

1 **Cuckoos are sensitive to host clutch size when choosing host nests for**
2 **parasitism**

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

60

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

63

64 **1. Introduction**

65 Avian brood parasites generally lay their eggs in nests of host species
66 such as small passerine birds, and then impose fitness costs by leaving
67 parental care of their offspring to the foster parents (Davies 2000).
68 Therefore, selection should favor counter-adaptations by hosts to resist
69 parasitism (Davies and Brooke 1988; Soler 2014). Such host-parasite
70 interactions provide a model system for the study of coevolution (Davies
71 2011; Feeney et al. 2014). During this arms race, female parasites have
72 evolved a series of behavioral adaptations such as rapid egg laying for
73 minimizing the time of laying within 10 seconds to avoid fierce
74 aggressiveness by host parents (Moksnes et al. 2000; Langmore 2013),
75 and parasitic eggs being laid prior to hatching of host eggs resulting in
76 parasitic chicks possessing innate advantage (Hauber 2003; Birkhead et al.
77 2011; Honza et al. 2007; Anderson et al. 2009).

78 Early hatching would have an advantage in terms of quick offspring
79 growth rate and successful fledging caused by nest evictors by the sole
80 cuckoo occupier of the host nest (Davies 2000; Honza et al. 2007; Grim
81 et al. 2009). However, some non-evicting parasites (e.g. cowbirds) share
82 the nest with the progeny of the host (Kilner et al. 2004; Medina and
83 Langmore 2015). Parasitic eggs would be failing to hatch if they were
84 laid incorrectly with respect to the egg stage (McMaster and Sealy 1998;
85 Hauber 2003), while parasitic chicks have low survival rate and even

86 suffer death caused by mixed broods with host nestmates (Rutilla et al.
87 2002; Grim et al. 2009). Therefore, egg-laying at right stage and parasitic
88 eggs early hatching are beneficial behavioral responses for parasites.
89 Gelsch et al. (2016) revealed that cuckoos' egg-laying occurred prior to
90 their hosts starting egg incubation would more successfully than cuckoos'
91 egg laid after the onset of host incubation. Similarly, female
92 brown-headed cowbirds (*Molothrus ater*) would allow synchrony of
93 laying with the number of host eggs thereby avoiding nests that most
94 likely had started incubation. This ability of cowbird females to
95 remember the number of eggs and compare changes in the number of
96 eggs allows them to select a suitable nest for parasitism (White et al.
97 2009). From the perspective of parasites, in theory, it is adaptive to have
98 evolved behavior that provides an optimal time for egg deposition in host
99 nests (White et al. 2009; Soler and Pérez-Contreras 2012; Šulc et al.
100 2016; Soler et al. 2020).

101 An interesting and puzzling question to scientists is whether
102 parasites make decisions on the optimal time of parasitism based on the
103 number of eggs. That is whether female parasites know which nests are
104 new and which nests have started incubation. Female cowbirds prefer a
105 suitable number of eggs in their nests under lab condition (White et al.
106 2007, 2009), and female American coots (*Fulica americana*) use visual
107 cues to adjust clutch size and recognize foreign eggs suggesting that they

108 can count eggs (Lyon 2003; but see Haywood 2016). In addition,
109 evidence suggests that other bird species may have elaborate
110 quantification skills (Hunt et al. 2008; Odell and Eadie 2010; Bogale et al.
111 2011; Scarf et al. 2011; Ditz and Nieder 2015, 2016). Therefore, parasites
112 potentially know the laying stage of host eggs, and they are sensitive to
113 clutch size. If the timing of egg laying affects reproductive success,
114 natural selection should favor female cuckoos that parasitize a nest not
115 too early neither too late during the laying sequence, because this benefits
116 their offspring over host nestlings at the time of hatching (Davies 2000;
117 Geltsch et al. 2016).

118 The common cuckoo (*Cuculus canorus*) is a brood parasite that
119 exploits the Oriental reed warbler (*Acrocephalus orientalis*) as its major
120 host in our Chinese study site. Cuckoo females usually deposit their eggs
121 in a warbler nest and remove an egg before laying their own (Yang et al.
122 2016a, 2017). Our purpose was to test whether cuckoos know the number
123 of host eggs and whether they are sensitive to clutch size variation.
124 Therefore, we 1) investigated cases of natural parasitism in 8 years
125 2012-2019, from which we recorded parasitism date in relation to host
126 clutch size; 2) designed a field experiment with artificial combinations of
127 nests (figure 1) to assess the parasitism by female cuckoos, as well as
128 their response to variation in host clutch size. We hypothesized that
129 common cuckoos are able to assess the host nest stage, that is, the number

130 of host egg-laying sequences, and parasitize the target nest at an optimal
131 time.

132

133 **2. Material and methods**

134 **(a) Study site and study species**

135 This study was performed in Zhalong National Nature Reserve
136 (46°48'-47°31' N, 123°51'-124°37' E) located in Heilongjiang, northeast
137 China. Field experiments were carried out during the breeding season
138 (June to August) in years 2012-2019. In our study system, habitats are
139 primarily reed swamps, and the common cuckoo is the only primary
140 parasite of the Oriental reed warbler, where warblers suffered a high
141 parasitism rate ranging from 34.3% to 65.5% among years (see Yang et al.
142 2017). Furthermore, the appearance of cuckoo eggs closely resembled
143 that of warbler host eggs (Yang et al. 2016b; Li et al. 2016).

144

145 **(b) Field experiment**

146 We systematically searched reed beds during the breeding season and
147 targeted warbler nests by monitoring the activities of host parents in
148 2015-2019. When we found a new warbler nest, we would monitor its
149 egg-laying stage every day, including the first egg laying date, clutch size,
150 parasitism status etc., our purpose being to know which day the cuckoo
151 female visited these nests and parasitism occurred. Multiple parasitism is

152 well known in this warbler population (Liang et al., 2014; Yang et al.,
153 2014), so we deliberately recorded parasitism date of the first female
154 cuckoo and the second one. After breeding ended, we collected natural
155 old warbler nests in order to produce experimental combinations of nests
156 for this study. During the breeding season, once warblers started to lay
157 eggs in their new nests, one experimental combination of nests was set up
158 to elicit cuckoo female egg-laying (Yang et al., 2016a, 2017). Our
159 eliciting design was to set up a combination of nests including four
160 collected old nests close to an active host nest (figure 1). Different
161 numbers (0, 1, 3 or 5) of white model eggs were inserted randomly into
162 these four nests (mean size of model eggs: 30.22 mm × 21.64 mm, 11.63
163 g). The combination of nests was located at a distance of ca. 1 m from the
164 active host nest (figure 1).

165 The locations of combinations of nests above were fixed following
166 the rule that they were in similar habitat as the matched naturally active
167 nest. Furthermore, in order to increase opportunities for cuckoo
168 parasitism, we specifically fixed the combination of nests higher (the nest
169 height hypothesis, Budnik et al. 2002; Patten et al. 2011) than the position
170 of active host nests, thereby making it easier for cuckoos to locate target
171 nests from their vantage points (the nest exposure hypothesis, Moskát and
172 Honza 2000; Clarke et al. 2001). These treatments were predicted to
173 facilitate the cuckoos' knowledge about status of nest contents (e.g. egg

174 number), when approaching target nests or approaching potential host
175 nests prior to egg-laying.

176 These field experimental nests were monitored daily for six
177 continuous days to confirm whether cuckoo parasitism occurred until
178 completion of the host clutch. These nests were checked once per day and
179 all nests were video recorded except on rainy days. Video devices (JWD
180 DV-58G, JWD Inc., Shenzhen, China) were installed in the morning and
181 were removed at dusk. No treatment was assigned to active warbler nests
182 except clutch size being checked and nest parasitism status being
183 monitored.

184

185 **(c) Statistical analysis**

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

191

192 **3. Results**

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

194 A total of 245 cases of parasitism were recorded in 8 years 2012-2019
195 (figure 2), a highly significant difference in frequency of parasitism

196 among nests with different clutch sizes (Chi-square test, $\chi^2 = 241.97$, $P <$
197 0.001). A proportion of 75% cuckoo eggs were parasitized at the 1-2 eggs
198 stage (1 egg: 49%, 120/245; 2 eggs: 26%, 63/245). By contrast, just ca. 1%
199 of cuckoo eggs were laid in 5-6 eggs nests (5 eggs: 0.8%, 2/245; 6 eggs:
200 0.4%, 1/245). Cuckoos biased parasitism towards nests with fewer host
201 eggs in nests (e.g., 1 or 2 eggs) for parasitism compared to the nests with
202 more eggs (e.g., 3-6 eggs) (figure 2).

203 A total of 43 cases of multiple parasitism were recorded during the
204 year 2012-2019, and 33 out of these cases are known clearly as the 1st
205 cuckoo female choosing the host clutch size for parasitism, as well as
206 known clearly the 2nd cuckoo egg-laying time in the same host nest
207 when multiple parasitism happened (figure 3), the rest of 10 cases are
208 vague due to the nest have already existed two cuckoo eggs in nest when
209 we found these nests. For the 1st cuckoo, 100% of cases were parasitized
210 before the 2 egg-laying stage, for the 2nd cuckoo, they delayed 1.03 day
211 deposition of their eggs. However, there were still 8 cases showing that
212 both the 1st and 2nd cuckoo females laid their eggs at the same day
213 when the host was at the one egg-laying stage. These findings showed
214 that all cuckoo females prefer smaller clutch sizes for parasitism (figure
215 3).

216

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

218 A total of 42 experimental combinations of nests were tested in the field,
219 and 32 cases of parasitism (figure 4) were recorded during 2015-2019.
220 There was a surprisingly high parasitism rate (76%, 32/42) in all
221 manipulated combinations of nests in this study. For the inserted clutch
222 size, the frequency of parasitism among four types of nests with numbers
223 0, 1, 3 and 5 model eggs showed a highly significant difference
224 (Chi-square test, $\chi^2 = 31.93$, $P < 0.001$), among these parasitism cases,
225 the vast majority of cuckoo eggs being found to parasitize at the 1-egg
226 stage (78%, 25/32).

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

231

232 **4. Discussion**

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

240 parasitism.

241 Egg-laying by cuckoos was described as a very quick process
242 (Wyllie 1981; Davies 2000). When approaching potential host nests,
243 female cuckoos usually perch at a vantage point and monitor host
244 activities (Honza et al. 2002; Moksnes et al. 2000). Empirical studies
245 revealed that cuckoos should know the status of host nests from the
246 activity of nest building, nest location, and even the onset of egg-laying
247 and incubation (Moksnes et al. 2000; Honza et al. 2002; Vogl et al. 2002;
248 Yang et al. 2016a, 2017; Honza et al. 2019). Therefore, cuckoo females
249 always lay their eggs during the laying period of the host rather than
250 earlier or later.

251 Parasitic eggs were laid early during the laying period of the host
252 thereby increasing hatching success and survival prospects for parasite
253 chicks (Fiorini et al. 2009; Geltsch et al. 2016; Yang et al. 2018). For
254 example, Geltsch et al. (2016) found that all cuckoo eggs hatched
255 earlier than those of their hosts great reed warbler (*Acrocephalus*
256 *arundinaceus*) when cuckoo eggs were laid prior to the egg-laying in a
257 clutch size of 4 host eggs. In contrast, if cuckoo eggs were laid after the
258 4-egg stage, they would lose the advantage of early hatching in one third
259 of nests (Geltsch et al. 2016). Parasitic eggs that were laid into host nests
260 too late may result in failure of hatching of these eggs (McMaster and
261 Sealy 1998; Strausberger 1998; Hauber 2003). Alternatively, chick death

262 may arise because of eviction failure or cohabitation with nest-mates
263 (Grim et al. 2009, 2011), the “help to the parasitic chick” hypothesis
264 stated that reduced host clutch size by the parasitic female can help their
265 chick lower energy expenditure in later ejection of nestmates, this may be
266 one reason why cuckoo females take a preference for hosts with smaller
267 clutches to decrease the costs of egg evictions, although a recent study
268 argued for a contrary finding that chicks evicting more eggs have a higher
269 growth rate than chicks that evicted fewer eggs in Horsfield’s
270 bronze-cuckoo (*Chalcites basalis*) (Medina et al. 2019). Therefore, given
271 above, cuckoo females would favored earlier egg laying during the host
272 egg-laying period as being early hatching and eviction.

273 Moksnes et al. (2000) found reed warblers (*Acrocephalus scirpaceus*)
274 are less active at their nest during the first and second laying days but
275 become increasingly active at the late stage. Additionally, Geltsch et al.
276 (2016) also revealed that parasitizing at the beginning of the host
277 egg-laying stage may help cuckoos to avoid intense host nest defence
278 because hosts start to incubate and thus increase their nest attentiveness
279 after the laying of their fourth egg. Therefore, female cuckoos prefer to
280 parasitize 1- or 2-egg stages rather than during the 4- to 6-egg stages, and
281 their preferences for hosts with smaller clutches in this study may also be
282 due to host nest attentiveness.

283 The “mimicry improvement” hypothesis states that the common

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

292 Davies and Brooke (1988) showed that 45 cuckoo eggs in their study
293 had none at pre-laying and clutch completion, with most being laid at the
294 1-egg stage. This finding was extremely similar to those of the present
295 study. Nevertheless, compared with our study, their findings generally
296 involved smaller sample sizes over fewer years with most nests checked
297 being completed clutches. Furthermore, Wyllie (1981) also found that 88%
298 (n=90) of cuckoo eggs were laid at the 1-, 2- or 3-egg stages, and none of
299 them were laid after the onset of incubation. However, White et al. (2007)
300 reported that female brown-headed cowbirds (*Molothrus ater*) preferred
301 nests containing 3 eggs under lab conditions, and they explained that
302 cowbird chicks may benefit from having more host chicks present thereby
303 increasing the amount of care provided by host parents (i.e., Kilner et al.
304 2005). This differs from common cuckoo nestlings, which are typically
305 raised alone in the nest with no siblings because of eviction behavior

306 (Davies 2000; Honza et al. 2007; Anderson et al. 2009). Therefore,
307 cuckoo nestlings benefitted the most when parasitism occurred earlier.
308 This may also explain why cases of laying by female cuckoos during the
309 4- to 6-egg stages were rare.

310 Hosts seemed to adopt the rule that ‘any egg appearing in the nest
311 before I start to lay cannot be mine, so reject it’ (Davies 2000).
312 Underlying this theory, cuckoo females should not parasitize during
313 pre-laying in empty nests thereby avoiding egg rejection/burial or nest
314 desertion (Moskát and Hauber 2007; Wang et al. 2015). We found some
315 cases of parasitism (17/245, 6.9%) subject to this scenario, and some
316 previous studies showed that 4 out of 90 cuckoo eggs (4.4%) were laid in
317 an empty nest (Wyllie 1981) and Honza et al. (2019) found 4.9% (28/577)
318 of all parasitized nests did cuckoos make laying errors by parasitizing
319 deserted and old nests including one nest (0.2%) that was even parasitized
320 by a cuckoo egg during the nestling stage during their ten years’ study.
321 The possible explanations were that 1) female cuckoos assessed the host
322 egg-laying stage by mistake. Some host nests were far away from vantage
323 viewpoints or concealed under vegetation, and it is difficult for cuckoos
324 to check them due to host nest defense (Feeney et al. 2014). Nest building
325 speed in some hosts may be different, if one host pair build nests slowly,
326 while female cuckoos detect this nest for a long time and decide to lay
327 eggs on a suitable day according to their assessment. However, when

328 cuckoos approach this target nest still empty with no egg, the cuckoo may
329 also be forced to deposit its egg in a hurry. For example, we only found
330 one cuckoo egg in a half-finished nest in year 2014 (figure 5). 2) Female
331 cuckoos had not enough time to make an optimal choice among different
332 available nests based on variation in number of eggs. Generally, hosts
333 always appear around their nests and are aggressive towards cuckoos
334 (Feeney et al. 2014; Ma et al. 2018; Zhang et al. 2019). For instance,
335 Nakamura et al. (2005) reported that the Oriental warbler (*Acrocephalus*
336 *orientalis*) drove off and repulsed female cuckoos when they attempted to
337 approach the nest for nine times. Furthermore, laying females were
338 injured or even killed by hosts (Davies 2000). In this study, we also found
339 that a female cuckoo was fiercely attacked and fell into swampy water
340 below the host nest until it was drowned in year 2014. 3) Empty nests had
341 sufficient space for cuckoo body size. The only evidence that larger nests
342 in many different species of birds are associated with the laying of larger
343 clutches (Møller et al. 2014) may be that empty nests are superior for
344 rapid egg-laying by cuckoos. 4) Cuckoo females may also follow a
345 ‘shotgun strategy’ as shown in shiny cowbirds (*Molothrus bonariensis*)
346 that laid 12.4% (33/267) eggs into incubated host clutches and 30.7%
347 (82/267) eggs into deserted nests (Kattan 1997).

348 In order to increase the opportunity of cuckoo parasitism of
349 experimental nests, we specifically fixed the nests higher and more

350 exposed than naturally active nests. Actually, these treatments promoted
351 parasitism rate to help elicit more cuckoos coming and laying eggs as
352 filmed in our video devices. These results are also consistent with the nest
353 height hypothesis (Budnik et al. 2002; Patten et al. 2011) and the nest
354 exposure hypothesis explaining variation in rate of cuckoo parasitism
355 (Moskát and Honza 2000; Clarke et al. 2001).

356 **5. Conclusion**

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

371

372 **Ethics.** The experiments comply with the current laws of China, where
373 they were performed. Fieldwork was carried out with permission (no.
374 ZL-GZNU-2019-06) from Zhalong National Nature Reserve,
375 Heilongjiang, China. Experimental procedures were in agreement with
376 the Animal Research Ethics Committee of Hainan Provincial Education
377 Centre for Ecology and Environment, Hainan Normal University (permit
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379 **Data accessibility.** All data analysed and videos for this study are
380 available at Dryad Digital Repository by Wang et al. 2020.

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

386 **Competing interest.** The authors declare that they have no competing
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400

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594

595 **Legends to figures**

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

599

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

604

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

608

609 **Figure 4.** Frequency distribution of cuckoos choosing experimental nests
610 in relation to the number of model eggs among four types nest (0, 1, 3 or
611 5 eggs) when parasitism happened. Numbers on the bars refer to the
612 result of cuckoos' choice toward the type nest.

613

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

616

617 **Electronic Supplementary Materials**

618

619 **ESM Video S1.** Female common cuckoo lay its egg in a nest with zero
620 experimental parasitic egg.

621

622 **ESM Video S2.** Female common cuckoo lays its egg in a nest with one
623 experimental parasitic egg.

624

625 **ESM Video S3.** Female common cuckoo lays its egg in a nest with three
626 experimental parasitic eggs.

627

628 **ESM Video S4.** Female common cuckoo lays its egg in a nest with five
629 experimental parasitic eggs.