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; Ellisson 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

Received: 22 February 2020; Accepted: 14 May 2020; Online: 21 May 2020

Foundation items: This work was supported by the National Natural Science Foundation of China (31660617 and 31960105 to L.W.W., 31772453 and 31970427 to W.L.). L.W.W. was funded by the Initial Fund Key Laboratories of Guizhou Province (2011-4005) and Joint Fund of the National Natural Science Foundation of China and the Karst Science Research Center of Guizhou Province (U1812401)

DOI: 10.24272/j.issn.2095-8137.2020.021

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; Martín-Gálvez 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 gentes (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 (Fossøy 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°48'–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 (Uniscom-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 (20 000 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 retrieving 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/share/9EhA4V4tI9emrU97VjREOhzmCYrE5ujC9owpPLL60VA).

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

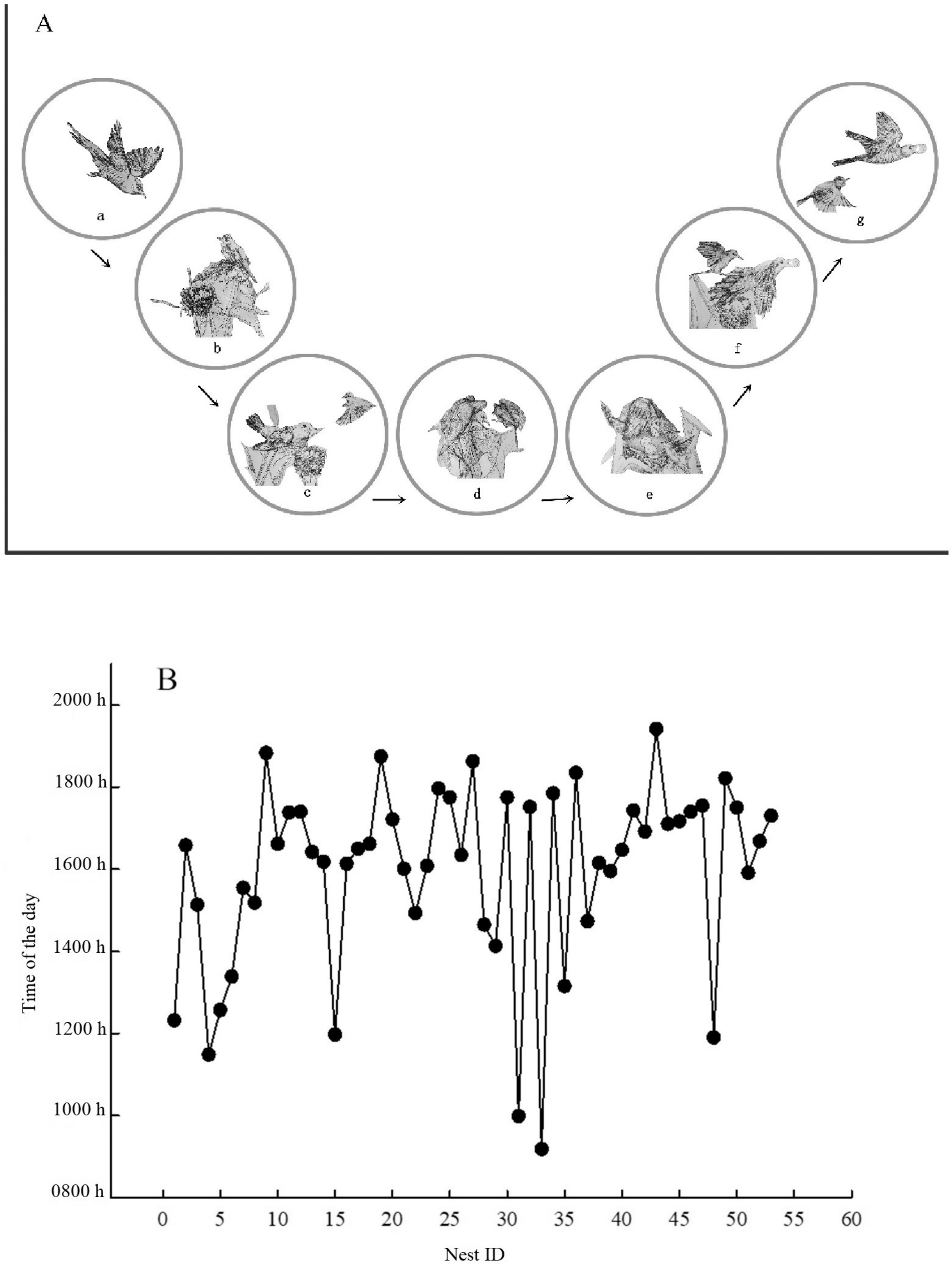

Figure 1 Illustration of egg-laying behaviors of common cuckoo females parasitizing oriental reed warbler host nests (A) and distribution of parasitism time by cuckoos across each daytime hour (in total, 53 nests experienced parasitism) (B)

a: Cuckoo flew down to target nest; b: Host guarded nest; c: Cuckoo perched on target nest; d: Cuckoo hid its head and started egg pecking/biting; e: Cuckoo hunched its body, pecked an egg, closed its tail, and opened its eyes; f: Cuckoo finished egg laying, sometimes removing an egg; g: Cuckoo flew away.

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	24.48±27.22	10.67±7.05	0.6±0.6
Present	1641 h	7.60±3.11	5.61±2.42	0.5±0.5
χ^2	0.164	35.355	26.902	0.406
df	1	1	1	1
P	0.686	<0.001	<0.002	0.524

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, χ^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=13.33±17.72 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 2.32 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, χ^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 (7.26±5.02 s, *n*=49). Four videos were not included in statistical analysis as the cuckoos 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, χ^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 (11/32) or present (21/32).

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, χ^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 they 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, χ^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., EMS 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 (Honza 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* *platyrhynchos domesticus*) of ~35 min. In brood parasites, however, egg laying usually takes less than 1 min, even as little 10 s (Davies & de L. Brooke, 1988; Gloag et al., 2014; Honza et al., 2002; Wyllie, 1981).

In this study, we found that common cuckoos usually pecked/bit one egg during egg laying, with some cuckoos (and some not) then removing the peaked egg soon after completion of egg laying. Moksnes et al. (2000) described one case in which the cuckoo ate two host eggs and held but did not remove a third before laying her own. This behavior is consistent with most cases of egg removal observed in our study. We hypothesize that, during such a short period of egg-laying, the seemingly superfluous action of egg biting was possibly a way to help reinforce the strength of fast egg-laying by the cuckoo.

Our results indicated that most cuckoos laid eggs in the afternoon, consistent with previous work (Honza et al., 2002; Moksnes et al., 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 cuckoo 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

We are grateful to Wenfeng Wang and Jianhua Ma from Zhalong National Nature Reserve for their help and cooperation. All experiments performed complied with the current laws of China. Fieldwork was carried out with permission (no. ZL-GZNU-2019-06) from Zhalong National Nature Reserve, Heilongjiang, China. Experimental procedures were in accordance with the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (no. HNECEE-2012-003).

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.

Long-Wu Wang[1], Guo Zhong[1], Gang-Bin He[1], Yu-Han Zhang[1], Wei Liang[2,*]

[1] *State Forestry Administration of China Key Laboratory for Biodiversity Conservation in Mountainous Areas of Southwest Karst*, *School of Life Sciences*, *Guizhou Normal University*, *Guiyang*, *Guizhou* 550001, *China*

[2] *Ministry of Education Key Laboratory for Ecology of Tropical Islands*, *College of Life Sciences*, *Hainan Normal University*, *Haikou*, *Hainan* 571158, *China*

*Corresponding author, E-mail: liangwei@hainnu.edu.cn

REFERENCES

Antonov A, Stokke BG, Moksnes A, Kleven O, Honza M, Røskaft E. 2006. Eggshell strength of an obligate brood parasite: a test of the puncture resistance hypothesis. *Behavioral Ecology and Sociobiology*, **60**(1): 11−18.

Antonov A, Stokke BG, Moksnes A, Røskaft E. 2007. First evidence of regular common cuckoo, *Cuculus canorus*, parasitism on eastern olivaceous warblers, *Hippolais pallida elaeica*. *Naturwissenschaften*, **94**(4): 307−312.

Antonov A, Stokke BG, Moksnes A, Røskaft E. 2008. Does the cuckoo benefit from laying unusually strong eggs?. *Animal Behaviour*, **76**(6): 1893−1900.

Brooker LC, Brooker MG, Brooker AMH. 1990. An alternative population/genetics model for the evolution of egg mimesis and egg crypsis in cuckoos. *Journal of Theoretical Biology*, **146**(1): 123−143.

Brooker MG, Brooker LC. 1991. Eggshell strength in cuckoos and cowbirds. *Ibis*, **133**(4): 406−413.

Chance EP. 1940. The Truth about the Cuckoo. London: Country Life.

Davies NB, de L. Brooke M. 1988. Cuckoos versus reed warblers: Adaptations and counteradaptations. *Animal Behaviour*, **36**(1): 262−284.

Davies NB. 2000. Cuckoos, Cowbirds and other Cheats. London: T & AD Poyser.

Davies NB. 2011. Cuckoo adaptations: trickery and tuning. *Journal of Zoology*, **284**(1): 1−14.

Deng ZQ, Lloyd H, Xia CW, Møller AP, Liang W, Zhang YY. 2019. Components of variation in female common cuckoo calls. *Behavioural Processes*, **158**: 106−112.

Edwards G, Hosking E, Smith S. 1950. Reactions of some passerine birds to a stuffed cuckoo. II. A detailed study of the willow-warbler. *British Birds*, **43**: 144−150.

Ellison KS, Fiorini VD, Gloag R, Sealy SG. 2020. Video recordings of brown-headed (*Molothrus ater*) and shiny (*M. bonariensis*) cowbirds reveal oviposition from an elevated position: implications for host–parasite coevolution. *The Wilson Journal of Ornithology*, **131**(4): 789−795.

Feeney WE, Medina I, Somveille M, Heinsohn R, Hall ML, Mulder RA, Stein JA, Kilner RM, Langmore NE. 2013. Brood parasitism and the evolution of cooperative breeding in birds. *Science*, **342**(6165): 1506−1508.

Feeney WE, Welbergen JA, Langmore NE. 2012. The frontline of avian brood parasite–host coevolution. *Animal Behaviour*, **84**(1): 3−12.

Feeney WE, Welbergen JA, Langmore NE. 2014. Advances in the study of coevolution between avian brood parasites and their hosts. *Annual Review of Ecology, Evolution, and Systematics*, **45**: 227−246.

Fossøy F, Sorenson MD, Liang W, Ekrem T, Moksnes A, Møller AP, Rutila J, Røskaft E, Takasu F, Yang CC, Stokke BG. 2016. Ancient origin and maternal inheritance of blue cuckoo eggs. *Nature Communications*, **7**: 10272.

Gloag R, Fiorini VD, Reboreda JC, Kacelnik A. 2013. The wages of violence: mobbing by mockingbirds as a frontline defence against brood-parasitic cowbirds. *Animal Behaviour*, **86**(5): 1023−1029.

Gloag R, Keller LA, Langmore NE. 2014. Cryptic cuckoo eggs hide from competing cuckoos. *Proceedings of the Royal Society B: Biological Sciences*, **281**(1792): 20141014.

Grim T. 2005. Host recognition of brood parasites: implications for methodology in studies of enemy recognition. *The Auk*, **122**(2): 530−543.

Grim T, Rutila J, Cassey P, Hauber ME. 2009. The cost of virulence: An experimental study of egg eviction by brood parasitic chicks. *Behavioral Ecology*, **20**(5): 1138−1146.

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. *Animal Behaviour*, **64**(6): 861−868.

Langmore NE, Kilner RM. 2009. Why do Horsfield's bronze-cuckoo *Chalcites basalis* eggs mimic those of their hosts?. *Behavioral Ecology and Sociobiology*, **63**(8): 1127−1131.

Li DL, Zhang ZW, Grim T, Liang W, Stokke BG. 2016. Explaining variation in brood parasitism rates between potential host species with similar habitat requirements. *Evolutionary Ecology*, **30**(5): 905−923.

Liang GX, Yang CC, Wang LW, Liang W. 2014. Variation in parasitism rates by common cuckoos among three populations of the Oriental reed warblers. *Sichuan Journal of Zoology*, **33**(5): 673−677. (in Chinese)

Ma LK, Yang CC, Liang W. 2018. Hawk mimicry does not reduce attacks of cuckoos by highly aggressive hosts. *Avian Research*, **9**(1): 35.

Martín-Gálvez D, Soler M, Soler JJ, Martín-Vivaldi M, Palomino JJ. 2005. Food acquisition by common cuckoo chicks in rufous bush robin nests and the advantage of eviction behaviour. *Animal Behaviour*, **70**(6): 1313−1321.

Medina I, Hall ML, Taylor CJ, Mulder RA, Langmore NE. 2019. Experimental increase in eviction load does not impose a growth cost for cuckoo chicks. *Behavioral Ecology and Sociobiology*, **73**(4): 44.

Moksnes A, Fossøy F, Røskaft E, Stokke BG. 2013. Reviewing 30 years of studies on the common cuckoo: accumulated knowledge and future perspectives. *Chinese Birds*, **4**(1): 3−14.

Moksnes A, Øskaft ER. 1995. Egg‐morphs and host preference in the common cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections. *Journal of Zoology*, **236**(4): 625−648.

Moksnes A, Røskaft E, Hagen LG, Honza M, Mørk C, Olsen PH. 2000. Common cuckoo *Cuculus canorus* and host behaviour at reed warbler *Acrocephalus scirpaceus* nests. *Ibis*, **142**(2): 247−258.

Nakamura H, Miyazawa Y, Kashiwagi K. 2005. Behavior of radio-tracked common cuckoo females during the breeding season in Japan. *Ornithological Science*, **4**(1): 31−41.

Payne RB, Payne LL, Woods JL, Sorenson MD. 2000. Imprinting and the origin of parasite–host species associations in brood-parasitic indigobirds, Vidua chalybeata. *Animal Behaviour*, **59**(1): 69−81.

Payne RB, Woods JL, Payne LL. 2001. Parental care in estrildid finches: experimental tests of a model of *Vidua* brood parasitism. *Animal Behaviour*, **62**(3): 473−483.

Peer BD. 2006. Egg destruction and egg removal by avian brood parasites: Adaptiveness and consequences. *The Auk*, **123**(1): 16−22.

Picman J, Pribil S. 1997. Is greater eggshell density an alternative mechanism by which parasitic cuckoos increase the strength of their eggs?. *Journal für Ornithologie*, **138**(4): 531−541.

Scardamaglia RC, Fiorini VD, Kacelnik A, Reboreda JC. 2017. Planning host exploitation through prospecting visits by parasitic cowbirds. *Behavioral Ecology and Sociobiology*, **71**(1): 23.

Scott DM, Weatherhead PJ, Ankney CD. 1992. Egg-eating by female brown-headed cowbirds. *The Condor*, **94**(3): 579−584.

Sealy SG. 1992. Removal of yellow warbler eggs in association with cowbird parasitism. *The Condor*, **94**(1): 40−54.

Sealy SG, Neudorf DL, Hill DP. 1995. Rapid laying by brown‐headed cowbirds *Molothrus ater* and other parasitic birds. *Ibis*, **137**(1): 76−84.

Soler J, Soler M. 2000. Brood-parasite interactions between great spotted cuckoos and magpies: a model system for studying coevolutionary relationships. *Oecologia*, **125**(3): 309−320.

Soler M. 2014. Long–term coevolution between avian brood parasites and their hosts. *Biological Reviews*, **89**(3): 688−704.

Soler M. 2017. Avian Brood Parasitism. Behaviour, Ecology, Evolution and Coevolution. Cham: Springer.

Spottiswoode CN, Colebrook-Robjent JFR. 2007. Egg puncturing by the brood parasitic greater honeyguide and potential host counteradaptations. *Behavioral Ecology*, **18**(4): 792−799.

Spottiswoode CN. 2010. The evolution of host‐specific variation in cuckoo eggshell strength. *Journal of Evolutionary Biology*, **23**(8): 1792−1799.

Šulc M, Procházka P, Capek M, Honza M. 2016. Common cuckoo females are not choosy when removing an egg during parasitism. *Behavioral Ecology*, **27**(6): 1642−1649.

Thorogood R, Davies NB. 2016. Combining personal with social information facilitates host defences and explains why cuckoos should be secretive. *Scientific Reports*, **6**(1): 19872.

Trnka A, Prokop P. 2012. The effectiveness of hawk mimicry in protecting cuckoos from aggressive hosts. *Animal Behaviour*, **83**(1): 263−268.

Wang XP, Yang SL, Lu M, Liu CG, Tan B, Yang RC, Zhou MD, Luo YJ, He ZQ. 2018. The egg-laying behavior of Sanshui duck. *Jiangsu Agricultural Sciences*, **46**(17): 188−191. (in Chinese)

Wyllie I. 1981. The Cuckoo. London: Batsford.

Yang CC, Huang QL, Wang LW, Du WG, Liang W, Møller AP. 2018. Keeping eggs warm: thermal and developmental advantages for parasitic cuckoos of laying unusually thick-shelled eggs. *The Science of Nature*, **105**(1–2): 10.

Yang CC, Liang W, Antonov A, Cai Y, Stokke BG, Fossøy F, Moksnes A, Røskaft E. 2012. Diversity of parasitic cuckoos and their hosts in China. *Chinese Birds*, **3**(1): 9−32.

Yang CC, Wang LW, Liang W, Møller AP. 2016a. Do common cuckoos (*Cuculus canorus*) possess an optimal laying behaviour to match their own egg phenotype to that of their Oriental reed warbler (*Acrocephalus orientalis*) hosts?. *Biological Journal of the Linnean Society*, **117**(3): 422−427.

Yang CC, Wang LW, Liang W, Møller AP. 2016b. Egg recognition as antiparasitism defence in hosts does not select for laying of matching eggs in parasitic cuckoos. *Animal Behaviour*, **122**: 177−181.

Yang CC, Wang LW, Liang W, Møller AP. 2017. How cuckoos find and choose host nests for parasitism. *Behavioral Ecology*, **28**(3): 859−865.

York JE, Davies NB. 2017. Female cuckoo calls misdirect host defences towards the wrong enemy. *Nature Ecology & Evolution*, **1**(10): 1520−1525.