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▶ **To cite this version:**

Longwu Wang, Canchao Yang, Gangbin He, Wei Liang, Anders Pape Møller. Cuckoos use host egg number to choose host nests for parasitism. Proceedings of the Royal Society. B, Biological Sciences, 2020, 287 (1928), pp.20200343. 10.1098/rspb.2020.0343 . hal-03026302

HAL Id: hal-03026302
https://cnrs.hal.science/hal-03026302

Submitted on 3 Dec 2020

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Cuckoos use host egg number to choose host nests for parasitism

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Word count: 5729

Running head: Cuckoos are sensitive to clutch size

Parasitic cuckoos evolved rapid egg laying into host nests, and eggs hatching earlier thereby providing advantages for quick chick growth and successful fledging caused by nest evictors. Therefore, adaptive behavior for seeking optimal time for egg deposition in host nests is helpful. Here we focused on whether common cuckoos (*Cuculus canorus*) possess the ability to choose a suitable nest for parasitism based on the clutch size according to 1) the egg-laying date of cases of natural parasitism during 8 years in relation to host clutch size, and 2) artificial combinations of eggs that elicited female cuckoos to parasitize nests with different numbers of model egg in nests of Oriental reed warbler hosts (*Acrocephalus orientalis*). Cuckoos preferred host nests at the onset of egg-laying (the 1- or 2-egg stage) rather than at other egg stages both in natural and experimental nests. To our knowledge, this is the first field experiment convincingly showing that cuckoos choose host nests for parasitism based on the number of host eggs when. We argue that cuckoo females estimate the host nest stage using egg number, and thus grasp the opportunity for timely parasitism.

Keywords: brood parasitism, common cuckoo, clutch size, egg number, Oriental reed warbler

1. Introduction

Avian interspecific brood parasites lay their eggs in nests of host species, often small passerine birds, and leave parental care of their offspring to the foster parents (Davies 2000). This imposes fitness costs on the host, selecting for counter-adaptations by hosts to resist parasitism (Davies and Brooke 1988; Soler 2014). Such host-parasite interactions provide a model system for the study of coevolution (Davies 2011; Feeney et al. 2014). The common cuckoo, *Cuculus canorus*, has evolved behavioral adaptations such as rapid egg laying of less than 10 seconds to avoid attack by host parents (Moksnes et al. 2000; Langmore 2013), and timing egg laying such that parasite eggs hatch before the host chicks hatch (Hauber 2003; Birkhead et al. 2011; Honza et al. 2007; Anderson et al. 2009).

Early hatching followed by eviction of all other eggs in the nest grants the chick of the common cuckoo the advantage of uncontested access to nest resources (Davies 2000; Honza et al. 2007; Grim et al. 2009). However, when the parasite egg is laid too late in the hosts laying sequence, the chick is unable to evict the larger chicks and must share the nest. Furthermore, when common cuckoos parasitize the common redstart (*Phoe*…) not all host eggs are evicted from all nests, and cuckoo chicks that cohabit with host nestlings have lower survival and fledging rates than those reared alone (Rutila et al. 2002; Grim et al. 2009). Therefore there is a clear advantage for the cuckoo to lay eggs into nests in a particular stage, for

example before the beginning of incubation (Gelsch et al. 2016), to ensure that the cuckoo chick hatches before the hosts. Indeed, it should be advantageous for cuckoos to be able to judge the appropriate time for egg laying in each host nest.

When a female cuckoo finds a host nest she can observe how much time the parents spend on the nest, whether other cuckoo females are in the vicinity and the number of eggs in the nest. Several bird species have been shown to have elaborate quantification skills (Hunt et al. 2008; Odell and Eadie 2010; Bogale et al. 2011; Scarf et al. 2011; Ditz and Nieder 2015, 2016). Female American coots (*Fulica americana*) use visual cues to adjust clutch size and recognize foreign eggs suggesting that they can count eggs (Lyon 2003; but see Haywood 2016). Brood-parasitic female cowbirds, under lab conditions, prefer to lay eggs into host nests containing a suitable number of eggs (White et al. 2007, 2009) though a similar effect was not observed for great spotted cuckoos under field conditions (Soler and Pérez-Contreras 2012; Šulc et al. 2016; Soler et al. 2020). Here we investigate whether female common cuckoos use variation in egg number to choose host nests for their eggs.

Similarly, female brown-headed cowbirds (*Molothrus ater*) would allow synchrony of laying with the number of host eggs thereby avoiding

105 nests that most likely had started incubation. This ability of cowbird
106 females to remember the number of eggs and compare changes in the
107 number of eggs allows them to select a suitable nest for parasitism (White
108 et al. 2009). From the perspective of parasites, in theory, it is adaptive to
109 have evolved behavior that provides an optimal time for egg deposition in
110 host nests (White et al. 2009; Soler and Pérez-Contreras 2012; Šulc et al.
111 2016; Soler et al. 2020).

112 An interesting and puzzling question to scientists is whether parasites
113 make decisions on the optimal time of parasitism based on the number of
114 eggs. That is whether female parasites know which host nests are new and
115 which host nests have females that already started incubation. Female
116 cowbirds prefer a suitable number of eggs in their nests under lab
117 conditions (White et al. 2007, 2009), and female American coots (*Fulica*
118 *americana*) use visual cues to adjust clutch size and recognize foreign eggs
119 suggesting that they can count eggs (Lyon 2003; but see Haywood 2016).
120 In addition, evidence suggests that other bird species may have elaborate
121 quantification skills (Hunt et al. 2008; Odell and Eadie 2010; Bogale et al.
122 2011; Scarf et al. 2011; Ditz and Nieder 2015, 2016). Therefore, parasites
123 potentially know the laying stage of host eggs, and they are sensitive to
124 clutch size. If the timing of egg laying affects reproductive success, natural
125 selection should favor female cuckoos that parasitize a nest not too early
126 neither too late during the laying sequence, because this benefits their

127 offspring over host nestlings at the time of hatching (Davies 2000; Geltsch
128 et al. 2016).

129 The common cuckoo (*Cuculus canorus*) is a brood parasite that
130 exploits the Oriental reed warbler (*Acrocephalus orientalis*) as its main
131 host in our Chinese study site. Cuckoo females usually remove a host egg
132 before depositing one of their own in a warbler nest (Yang et al. 2016a,
133 2017). Here we test whether cuckoos distinguish among nests with more
134 or fewer host eggs using observations and a field experiment. For all cases
135 of natural parasitism we observed over 8 years 2012-2019 we recorded the
136 date of parasitism and host clutch size. Our field experiment varied the
137 number of host eggs in each of 4 nests placed in replicated experimental
138 arrays (figure 1) to assess the parasitism by female cuckoos, as well as their
139 response to variation in host clutch size. We hypothesized that common
140 cuckoos assess whether a nest is appropriate for parasitism based on the
141 number of eggs it contains.

142

143 ## 2. Material and methods

144 ### (a) Study site and study species

145 This study was performed in reed swamps in the Zhalong National Nature
146 Reserve (46°48′-47°31′ N, 123°51′-124°37′ E) in Heilongjiang, northeast
147 China. Field experiments were carried out each breeding season (June to
148 August) from 2012 to 2019. In this habitat the Oriental reed warbler suffers

parasitism by the common cuckoo ranging from 34.3% to 65.5% among years (see Yang et al. 2017). Furthermore, the cuckoo eggs observed closely resemble those of the warbler host (Yang et al. 2016b; Li et al. 2016).

(b) Field experiment

We systematically searched reed beds during the breeding season and targeted warbler nests by monitoring the activities of host parents in 2015-2019. When we found a new warbler nest, we visited it daily and recorded the date of the first egg laid, total clutch size, parasitism status etc., to know which day the cuckoo female laid her egg. Multiple parasitism occurs in this warbler population (Liang et al., 2014; Yang et al., 2014) so we recorded the date of appearance of the first and second cuckoo egg if such appeared. After breeding ended, we collected warbler nests for the experimental nests described below.

(c) Field experiment

During each breeding season, once warblers started to lay eggs, a set of four experimental nests from the year before was set up within about 1 meter of each active host nest. Within each set of nests there was a nest containing 0, 1, 3 and 5 white model eggs (mean size of model eggs: 30.22 mm × 21.64 mm, 11.63 g) (figure 1). These sets of nests were placed in similar habitat to the matched naturally active nest but HOW MUCH

171 higher in the vegetation to make it easier for cuckoos to find (Moskát and
172 Honza 2000; Clarke et al. 2001) and to parasitise (Budnik et al. 2002;
173 Patten et al. 2011).

174 Experimental nests were monitored for cuckoo parasitism by daily
175 visits and video recordings for six days until completion of the host clutch.
176 Video devices (JWD DV-58G, JWD Inc., Shenzhen, China) were installed
177 in the morning and were removed at dusk except on rainy days.

178

179 **(d) Statistical analysis**

180 Chi-square tests were used to test for frequency of parasitism and
181 preference during nest choice. Fisher exact test was used if effective
182 sample size was less than five. Differences were considered to be
183 significant at the 0.05 level. Statistical analysis was conducted using IBM
184 SPSS Version 22.0 (IBM Corp., Armonk, NY, USA).

185

186 **3. Results**

187 **(a) Natural frequency of parasitism**

188 A total of 245 cases of parasitism were recorded in 8 years 2012-2019
189 (figure 2), a highly significant difference in frequency of parasitism among
190 nests with different clutch sizes (Chi-square test, $\chi^2 = 241.97$, $P < 0.001$).
191 A proportion of 75% cuckoo eggs were parasitized at the 1-2 eggs stage (1
192 egg: 49%, 120/245; 2 eggs: 26%, 63/245). By contrast, just ca. 1% of

193 cuckoo eggs were laid in 5-6 eggs nests (5 eggs: 0.8%, 2/245; 6 eggs: 0.4%,
194 1/245). Cuckoos biased parasitism towards nests with fewer host eggs in
195 nests (e.g., 1 or 2 eggs) for parasitism compared to the nests with more
196 eggs (e.g., 3-6 eggs) (figure 2).

197 A total of 43 cases of multiple parasitism were recorded during 2012-
198 2019, and 33 of these cases were known as the 1st cuckoo female choosing
199 the clutch size of the host for parasitism. We knew clearly that the time of
200 laying by the 2nd cuckoo happened in the same host nest when multiple
201 parasitism occurred (figure 3). The remaining 10 cases are ambiguous
202 because the nest already had two cuckoo eggs in the nest when found by
203 us. For the 1st cuckoo, 100% of cases were parasitized before the 2 egg-
204 laying stage, while for the 2nd cuckoo, they delayed deposition of their
205 eggs by 1.03 days. However, there were still 8 cases showing that both the
206 1st and 2nd cuckoo females laid their eggs at the same day when the host
207 was at the one egg-laying stage. These findings showed that all cuckoo
208 females prefer smaller clutch sizes for parasitism (figure 3).

209

210 **(b) Experiments for attracting cuckoo parasitism**

211 A total of 42 experimental combinations of nests were tested in the field,
212 and 32 cases of parasitism (figure 4) were recorded during 2015-2019.
213 There was a surprisingly high parasitism rate (76%, 32/42) in all
214 manipulated combinations of nests in this study. For the inserted clutch size,

215 the frequency of parasitism among four types of nests with numbers 0, 1,
216 3 and 5 model eggs showed a highly significant difference (Chi-square test,
217 $\chi^2 = 31.93$, $P < 0.001$), among these parasitism cases, the vast majority of
218 cuckoo eggs being found to parasitize at the 1-egg stage (78%, 25/32).

219 Additionally, no cuckoo parasitism occurred in naturally active host
220 nests during the egg-laying stage. Video recordings showed cuckoo female
221 egg-laying behavior in nests with artificially inserted 0, 1, 3 and 5 model
222 eggs, respectively (ESM Video S1-S4).

223

224 **4. Discussion**

225 Female cuckoos generally biased their nest preference towards smaller
226 clutch sizes versus other sizes both in natural nests and experimental ones.
227 That is, the day of onset of egg-laying by the host is the optimal timing for
228 cuckoo parasitism as theory predicts. Our results suggested that female
229 cuckoos have a preference for a certain number of host eggs, and they are
230 able to distinguish host nests based on clutch size. They could estimate
231 time of the host nest stage and grasp the opportunity for timely parasitism.

232 Egg-laying by cuckoos was described as a very quick process (Wyllie
233 1981; Davies 2000). When approaching potential host nests, female
234 cuckoos usually perch at a vantage point and monitor host activities (Honza
235 et al. 2002; Moksnes et al. 2000). Empirical studies revealed that cuckoos
236 should know the status of host nests from the activity of nest building, nest

location, and even the onset of egg-laying and incubation (Moksnes et al. 2000; Honza et al. 2002; Vogl et al. 2002; Yang et al. 2016a, 2017; Honza et al. 2019). Therefore, cuckoo females always lay their eggs during the laying period of the host rather than earlier or later.

Parasitic eggs were laid early during the laying period of the host thereby increasing hatching success and survival prospects for parasite chicks (Fiorini et al. 2009; Geltsch et al. 2016; Yang et al. 2018). For example, Geltsch et al. (2016) found that all cuckoo eggs hatched earlier than those of their great reed warbler hosts (*Acrocephalus arundinaceus*), because cuckoo eggs were laid prior to laying in a clutch of 4 host eggs. In contrast, if cuckoo eggs were laid after the 4-egg stage, they would lose the advantage of early hatching in one third of nests (Geltsch et al. 2016). Parasitic eggs that were laid into host nests too late may result in failure of hatching of these eggs (McMaster and Sealy 1998; Strausberger 1998; Hauber 2003). Alternatively, chick death may arise because of eviction failure or cohabitation with nest-mates (Grim et al. 2009, 2011), the "help to the parasitic chick" hypothesis stated that reduced host clutch size by the parasitic female can help their chick lower energy expenditure in later ejection of nestmates, this may be one reason why cuckoo females take a preference for hosts with smaller clutches to decrease the costs of egg evictions, although a recent study argued for a contrary finding that chicks evicting more eggs have a higher growth rate than chicks that evicted fewer

eggs in Horsfield's bronze-cuckoo (*Chalcites basalis*) (Medina et al. 2019). Therefore, cuckoo females should favor earlier laying during the egg-laying period of the host resulting in early hatching and eviction.

Moksnes et al. (2000) found reed warblers (*Acrocephalus scirpaceus*) are less active at their nest during the first and second laying days but become increasingly active at the late stage. Additionally, Geltsch et al. (2016) also revealed that parasitizing at the beginning of the host egg-laying stage may help cuckoos to avoid intense host nest defence because hosts start to incubate and thus increase their nest attentiveness after the laying of their fourth egg. Therefore, female cuckoos prefer to parasitize 1- or 2-egg stages rather than during the 4- to 6-egg stages, and their preferences for hosts with smaller clutches in this study may also be due to host nest attentiveness.

The "mimicry improvement" hypothesis states that the common cuckoo female removes one host egg to improve mimicry of its egg in the host clutch and thus increase the chance of acceptance (Šulc et al. 2016), that is, the less eggs at the nest, the higher the chance of acceptance for cuckoo eggs. Mikami et al. (2015) also showed that hosts with smaller clutch sizes are discouraged to reject cuckoo eggs due to the lower relative payoff. In these scenarios, it would be adaptive for cuckoos to select nests with smaller clutch sizes for parasitism in terms of egg acceptance.

Davies and Brooke (1988) showed that 45 cuckoo eggs in their study

had none at pre-laying and clutch completion, with most being laid at the 1-egg stage. This finding was extremely similar to those of the present study. Nevertheless, compared with our study, their findings generally involved smaller sample sizes over fewer years with most nests checked being completed clutches. Furthermore, Wyllie (1981) also found that 88% (n=90) of cuckoo eggs were laid at the 1-, 2- or 3-egg stages, and none of them were laid after the onset of incubation. However, White et al. (2007) reported that female brown-headed cowbirds (*Molothrus ater*) preferred nests containing 3 eggs under lab conditions, and they explained that cowbird chicks may benefit from having more host chicks present thereby increasing the amount of care provided by host parents (i.e., Kilner et al. 2005). This differs from common cuckoo nestlings, which are typically raised alone in the nest with no siblings because of eviction behavior (Davies 2000; Honza et al. 2007; Anderson et al. 2009). Therefore, cuckoo nestlings benefitted the most when parasitism occurred earlier. This may also explain why cases of laying by female cuckoos during the 4- to 6-egg stages were rare.

Hosts seemed to adopt the rule that 'any egg appearing in the nest before I start to lay cannot be mine, so reject it' (Davies 2000). Underlying this theory, cuckoo females should not parasitize during pre-laying in empty nests thereby avoiding egg rejection/burial or nest desertion (Moskát and Hauber 2007; Wang et al. 2015). We found some cases of

303 parasitism (17/245, 6.9%) subject to this scenario, and some previous
304 studies showed that 4 out of 90 cuckoo eggs (4.4%) were laid in an empty
305 nest (Wyllie 1981) and Honza et al. (2019) found 4.9% (28/577) of all
306 parasitized nests did cuckoos make laying errors by parasitizing deserted
307 and old nests including one nest (0.2%) that was even parasitized by a
308 cuckoo egg during the nestling stage during their ten years' study. The
309 possible explanations were that 1) female cuckoos assessed the host egg-
310 laying stage by mistake. Some host nests were far away from vantage
311 viewpoints or concealed under vegetation, and it is difficult for cuckoos to
312 check them due to host nest defense (Feeney et al. 2014). Nest building
313 speed in some hosts may be different, if one host pair build nests slowly,
314 while female cuckoos detect this nest for a long time and decide to lay eggs
315 on a suitable day according to their assessment. However, when cuckoos
316 approach this target nest still empty with no egg, the cuckoo may also be
317 forced to deposit its egg in a hurry. For example, we only found one cuckoo
318 egg in a half-finished nest in year 2014 (figure 5). 2) Female cuckoos had
319 not enough time to make an optimal choice among different available nests
320 based on variation in number of eggs. Generally, hosts always appear
321 around their nests and are aggressive towards cuckoos (Feeney et al. 2014;
322 Ma et al. 2018; Zhang et al. 2019). For instance, Nakamura et al. (2005)
323 reported that the Oriental warbler (*Acrocephalus orientalis*) drove off and
324 repulsed female cuckoos when they attempted to approach the nest for nine

times. Furthermore, laying females were injured or even killed by hosts (Davies 2000). In this study, we also found that a female cuckoo was fiercely attacked and fell into swampy water below the host nest until it was drowned in year 2014. 3) Empty nests had sufficient space for cuckoo body size. The only evidence that larger nests in many different species of birds are associated with the laying of larger clutches (Møller et al. 2014) may be that empty nests are superior for rapid egg-laying by cuckoos. 4) Cuckoo females may also follow a 'shotgun strategy' as shown in shiny cowbirds (*Molothrus bonariensis*) that laid 12.4% (33/267) eggs into incubated host clutches and 30.7% (82/267) eggs into deserted nests (Kattan 1997).

In order to increase the opportunity of cuckoo parasitism of experimental nests, we specifically fixed the nests higher and more exposed than naturally active nests. Actually, these treatments promoted parasitism rate to help elicit more cuckoos coming and laying eggs as filmed in our video devices. These results are also consistent with the nest height hypothesis (Budnik et al. 2002; Patten et al. 2011) and the nest exposure hypothesis explaining variation in rate of cuckoo parasitism (Moskát and Honza 2000; Clarke et al. 2001).

5. Conclusion

In summary, this study considerably improved our knowledge of the cuckoos being able to discriminate and make decisions based on the

number of eggs in a host nest. We provided strong field experimental evidence to suggest that female cuckoos generally preferred host nests at the onset of egg laying rather than other egg stages because of hatching efficiency. Furthermore, cuckoos were better able to find host nests located higher and more exposed to parasitism, this finding being consistent with the nest height and the nest exposure hypotheses. To our knowledge, this is the first field experiment that convincingly shows that cuckoos are sensitive to the number of eggs, and that cuckoos can distinguish among host nests based on differences in clutch size. Future research should focus on experimental test of cognitive ability of the common cuckoo and should expand on the mechanism driving the findings of this study.

Ethics. The experiments comply with the current laws of China, where they were performed. Fieldwork was carried out with permission (no. ZL-GZNU-2019-06) from Zhalong National Nature Reserve, Heilongjiang, China. Experimental procedures were in agreement with the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (permit no. HNECEE-2012-003).

Data accessibility. All data analysed and videos for this study are available at Dryad Digital Repository by Wang et al. 2020.

Authors' contributions. WL and LW designed the study; LW and GH carried out field experiments; LW and CY performed carried out laboratory and statistical analyses. LW wrote the draft manuscript, and WL and APM involved in discussion, and helped improve the manuscript. All authors approved the final submission.

Competing interest. The authors declare that they have no competing interest.

Fundings. This work was supported by the National Natural Science Foundation of China (Nos. 31660617 and 31960105 to LW, 31672303 to CY, 31772453 and 31970427 to WL). LW was funded by a PhD grant from Guizhou Normal University (No. 0516009), the Initial Fund Key Laboratories of Guizhou Province (grant No. 2011-4005), the Joint Fund of the National Natural Science Foundation of China and the Karst

Science Research Center of Guizhou Province (No. U1812401).

Acknowledgments. We would like to thank Professor Hans Heesterbeek, the Associate Editor, and two referees for their constructive comments on this manuscript. We are grateful to Wenfeng Wang and Jianhua Ma from Zhalong National Nature Reserve for their help and co-operation. We thank Tinggao Yang and Hailin Lu for their assistance with fieldwork.

References

Anderson MG, Moskát C, Bán M, Grim T, Cassey P, Hauber ME. 2009. Egg eviction imposes a recoverable cost of virulence in chicks of a brood parasite. *PLoS One*. **4**, e7725. (doi: 10.1371/journal.pone.0007725)

Birkhead TR, Hemmings N, Spottiswoode CN, Mikulica O, Moskát C, Bán M, Schulze-Hagen K. 2011. Internal incubation and early hatching in brood parasitic birds. *Proc. R. Soc. Lond. B.* **278**, 1019-1024. (doi.org/10.1098/rspb.2010.1504)

Budnik JM, Thompson III FR, Ryan MR. 2002. Effect of habitat characteristics on the probability of parasitism and predation of Bell's vireo nests. *J. Wildl. Manage*. **66**, 232–239. (doi: 10.2307/3802889)

Bogale BA, Kamata N, Mioko K, Sugita S. 2011. Quantity discrimination in jungle crows, *Corvus macrorhynchos*. *Anim. Behav*. **82**, 635–641. (doi.org/10.1016/j.anbehav.2011.05.025)

Clarke AL, Øien IJ, Honza M, Moksnes A, Røskaft E. 2001. Factors affecting reed warbler risk of brood parasitism by the common cuckoo. *Auk*. **118**, 534–538. (doi: 0.1093/auk/118.2.534)

Davies NB, Brooke MdeL. 1988. Cuckoos versus reed warblers: Adaptations and counteradaptations. *Anim. Behav*. **36**, 262–284. (doi: 10.1016/S0003-3472(88)80269-0)

Davies NB. 2000. Cuckoos, cowbirds and other cheats. T & AD Poyser,

London.

Davies NB. 2011. Cuckoo adaptations: trickery and tuning. *J. Zool*. **284**, 1–14. (doi: 10.1111/j.1469-7998.2011.00810.x)

Ditz HM, Nieder A. 2015. Neurons selective to the number of visual items in the corvid songbird endbrain. *Proc. Natl. Acad. Sci. USA*. **112**, 7827–7832. (doi: 10.1073/pnas.1504245112)

Ditz HM, Nieder A. 2016. Numerosity representations in crows obey the Weber–Fechner law. *Proc. R. Soc. Lond. B.* **283**, 20160083. (doi: 10.1098/rspb.2016.0083)

Feeney WE, Welbergen JA, Langmore NE. 2014. Advances in the study of coevolution between avian brood parasites and their hosts. *Annu. Rev. Ecol. Evol. Syst.* **45**, 227–246. (doi: 10.1146/annurev-ecolsys-120213-091603)

Geltsch N, Bán M, Hauber ME, Moskát C. 2016. When should common cuckoos *Cuculus canorus* lay their eggs in host nests? *Bird Study.* **63**, 46–51. (doi: 10.1080/00063657.2015.1125851)

Gloag R, Keller LA, Langmore NE. 2014. Cryptic cuckoo eggs hide from competing cuckoos. *Proc. R. Soc. Lond. B.* **281**, 20141014. (doi: 10.1098/rspb.2014.1014)

Grim T, Rutila J, Cassey P, Hauber ME. 2009. Experimentally constrained virulence is costly for common cuckoo chicks. *Ethology.* **115**, 14–22. (doi: 10.1111/j.1439-0310.2008.01574.x)

Grim T, Samaš P, Moskát C, Kleven O, Honza M, Moksnes A, Stokke BG. 2011. Constraints on host choice: why do parasitic birds rarely exploit some common potential hosts? *J. Anim. Ecol.* **80**, 508–518. (doi: 10.1111/j.1365-2656.2010.01798.x)

Hauber ME. 2003. Hatching asynchrony, nestling competition, and the cost of interspecific brood parasitism. *Behav. Ecol.* **14**, 227–235. (doi: 10.1093/beheco/14.2.227)

Haywood S. 2016. Can birds count eggs in their nests? *Ibis*. **158**, 195–198. (doi: 10.1111/ibi.12328)

Honza M, Taborsky B, Taborsky M, Teuschl Y, Vogl W, Moksnes A, Røskaft E. 2002. Behaviour of female common cuckoos, *Cuculus canorus*, in the vicinity of host nests before and during egg laying: A radiotelemetry study. *Anim. Behav*. **64**, 861–868. (doi: 10.1006/anbe.2002.1969)

Honza M, Voslajerová K, Moskát C. 2007. Eviction behaviour of the common cuckoo *Cuculus canorus* chicks. *J. Avian Biol.* **38**, 385–389. (doi: 10.1111/j.2007.0908-8857.03901.x)

Hunt S, Low J, Burns KC. 2008. Adaptive numerical competency in a food-hoarding songbird. *Proc. R. Soc. Lond. B.* **275**, 2373–2379. (doi: 10.1098/rspb.2008.0702)

Kattan GH. 1997. Shiny cowbirds follow the 'shotgun' strategy of brood parasitism. *Anim. Behav*. **53**, 647–654. (doi:10.1006/anbe.1996.0339)

454 Kilner RM, Madden JR, Hauber ME. 2004. Brood parasitic cowbird
455 nestlings use host young to procure resources. *Science.* **305**, 877–879.
456 (doi: 10.1126/science.1098487)
457 Langmore NE. 2013. Australian cuckoos and their adaptations for brood
458 parasitism. *Chin. Birds.* **4**, 86–92. (doi: 10.5122/cbirds.2013.0007)
459 Liang G, Yang C, Wang L, Liang W. 2014. Variation in parasitism rates by
460 common cuckoos among three populations of the Oriental reed
461 warblers. *Sichuan J. Zool.* **33**, 673-677. (doi: 10.3969/j.issn.1000-70
462 83.2014.05.006)
463 Li D, Ruan Y, Wang Y, Chang AK, Wan D, Zhang Z. 2016a. Egg-spot
464 matching in common cuckoo parasitism of the Oriental reed warbler:
465 effects of host nest availability and egg rejection. *Avian Res.* **7**, 21.
466 (doi: 10.1186/s40657-016-0057-y)
467 Lyon BE. 2003. Egg recognition and counting reduce costs of avian
468 conspecific brood parasitism. *Nature.* **422**, 495–499. (doi:
469 10.1038/nature01505)
470 Ma L, Yang C, Liang W. 2018. Hawk mimicry does not reduce attacks of
471 cuckoos by highly aggressive hosts. *Avian Res*. **9**, 35. (doi:
472 10.1186/s40657-018-0127-4)
473 McMaster DG, Sealy SG. 1998. Short incubation periods of brown headed
474 cowbird: how do cowbird eggs hatch before yellow warbler eggs?
475 *Condor.* **100**, 102–111. (doi: 10.2307/1369901)

476 Medina I, Langmore NE. 2015. The costs of avian brood parasitism explain
477 variation egg rejection behaviour in hosts. *Biol. Lett.* **11**, 20150296.
478 (doi: 10.1098/rsbl.2015.0296)
479 Medina I, Hall ML., Taylor CJ, Mulder RA, Langmore NE. 2019.
480 Experimental increase in eviction load does not impose a growth cost
481 for cuckoo chicks. *Behav. Ecol. Sociobiol.* **73**, 44-48. (doi:
482 10.1007/s00265-019-2655-2)
483 Mikami OK, Sato NJ, Ueda K, Tanaka KD. 2015. Egg removal by cuckoos
484 forces hosts to accept parasite eggs. *J. Avian Biol*. **46**, 275–282.
485 (10.1111/jav.00410)
486 Moskát C, Honza M. 2000. Effect of nest and nest site characteristics on
487 the risk of cuckoo *Cuculus canorus* parasitism in the great reed
488 warbler *Acrocephalus arundinaceus*. *Ecography.* **23**, 335–341. (doi:
489 10.1111/j.1600-0587.2000.tb00289.x)
490 Moskát C, Hauber ME. 2007. Conflict between egg recognition and egg
491 rejection decisions in common cuckoo (*Cuculus canorus*) hosts. *Anim.*
492 *Cogn.* **10**, 377–386. (doi: 10.1007/s10071-007-0071-x)
493 Møller AP, Adriaensen F, Artemyev Ac, Bańbura J, Barba E, Biard C,
494 Cecere F. 2014. Variation in clutch size in relation to nest size in birds.
495 *Ecol. Evol.* **4**, 3583-3595. (doi: 10.1002/ece3.1189)
496 Moksnes A, Røskaft E, Hagen LG, Honza M, Mørk C, Olsen PH. 2000.
497 Common cuckoo *Cuculus canorus* and host behaviour at reed warbler

498 *Acrocephalus scirpaceus* nests. *Ibis*. **142**, 247–258. (doi:
499 10.1111/j.1474-919X.2000.tb04864.x)
500 Nakamura H, Miyazawa Y, Kashiwagi K. 2005. Behavior of radio-tracked
501 common cuckoo females during the breeding season in Japan.
502 *Ornithol*. Sci. **4**, 31– 41. (doi: 10.2326/osj.4.31)
503 Odell NS, Eadie JM. 2010. Do wood ducks use the quantity of eggs in a
504 nest as a cue to the nest's value? *Behav. Ecol.* **21**, 794–801. (doi:
505 10.1093/beheco/arq055)
506 Patten MA, Reinking DL, Wolfe DH. 2011. Hierarchical cues in brood
507 parasite nest selection. *J. Ornithol*. **152**, 521–532. (doi:
508 10.1007/s10336-010-0608-7)
509 Peer BD. 2006. Egg destruction and egg removal by avian brood parasites:
510 Adaptiveness and consequences. *Auk.* **123**, 16–22. (doi:
511 10.1642/0004-8038(2006)123[0016:EDAERB]2.0.CO;2)
512 Rutila J, Latja R, Koskela K. 2002. The common cuckoo *Cuculus canorus*
513 and its cavity nesting host, the redstart *Phoenicurus phoenicurus*: a
514 peculiar cuckoo - host system? *J. Avian Biol.* **33**, 414–419. (doi:
515 10.1034/j.1600-048X.2002.02937.x)
516 Scarf D, Hayne H, Colombo M. 2011. Pigeons on par with primates in
517 numerical competence. *Science*. **334**, 1664. (doi: 10.1126/science.12
518 13357)
519 Sealy SG, Underwood TJ. 2012. Egg discrimination by hosts and obligate

520 brood parasites: a historical perspective and new synthesis. *Chin.*
521 *Birds*. **3**, 274–294. (doi: 10.5122/cbirds.2012.0042)
522 Soler M. 2014. Long–term coevolution between avian brood parasites and
523 their hosts. *Biol. Rev*. **89**, 688–704. (doi: 10.1111/brv.12075)
524 Soler M, Pérez-Contreras T. 2012. Location of suitable nests by great
525 spotted cuckoos: an empirical and experimental study. *Behav. Ecol.*
526 *Sociobiol*. **66**, 1305–1310. (doi: 10.1007/s00265-012-1385-5)
527 Soler M, Pérez-Contreras T, Soler JJ. 2020. Great spotted cuckoos show
528 dynamic patterns of host selection during the breeding season: The
529 importance of laying stage and parasitism status of magpie
530 nests. *Behav. Ecol*. In press. (doi: 10.1093/beheco/arz208)
531 Strausberger BM. 1998. Temperature, egg mass, and incubation time: a
532 comparison of brown-Headed cowbirds and red-winged blackbirds.
533 *Auk*. **115**, 843–850. (doi: 10.2307/4089503)
534 Šulc M, Procházka P, Capek M, Honza M. 2016. Common cuckoo females
535 are not choosy when removing an egg during parasitism. *Behav. Ecol*.
536 **27**, 1642–1649. (doi: 10.1093/beheco/arw085)
537 Vogl W, Taborsky M, Taborsky B, Teusch Y, Honza M. 2002. Cuckoo
538 females preferentially use specific habitats when searching for host
539 nests. *Anim. Behav*. **64**, 843–850. (doi: 10.1006/anbe.2003.1967)
540 Wang L, Yang C, He G, Liang W, Møller AP. 2020. Data from: Cuckoos
541 are sensitive to host clutch size when choosing host nests for

parasitism. Dryad Digital Repository. (doi: 10.5061/dryad.47d7wm396)

Wang L, Yang C, Møller AP, Liang W, Lu X. 2015. Multiple mechanisms of egg recognition in a cuckoo host. *Behav. Ecol. Sociobiol*. **69**, 1761–1767. (doi: 10.1007/s00265-015-1988-8)

White DJ, Ho L, Freed-Brown G. 2009. Counting chicks before they hatch: female cowbirds can time readiness of a host nest for parasitism. *Psychol. Sci*. **20**, 1140–1145. (doi.org/10.1111/j.1467-928 0.2009.02418.x)

White DJ, Ho L, Santos G de los, Godoy I. 2007. An experimental test of preferences for nest contents in an obligate brood parasite, *Molothrus ater*. *Behav. Ecol.* **18**, 922–928. (doi: 10.1093/beheco/arm062)

Wyllie I. 1981. The cuckoo. Batsford, London.

Yang C, Li D, Wang L, Liang G, Zhang Z, Liang W. 2014. Geograpcchic variation in parasitism rates of two sympatric cuckoo hosts in China. *Zool. Res*. **35**, 67–71. (doi: 10.11813/j.issn.0254-5853.2014.1.067)

Yang C, Huang Q, Wang L, Du W-G, Liang W, Møller AP. 2018. Keeping eggs warm: Thermal and developmental advantages for parasitic cuckoos of laying unusually thick-shelled eggs. *Sci. Nat.* **105**, 10. (doi: 10.1007/s00114-017-1532-y)

Yang C, Wang L, Liang W, Møller AP. 2016a. Egg recognition as antiparasitism defence in hosts does not select for laying of matching

564 eggs in parasitic cuckoos. *Anim. Behav*. **122**, 177–181. (doi:
565 10.1016/j.anbehav.2016.10.018)
566 Yang C, Wang L, Liang W, Møller AP. 2016b. Do common cuckoos
567 (*Cuculus canorus*) possess an optimal laying behaviour to match their
568 own egg phenotype to that of their Oriental reed warbler
569 (*Acrocephalus orientalis*) hosts? *Biol. J. Linn. Soc.* **117**, 422–427. (doi:
570 10.1111/bij.12690)
571 Yang C, Wang L, Liang W, Møller AP. 2017. How cuckoos find and choose
572 host nests for parasitism. *Behav. Ecol.* **28**, 859–865. (doi:
573 10.1093/beheco/arx049)
574 Zhang J, Shi J, Deng W, Liang W. 2019. Nest defense and egg recognition
575 in the grey-backed thrush (*Turdus hortulorum*): Defense against
576 interspecific or conspecific brood parasitism? *Behav. Ecol.*
577 *Sociobiol.* **73**, 148–155. (doi: 10.1007/s00265-019-2759-8)
578

Legends to figures

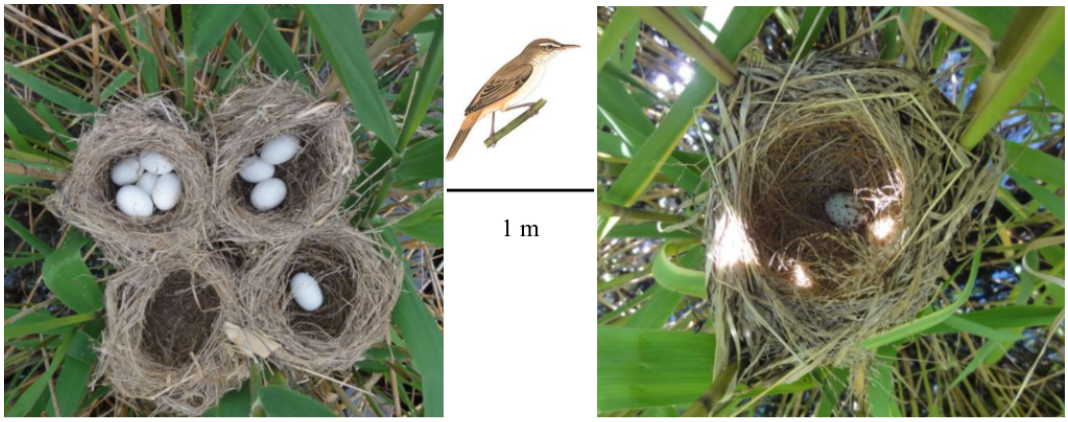
Figure 1. Example of combination of host nests for eliciting cuckoo parasitism in this study. Four nests showed the 0-1-3-5 combination of nests with white model eggs, respectively.

Figure 2. Frequency of level of natural parasitism of cuckoos choosing host nests in relation to clutch size during the egg-laying stage in 8 years from 2012 to 2019 in the same study site. Numbers on the bars refer to sample size.

Figure 3. Frequency of the 1st cuckoo female and the 2nd one choosing the nest in relation to clutch size for parasitism when multiple cases of parasitism occurred. Numbers on the bars refer to sample size.

Figure 4. Frequency distribution of cuckoos choosing experimental nests in relation to the number of model eggs among four types nest (0, 1, 3 or 5 eggs) when parasitism happened. Numbers on the bars refer to the result of cuckoos' choice toward the type nest.

Figure 5. One case of cuckoo female depositing its egg in a half-finished nest of Oriental reed warbler on July 10, 2014.



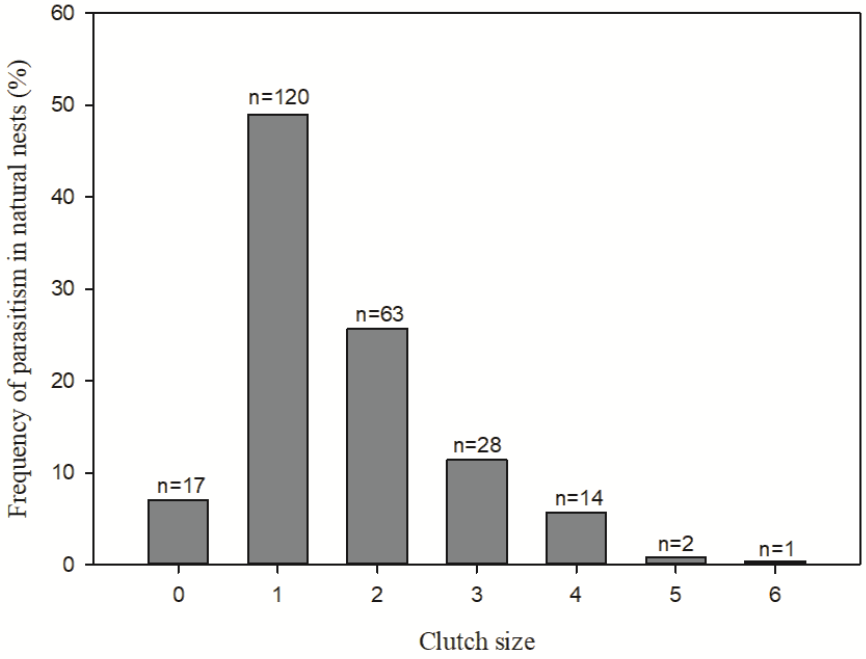
Combination of nests

Active host nest

602

603 Fig. 1

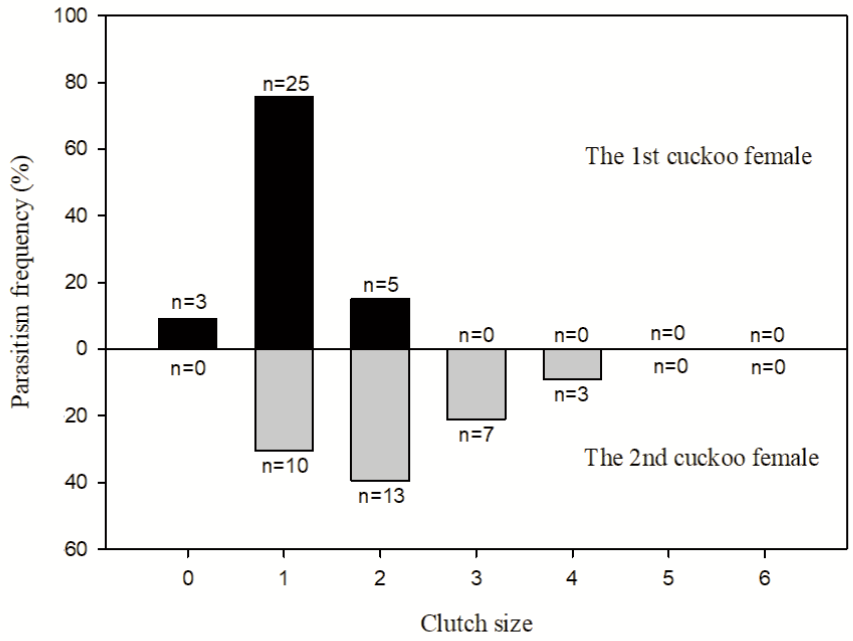
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606 Fig. 2

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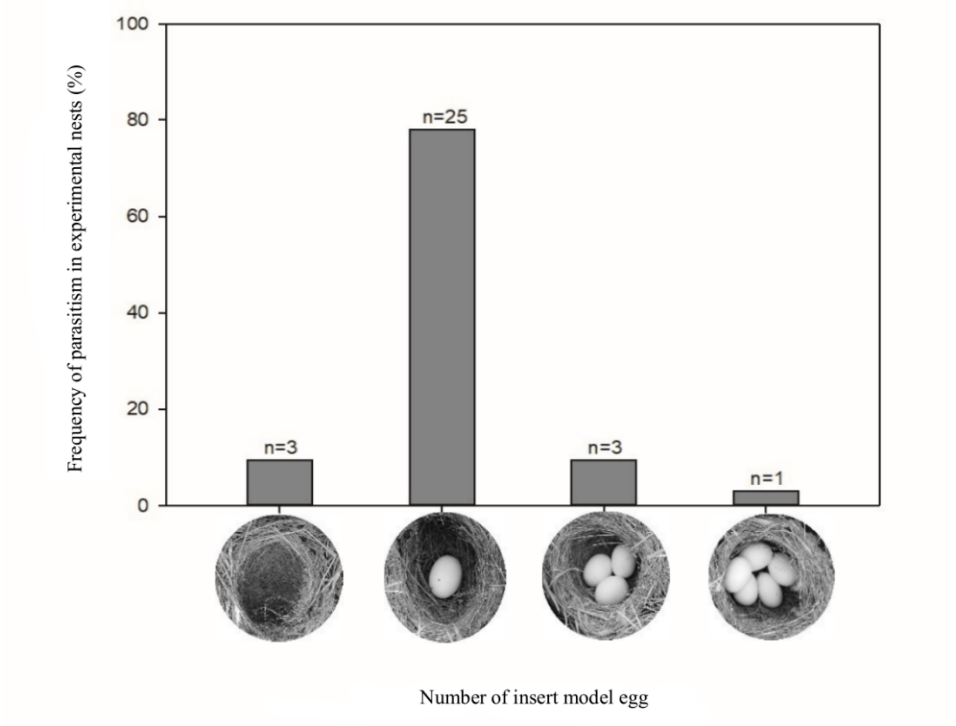


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609 Fig. 3

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613 Fig. 4

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Fig. 5