Egg laying behavior of common cuckoos (Cuculus canorus): Data based on field video-recordings

DEAR EDITOR,

The egg laying behavior of brood parasites is at the heart of studies on host co-evolution. Therefore, research on egg laying behavior can improve our understanding of brood parasitism and associated processes. Over a seven year study period, we monitored 455 oriental reed warbler (Acrocephalus orientalis) nests during the egg laying period, 250 of which were parasitized by common cuckoos (Cuculus canorus). We collected 53 clear videos of common cuckoo parasitism, analyzed all recorded parasitic behavior in detail, and summarized the process of brood parasitism. Furthermore, based on analyses of the field video recordings, we propose a new explanation for egg removal behavior, namely the delivery hypothesis, i.e., egg pecking and biting by cuckoos may facilitate fast egg-laying and parasitism by reducing host attention and attack, with egg removal a side effect of egg pecking and biting. We concluded that common cuckoos change their behavior when hosts are present at the nest, with a set of behaviors performed to deal with host attack and successfully complete parasitic egg-laying regardless of time of day.

Obligate brood parasites lay their eggs in the nests of other birds and provide no parental care to their offspring (Davies, 2000; Soler, 2017). Because the cost of parasitism to the host is high, it can provoke strong host resistance, such as anti-parasitic nest defense and egg rejection (Davies, 2000; Soler, 2014, 2017). Parasitic birds lay eggs in host nests rapidly to reduce the chance of discovery and attack by the host (Chance, 1940; Davies & de L. Brooke, 1988; Davies, 2000). The arms race between parasites and hosts is present throughout their lives (Davies, 2011; Feeney et al., 2014), but their most intense “bodily combat” takes place when parasites attempt to lay eggs (Feeney et al., 2012, 2013; Gloag et al., 2013; Moksnes et al., 2000).

The egg laying process varies with avian brood parasites. In terms of time, some parasites, such as common cuckoos, are known to lay their eggs in the afternoon or evening (Nakamura et al., 2005; Wyllie, 1981). As hosts lay eggs and stay close to the nest in the morning, but rarely in the afternoon, afternoon parasitism reduces the risk of detection by the host and the possibility of parasitic egg rejection (Davies & de L. Brooke, 1988). However, some parasites such as cowbirds (Molothrus spp.) complete egg laying before sunrise (Gloag et al., 2013; Sealy, 1992). The entire process of egg laying by a brood parasite is usually short (less than 10 s) (Davies & de L. Brooke, 1988;Ellison et al., 2020; Moksnes et al., 2000; Scardamaglia et al., 2017; Soler & Soler, 2000); despite this, in addition to egg laying, brood parasites also display other complex behaviors. For instance, cowbirds often remove or puncture host eggs during egg laying (Gloag et al., 2013; Sealy, 1992), a behavior also noted in honeyguides (family Indicatoridae) (Spottiswoode & Colebrook-Robjent, 2007). Indigobirds and whydahs (Viduidae) occasionally eat host eggs (Payne et al., 2000, 2001), and most female cuckoos prefer to remove or eat 1–2 host eggs (Gloag et al., 2014; Langmore & Kilner, 2009; Moksnes et al., 2000). Even within the same species, such as the common cuckoo, some individuals may remove eggs even under strong attack by a host, whereas others leave quickly after laying eggs (Moksnes et al., 2000).

So far, several hypotheses have been proposed to explain why parasites remove eggs (reviewed in Šulc et al., 2016). Among them, the “parasite competition hypothesis” suggests that egg removal behavior acts to prevent previously laid parasitic eggs from hatching, thereby improving the chances of success of the second-laid parasitic eggs (Brooker et al., 1990). This hypothesis is supported in little bronze-cuckoos (Chalcites minutillus) and their host, i.e., large-billed gerygones (Gerygone magnirostris). Gerygones rarely reject parasitized eggs (Gerygone magnirostris) (Chalcites minutillus) and their host, i.e., large-billed gerygones (Gerygone magnirostris).

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foreign eggs; nonetheless, cuckoos usually remove or eat eggs during parasitism (Gloag et al., 2014). However, common cuckoo females are not selective when removing eggs from the nest (Šulc et al., 2016), which does not support this hypothesis. The “help to the parasitic chick hypothesis” is supported by evidence from non-evicting brood parasites, such as cowbirds. Removing eggs can indeed reduce subsequent food competition among nestmates, whereas in the case of evicting species (e.g., common cuckoos), egg removal may allow parasitic offspring to expend less energy and effort removing host eggs, with consequences for their growth (Grim et al., 2009; Martin-Gámez et al., 2005). Recent study has suggested that cuckoo nestlings may grow faster when they remove more eggs (Medina et al., 2019). In contrast, some hypotheses, such as the “free meal hypothesis”, remain poorly tested (Peer, 2006; Scott et al., 1992) as it is difficult to determine whether or not parasites lack nutrition, especially calcium.

The common cuckoo is one of the most widely studied parasitic species, with more than 125 host species recorded (Moksnes et al., 2013). In Europe, common cuckoos have at least 20 different females (female-lines) in different populations with various egg morphs (Antonov et al., 2007; Moksnes & Øskaft, 1995). In China, there are 17 different species of parasitic cuckoos, with common cuckoos comprising different gentes, each parasitizing a single host (Fossey et al. 2016; Yang et al., 2012). Moksnes et al. (2000) video-recorded the egg laying behavior of the common cuckoo in the Czech Republic; however, the recordings failed to capture some details inside the nest and the sample size (n=14) was small, making it difficult to conclusively establish common cuckoo-specific behaviors. Therefore, further studies on the egg-laying behavior of cuckoos in different populations are necessary to obtain greater insight and knowledge in this field.

To this end, we analyzed 53 videos recorded in the field over a seven-year study period and used accurate video analysis software to analyze egg-laying details of common cuckoos in the nests of oriental reed warblers. In addition, we propose a new hypothesis for the interpretation of egg removal behavior in common cuckoos.

This study was performed in Zhalong National Nature Reserve (N46°45′–47°31′; E123°51′–124°37′) in Heilongjiang, northeast China. We systematically searched for oriental reed warbler nests during the breeding season (June to August) from 2013 to 2019. In our study area, common cuckoos mainly parasitize oriental reed warbler hosts, with a parasitism rate ranging from 34.3% to 65.5% (Yang et al., 2016a, 2017). The habitats include reed swamps, open water, and grasslands, with oriental reed warbler nests often built among reed stems with dry reed leaves. Newly built nests were checked every morning before 0800 h for the presence of host eggs. Once the host began egg laying, the nest was video recorded continuously from 0800 h to 2000 h, so that subsequent cuckoo parasitism could be accurately identified.

We used mini digital cameras (Uniscan-T71, 70 mm×26 mm×12 mm; Mymahdi Technology Co. Ltd., China) to capture cuckoo parasitism. To achieve longer battery life, the camcorders were equipped with an external power supply (20000 mAh, Romoss-Sense 6; Romoss Technology Co. Ltd., China). Recording usually started at 0800 h in the morning and the device was retrieved before sunset at 2000 h to prevent rain damage at night and to recharge the batteries.

The recording device was suspended ca. 1 m above the nest to avoid interference and to allow the target to appear in the device’s field of vision. We camouflaged the camera with reed leaves and wrapped it in plastic to avoid rain damage. We chose to record on sunny or non-rainy days to avoid rain damage of recording devices; however, we managed to record several cases of parasitism on days with unexpected rain.

When reviewing the video each day, we first checked whether parasitism had occurred, and then trimmed the video to include vision of the parasitic episode to analyze cases of egg laying by cuckoos. For each target nest, the device was installed for a maximum of 6 days. This was because oriental reed warblers usually have a clutch size of 4–6 eggs (Liang et al., 2014), and the cuckoo usually parasitizes during the egg laying period of the host (Li et al., 2016; Yang et al., 2016a, 2016b, 2017). We stopped recordings when the hosts began to incubate. Well-recorded videos were used for analysis of the egg laying process of cuckoos and warblers. Supplementary materials, including the 53 videos (ESM Videos S1-S53) and data referred to this study, can be found at the Dryad Digital Repository (https://datadryad.org/stash/shares/9EhA4V4f9emrU97VR0HzmCYrE5uC9owpPLL60VA).

We used video-analysis software (Aijianji; accuracy: 0.04 s per frame; Wangxu Technology Co. Ltd., China) to analyze the egg-laying process and to record all egg-laying details of cuckoos—from the time the parasites entered the device’s field of vision until they left, including the time at which parasitism occurred, presence of the host, time spent by cuckoos around the nest, time spent laying, number of eggs removed by cuckoos, and behaviors such as pecking/biting eggs or opening eyes during egg laying. In cases where nest surroundings were not visible in the video footage, we used sound to quantify the time cuckoos arrived at the nest as hosts would make a warning call or cuckoos would make noise when parasitism occurred.

Generalized linear mixed models (GLMMs) and log-link function were used to compare differences in egg-laying duration (gamma error structure) and number of eggs removed (Poisson error structure) by cuckoos between nests where hosts were or were not present. For all GLMMs, years were treated as a random term and all predicted variables were treated as fixed terms. All data were analyzed using R 3.6.1 software (http://www.r-project.org). Chi-square tests were used to test for the frequency of egg removal by cuckoos. Differences were considered significant at the 0.05 level.

In total, we observed 455 oriental reed warbler nests during the egg-laying period, 250 of which were parasitized by common cuckoos. We recorded 53 clear videos of parasitism by cuckoos (ESM Video S1-S53).
The cuckoo parasitism process involved the following steps. The cuckoo first approached the nest (Figure 1A, a), regardless of whether the host was present (Figure 1A, b); it then stood on the edge of the nest to start egg laying.
Table 1  Details of common cuckoo visits to host nests

| Host activity | Time of day | Duration of stay at nest (s) | Duration of egg laying (s) | No. of eggs removed (n) |
|---------------|-------------|------------------------------|---------------------------|-------------------------|
| Absent        | 1616 h      | 24.4±27 22                   | 10.67±7.05                | 0.6±0.6                 |
| Present       | 1641 h      | 7.6±3.11                     | 5.6±2.42                  | 0.5±0.5                 |

\[ \chi^2 = 0.164, df = 1, P = 0.686 \]

Data are means±SD of duration of egg laying, duration of stay, and number of eggs removed by cuckoo females when host was absent from \( n=18 \) and present \( n=35 \) at the nest.

(Figure 1A, c); used its bill to grasp eggs in the nest (Figure 1A, d); concealed its head and peaked an egg; bowed its body; spread its wings; laid its tail very close to the bottom of the nest; kept its eyes open the entire time (Figure 1A, e); raised its head at the end of egg laying (Figure 1A, f); removed one egg (or no eggs in some cases) and flew away quickly (Figure 1A, g).

Cuckoos laid eggs throughout the day, from 0911 h to 1925 h \( n=53 \), with a median time of 1630 h (Figure 1B). When the host was absent, cuckoos laid eggs from 0911 h to 1925 h \( n=18 \), with a median time of 1616 h (Table 1). When the host was present, the cuckoos laid eggs from 1129 h to 1850 h \( n=35 \), with a median time of 1641 h (Table 1). Regardless of whether the host was present, there was no significant difference in the time of the day when cuckoos visited nests to parasitize (GLMMs, \( \chi^2=0.164, df=1, P=0.686 \)).

The duration of stay by the cuckoos around the nests was defined as the sum of time spent by the cuckoo in and around the host nest during the entire egg-laying process. In addition to actual egg laying, time was spent on other actions, including pecking and removing eggs, watching the nest, and avoiding host attacks. The laying process lasted between 2.32 s and 102.00 s (mean=13.3±7.7 s, \( n=53 \)). When the host was absent, the duration lasted between 3.92 s and 102.00 s (mean=24.48±27.23 s, \( n=18 \)), whereas, when the host was present, duration lasted between 3.32 s and 13.36 s (mean=7.60±3.11 s, \( n=35 \)). The time spent in the nest was significantly longer when the host was absent (GLMMs, \( \chi^2=35.355, df=1, P=0.001 \), Table 1).

Actual egg-laying time was defined as the time it took for a cuckoo to stand on the edge of the nest to commence laying until it raised its head and flew away, excluding the time spent on actions like removing eggs and observing. Egg-laying time was between 2.56 s and 26.28 s (7.28±5.02 s, \( n=49 \)). Four videos were not included in statistical analysis as the cuckoo did not lay eggs in these cases, although they did remove host eggs. In the absence of the host, egg-laying time was between 3.72 s and 26.28 s (10.67±7.05 s, \( n=16 \)), whereas in the presence of the host, actual egg-laying time was between 2.56 s and 12.84 s (5.61±2.42 s, \( n=33 \)). Thus, cuckoos laid eggs significantly faster when the host was present (GLM Ms, \( \chi^2=26.902, df=1, P=0.001 \), Table 1).

In the 53 videos analyzed, head hiding behavior was not recorded in two videos and was unclear in one video, with all other recordings showing cuckoos hiding their heads near the bottom of the nest \( n=50 \). Among these 50 videos, 18 were not clear enough to observe the cuckoos’ eyes, but in the remaining 32, their eyes remained open during the egg-laying process, regardless of whether hosts were absent \( n=32 \) or present \( n=21 \).

Based on observations from the 53 parasitism recordings, cuckoos usually laid eggs on sunny or non-rainy days \( 51/53 \). Only two cases of parasitism occurred on a rainy day \( 2/53 \), ESM Videos 17, 44), one of which was during heavy rain (see ESM Video 44).

During the egg-laying process \( n=53 \), host eggs were not removed by the cuckoos in 27 nests but were removed in 26 nests, usually one \( 24/26 \) or occasionally two \( 2/26 \) eggs in each case. Thus, there was no difference in the number of eggs removed by cuckoos in the presence or absence of the host (GLMM, \( \chi^2=0.406, df=1, P=0.524 \), Table 1).

Except for six videos in which egg removal behavior was not clearly visible, cuckoos \( n=47 \) were observed pecking/biting one egg in the nest before quickly laying their own egg and then flying away. When leaving, some cuckoos carried the pecked egg \( n=21 \) with them, while others left it in the nest \( n=26 \). This suggests that removing the pecked egg was not an essential part of their parasitic process (Chi-square test, \( \chi^2=0.531, P=0.465 \)). In one case, a cuckoo female held an egg in her bill and threw it away before egg laying. She then pecked another egg while laying her own but did not remove this host egg when finished (e.g., ESM Video 44).

Based on our observations, we propose a new explanation for egg removal behavior in cuckoos, namely, the delivery hypothesis. Specially, egg pecking/biting may help the parasitic cuckoo lay eggs more quickly to avoid host attention (Thorogood & Davies, 2016) and reduce host attacks (Ma et al., 2018), with egg removal being a side effect of egg pecking, although cuckoos sometimes removed the egg and sometimes did not.

In cuckoos, holding eggs in their bill during egg laying could waste time and energy and could increase host attack (Honzà et al., 2002; Moksnes et al., 2000; Sealy et al., 1995). Thus, reducing the time spent laying eggs is likely to be a critical factor, as fast egg laying can reduce the probability of detection and attack by the host (Sealy et al., 1995; Thorogood & Davies, 2016). Sealy et al. (1995) reviewed the egg-laying time of 19 species of nonparasitic birds and found that time varied from 20.7 min to 103.7 min. Wang et al. (2018) reported an egg-laying time in domestic ducks (Anas
if more nests were observed on rainy days, more cases of were recorded unexpectedly in rainy weather. We believe that videos were recorded on sunny days. However, two videos rain, we tried to record videos in dry weather. As such, most 2017). To ensure the recording devices were not damaged by reed warbler 2000; Nakamura et al., 2005). However, we also found some hitherto unreported behavior. A small number of cuckoos laid eggs from 0900 h to 1200 h, irrespective of the presence of the host. This suggests that cuckoos can lay eggs over the whole day, except in the early morning when warbler hosts lay their own eggs. In theory, any time of the day would be reasonable for cuckoos to lay eggs. However, it would be unsafe to parasitize before the hosts lay their own eggs as parasitic eggs can be easily rejected in that case (Davies, 2000). As cuckoos spend a great deal of time observing the nesting activities of their host (Honza et al., 2002), visiting the host nests too early would likely decrease the cuckoos’ rate of success, thus it would be an adaptive advantage to lay their eggs in the afternoon or before sunset.

If the host is absent during the egg-laying process, cuckoos have more time to expend on other activities, e.g., eating host eggs or waiting and watching, before they lay their own eggs and leave (see also Moksnes et al., 2000). This scenario was fully reflected in EMS Video 8: i.e., the female cuckoo finished laying her eggs, left for a while, returned to the same nest, removed one host egg, and then left again. In contrast, if the host is present and constantly attacking, the cuckoo has limited time and opportunity to perform time-consuming behaviors such as eating eggs or observing, instead rapidly laying eggs and fleeing. Therefore, we found significant differences in the duration of time spent at the nest and in actual egg-laying time when host was absent or present.

In this study, we recorded only two cases of parasitism on rainy days. Cuckoos are more vocally active in sunny than in rainy weather (Deng et al., 2019), with a recent study also suggesting that female cuckoo calls serve as a distraction for the host parent during cuckoo egg laying (e.g., as reported in reed warbler Acrocephalus scirpaceus by York & Davies, 2017). To ensure the recording devices were not damaged by rain, we tried to record videos in dry weather. As such, most videos were recorded on sunny days. However, two videos were recorded unexpectedly in rainy weather. We believe that if more nests were observed on rainy days, more cases of cuckoo egg laying on such days would be found.

When attacking the cuckoo, the host usually attacks the head, especially the eyes, which are the most vulnerable part of a bird’s head (Edwards et al., 1950; Grim, 2005; Trnka & Prokop, 2012). To reduce injury from host attacks, especially to the eyes, it is expected that brood parasites will close their eyes tightly when laying their parasitic eggs. In the current study, however, we found that when the brood approached the host nest, it lowered its head to the bottom of the nest and spread its wings, keeping its eyes open during the entire egg-laying process.

One explanation for this behavior may be that open eyes allow cuckoos to see the host eggs more clearly, making it easier to pick up the egg and identify the direction in which to fly at the completion of egg laying. Because cuckoos may lower their heads and protect their heads using their spreading wings, leaving only their backs exposed to host attacks, and this, coupled with short exposure time, may reduce the impact of host attack. For that reason, the presence of the host in the nest did not appear to affect cuckoo egg-laying behavior. As long as the cuckoo could locate its target, it continued to lay eggs, without fear of host attack, contrary to previous suggestions that egg laying by cuckoos occurs in secret (Chance, 1940; Davies & de L. Brooke, 1988; Davies, 2000; Thorogood & Davies, 2016).

During egg laying, the cuckoo bowed its body and laid its tail close to the bottom of the nest. No broken cuckoo or host eggs were found in any parasitized nest observed over the seven years in our study site. Brood parasite eggs exhibit unusual eggshell strength (Antonov et al., 2008; Brooker & Brooker, 1991; Picman & Pribil, 1997; Spottiswoode, 2010). Laying thick-shelled eggs can prevent rejection by the host (Antonov et al., 2006), is beneficial in terms of better heat preservation during hatching (Yang et al., 2018), and can offer protection from breakage during egg-laying (Ellison et al., 2020; Spottiswoode, 2010). Parasitic brown-headed (Molothrus ater) and shiny cowbirds (M. bonariensis) have been observed dropping their eggs into nests from an estimated height of 4–8 cm while laying; this elevated position may have selected for the high eggshell strength in cowbirds because stronger eggshells would be less likely to crack during egg laying (Ellison et al., 2020). In our videos, the egg-laying height of the cuckoos was close to zero; therefore, we suggest that the egg breakage hypothesis (Ellison et al., 2020) does not apply to the egg-laying process of cuckoos.

In conclusion, through field video analysis, we recorded a series of brood parasitism-related behaviors in common cuckoos. We also proposed a new hypothesis explaining their egg removal behavior, namely the delivery hypothesis, i.e., egg pecking/biting may help the cuckoo lay eggs more quickly to avoid host attention and reduce host attacks, with egg removal being a side effect of egg pecking and biting. Cuckoos will forcibly complete the egg-laying process regardless of whether the host is present as they have a set of behaviors to deal with host attack and can successfully
complete brood parasitism at any time. Thus, future research should clarify the function of egg-biting behavior, determine whether the proposed delivery hypothesis is applicable to other parasitic cuckoos, such as the lesser cuckoo (Cuculus poliocephalus) and large hawk cuckoo (Hierococcyx sparverioides), and explore whether egg-laying behavior in other parasitic cuckoos is similar to that in common cuckoos.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

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COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS’ CONTRIBUTIONS

W.L. and L.W.W. designed the study; L.W.W., G.Z., G.B.H., and Y.H.Z. carried out the field experiments; L.W.W. performed the laboratory and statistical analyses. L.W.W. wrote the draft manuscript with help and involvement from W.L. All authors read and approved the final version of the manuscript.

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