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

An interesting and puzzling question to scientists is whether parasites make decisions on the optimal time of parasitism based on the number of eggs. That is whether female parasites know which host nests are new and which host nests have females that already started incubation. Female cowbirds prefer a suitable number of eggs in their nests under lab conditions (White et al. 2007, 2009), and 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). In addition, evidence suggests that other bird species may 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). Therefore, parasites potentially know the laying stage of host eggs, and they are sensitive to clutch size. If the timing of egg laying affects reproductive success, natural selection should favor female cuckoos that parasitize a nest not too early neither too late during the laying sequence, because this benefits their offspring over host nestlings at the time of hatching (Davies 2000; Geltsch et al. 2016).

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

2. Material and methods

(a) Study site and study species

This study was performed in reed swamps in the Zhalong National Nature Reserve (46°48′-47°31′ N, 123°51′-124°37′ E) in Heilongjiang, northeast China. Field experiments were carried out each breeding season (June to 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 higher in the vegetation to make it easier for cuckoos to find (Moskát and Honza 2000; Clarke et al. 2001) and to parasitise (Budnik et al. 2002; Patten et al. 2011).

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

(d) Statistical analysis

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

3. Results

(a) Natural frequency of parasitism

A total of 245 cases of parasitism were recorded in 8 years 2012-2019 (figure 2), a highly significant difference in frequency of parasitism among nests with different clutch sizes (Chi-square test, $\chi^2 = 241.97$, $P < 0.001$). A proportion of 75% cuckoo eggs were parasitized at the 1-2 eggs stage (1 egg: 49%, 120/245; 2 eggs: 26%, 63/245). By contrast, just ca. 1% of cuckoo eggs were laid in 5-6 eggs nests (5 eggs: 0.8%, 2/245; 6 eggs: 0.4%, 1/245). Cuckoos biased parasitism towards nests with fewer host eggs in nests (e.g., 1 or 2 eggs) for parasitism compared to the nests with more eggs (e.g., 3-6 eggs) (figure 2).

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

(b) Experiments for attracting cuckoo parasitism

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

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

4. Discussion

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

Egg-laying by cuckoos was described as a very quick process (Wyllie 1981; Davies 2000). When approaching potential host nests, female cuckoos usually perch at a vantage point and monitor host activities (Honza et al. 2002; Moksnes et al. 2000). Empirical studies revealed that cuckoos 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 parasitism (17/245, 6.9%) subject to this scenario, and some previous studies showed that 4 out of 90 cuckoo eggs (4.4%) were laid in an empty nest (Wyllie 1981) and Honza et al. (2019) found 4.9% (28/577) of all parasitized nests did cuckoos make laying errors by parasitizing deserted and old nests including one nest (0.2%) that was even parasitized by a cuckoo egg during the nestling stage during their ten years' study. The possible explanations were that 1) female cuckoos assessed the host egg-laying stage by mistake. Some host nests were far away from vantage viewpoints or concealed under vegetation, and it is difficult for cuckoos to check them due to host nest defense (Feeney et al. 2014). Nest building speed in some hosts may be different, if one host pair build nests slowly, while female cuckoos detect this nest for a long time and decide to lay eggs on a suitable day according to their assessment. However, when cuckoos approach this target nest still empty with no egg, the cuckoo may also be forced to deposit its egg in a hurry. For example, we only found one cuckoo egg in a half-finished nest in year 2014 (figure 5). 2) Female cuckoos had not enough time to make an optimal choice among different available nests based on variation in number of eggs. Generally, hosts always appear around their nests and are aggressive towards cuckoos (Feeney et al. 2014; Ma et al. 2018; Zhang et al. 2019). For instance, Nakamura et al. (2005) reported that the Oriental warbler (*Acrocephalus orientalis*) drove off and 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.

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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.

Fig. 1

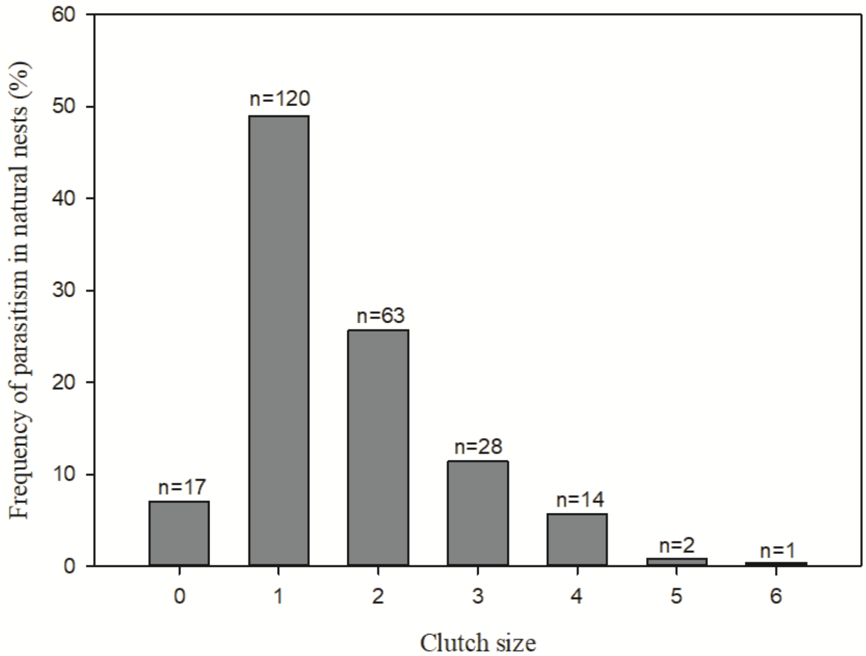

Frequency of parasitism in natural nests (%)
60
50
40
30
20
10
0
n=17
n=120
n=63
n=28
n=14
n=2
n=1
0
1
2
3
4
5
6
Clutch size

Fig. 2

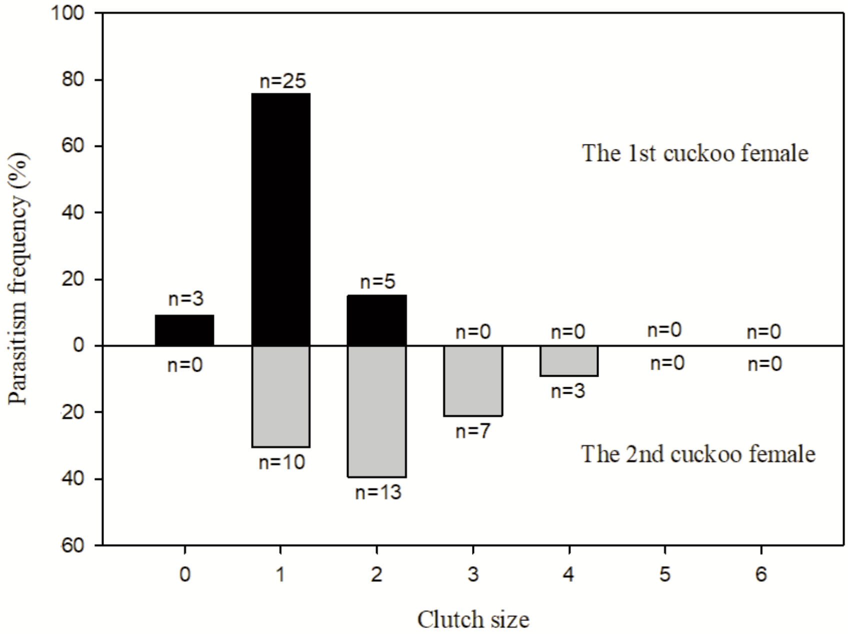
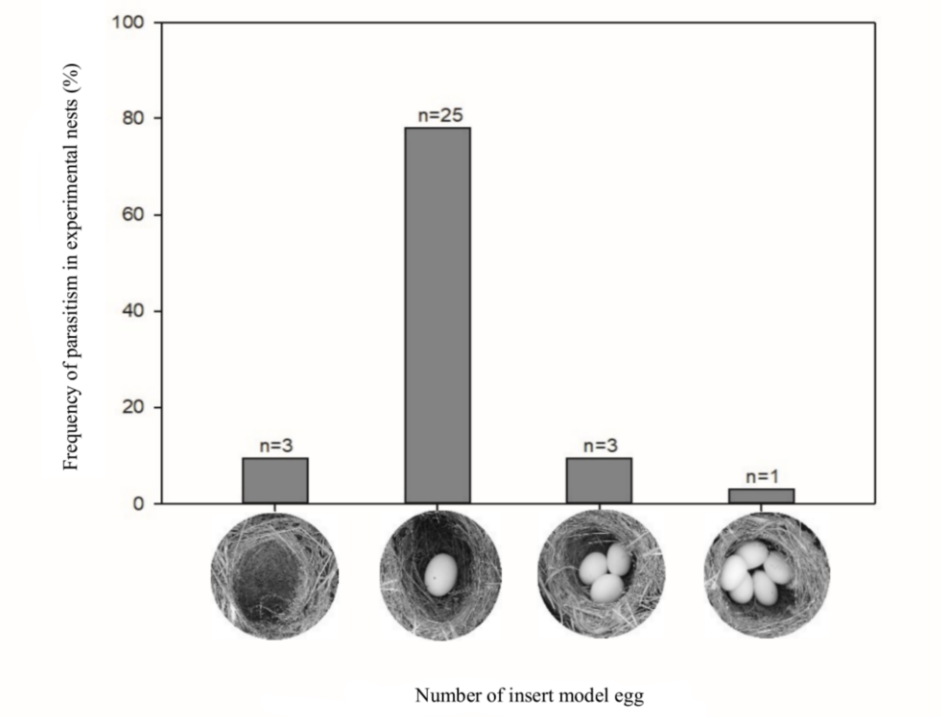

Parasitism frequency (%)
Clutch size
The 1st cuckoo female
The 2nd cuckoo female
100
80
60
40
20
0
20
40
60
0
1
2
3
4
5
6
n=3
n=25
n=5
n=0
n=0
n=0
n=0
n=0
n=10
n=13
n=7
n=3
n=0
n=0

Fig. 3



100
80
60
40
20
0
n=3
n=25
n=3
n=1
Frequency of parasitism in experimental nests (%)
Number of insert model egg

Fig. 4


Fig. 5