Nest size matters: common cuckoos prefer to parasitize larger nests of Oriental reed warblers

Longwu Wang1 · Gangbin He1 · Canchao Yang2 · Anders Pape Møller3 · Wei Liang2

Received: 30 August 2021 / Revised: 30 August 2021 / Accepted: 1 November 2021 / Published online: 12 November 2021
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract
Avian brood parasites leave parental care of their offspring to foster parents. Theory predicts that parasites should select for large host nests when they have sufficient available host nests at a given time. We developed an empirical experimental design to test cognitive ability of female cuckoos in nest size by studying nest choice of common cuckoos (Cuculus canorus) among nests of its Oriental reed warbler (Acrocephalus orientalis) hosts. We presented three groups of experimental nests: 1) nest dyads tied together including one large and one small artificial nest from reed leaves, 2) nest triads tied together used the old modified warbler’s own nests including enlarged, reduced and medium-sized nests, and 3) nest dyads are similar to group 1, but not tied together to elicit parasitism by common cuckoos. We predict that cuckoos prefer larger nest than medium one, the next is smaller nest. Our findings showed that common cuckoo females generally prefer large nests over medium or small sized nests in all three experimental groups. Furthermore, cuckoo parasitism was significantly more common than in previous studies of the same warbler population, implying that larger, higher and more exposed host nests effectively increased the probability of cuckoo parasitism.

Keywords Brood parasitism · Common cuckoo · Nest preference · Nest size · Oriental reed warbler

Introduction
Avian brood parasites increase their fitness through evolved egg-laying behaviour in the nests of hosts while leaving parental care of their offspring to the hosts (Davies 2000; Soler 2014). Brood parasites always depend on parasitized hosts for the care of their offspring. However, foster parents differ in their food provisioning ability of cuckoo nestlings caused by variation in parental quality (Brooke and Davies 1989; Grim et al. 2017). Therefore, if altricial obligate brood parasites maximize the benefits from the parental effort of their hosts, cuckoos should search for and select host nests with better quality during parasitism (de Neve et al. 2004; Álvarez and Barba 2008; Jelínek et al. 2016).

Birds’ nests are used for containing the eggs and/or offspring during breeding (Hansell 2000, 2007), the potential signaling function of a high-quality nest being important for successful fledging to avoid hosts from suffering from predation or from falling out of the nest (Álvarez and Barba 2008; Heenan and Seymour 2011; Møller et al. 2014; Møller 2017; Honza et al. 2020). Thus, parasites should search for the most suitable host nest (Davies 2000). How cuckoos find and choose host nests for parasitism is still poorly understood,
and previous studies suggested that egg laying by cuckoos should match the phenotypes or appearance of their host eggs (Avilés et al. 2006; Cherry et al. 2007; Honza et al. 2014; Li et al. 2016a, b), while other studies challenged these ideas and suggested that cuckoos randomly searched host nests for parasitism (Antonov et al. 2012; Yang et al. 2016b). Recent empirical work showed that when experimental nests in which some have different model eggs were given a similar opportunity for cuckoo parasitism, cuckoos selected these nests for parasitism without use of the content of nests including egg color, shape and size as search cues (Yang et al. 2016a). They randomly selected any one nest for parasitism and neglected the egg categories in the nest. Furthermore, the cuckoo parasitism frequency in their population associated with host nest size tended to be higher in large compared to small nests, they found that cuckoo females more often selected larger Oriental reed warbler nests (Acrocephalus orientalis) over smaller ones of black-browed reed warbler (Acrocephalus bistrigiceps) when these two types of nests were available for cuckoo choice (Yang et al. 2017), which could be explained by difference in host species, but also indicated that nest size plays a role in the cuckoo’s nest selection for parasitism.

The optimal egg-laying strategy proposes that when there are sufficiently many available nests at a given time, cuckoo females should prefer the nest made by the best quality hosts (Hauber 2007; Parejo and Avilés 2007; Trnka and Prokop 2011; Jelinek et al. 2014). In this scenario, cuckoos may select larger nests associated with increased fitness because larger nests may indicate superior parenting ability (Soler et al. 1998; de Neve et al. 2004; Avilés et al. 2009). A study spanning eight consecutive years showed that large magpie (Pica pica) nests were more likely to be parasitized by great spotted cuckoo (Clamator glandarius) than smaller nests when cuckoos have a larger availability of host nests among which to choose. Therefore, selection of active host nests may arise from nest choice by the great spotted cuckoo (Molina-Morales et al. 2016), probably because nest size correlates positively with parental abilities of magpies (Soler et al. 1995).

Here, we developed a field experimental method to test whether nest-size manipulation affects parasites’ cognitive ability in nest preference when there are sufficiently many available different nest-size nests. The common cuckoo (Cuculus canorus) is the most common brood parasite using the Oriental reed warbler as its major host in our study area (Yang et al. 2016a, 2017; Wang et al. 2020a). Different types of artificial experimental nests can be categorized as large, medium or small size, and we divided these nests into two groups (nest dyads and triads) to test our hypotheses. We predicted that cuckoos would lay their eggs in larger host nests in both the two groups if they had evolved the ability to discriminate among different nest sizes.

### Materials and methods

#### Study site and study species

This study was performed in Zhalong National Nature Reserve (47° 19’ N, 124° 22’ E), which is located in Heilongjiang, and another study site in Sifangtuosi farm (46° 12’ N, 123° 84’ E), Jilin, China, where is 100 km far from Zhalong. Fieldwork was carried out during the breeding season (June–August) in years 2015–2019, and 2021. Habitats were both primarily reed swamps with several small villages (Yang et al. 2017; Wang et al. 2020b). The Oriental reed warbler females build the nest independently, and the common cuckoo is the main parasitic cuckoo in both study areas, with a high parasitism rate ranging from 34.3 to 65.5% among years in Zhalong for warbler nests (Yang et al. 2017), cuckoos often remove one or two eggs before they parasitize the host nest (Wang et al. 2020a). Furthermore, the appearance of cuckoo eggs resembled the eggs of their hosts well (Yang et al. 2016b; Li et al. 2016a).

#### Experimental nest manufacture

We designed three experiments to test the nest size hypothesis. For group 1, one large nest (internal diameter, mean ± SD: 86.42 ± 0.91 mm, n = 36) and one small nest (internal diameter, 67.57 ± 1.05 mm, n = 36) were tied together as a combination of nests (Fig. 1, group 1). We tied two randomly chosen and different-sized nests together to constrain the choice of host nests to the experimental variable of nest size. This constrained the choice between the nest dyads, avoiding an absence of selection caused by distance between nests. This was because if these two experimental nests were located at a far distance, the cuckoo might not find them simultaneously and compare the two different-sized nests, especially when nests were located in dense reeds. These nests were weaved together with a mixture of dry reed leaves and sticks, sewing them with a needle and string. The purpose of this experiment was to control the nest structure, including reed material, shape, duration of nest construction, except for nest size, which was a unique character dividing nests into two categories. This helped us determine the relevance of nest size choice by cuckoos.

For group 2, ‘triple nests’ were installed in the field including large, medium and small sized old nests as described above. All nests used for this study were modified from natural old Oriental reed warbler nests. We used natural warbler nests as the medium category (internal diameter: 57.88 ± 5.00 mm, n = 33), while large nests were enlarged by 20 mm (internal diameter: 78.74 ± 4.34 mm,
Similarly, small nests were reduced by approximately 20 mm (internal diameter: 39.18 ± 3.42 mm, $n=33$). Similarly, small nests were reduced by approximately 20 mm (internal diameter: 39.18 ± 3.42 mm, $n=33$).

For group 3, one large nest (mean ± SD: 85.68 ± 1.04 mm, $n=12$) and one small nest (67.29 ± 1.26 mm, $n=12$) were at 1.0 m distance to attract cuckoos for parasitism (Fig. 1, group 3). This treatment was different group 1 and helped make two artificial nests look more natural and similar to the real ones (Yang et al. 2016a, 2017; Wang et al. 2020b, 2021).

We collected natural old nests that had fledged young or were deserted the previous year. Nests were collected and preserved in cardboard boxes. For the large nest treatment, we selected two old nests that were most similar in appearance (size, shape and nest materials) for our experiment. First, we randomly selected one nest and made a cut in the rim of the nest with scissors. Second, we put one-third of the other nest piece together with the rim cut and sewed it up. Similarly, for small nests, we cut nest material and re-sewed...
them to keep the internal diameter at approximately 40 mm. For the medium nests, we did not cut them, although we also sewed them with the same color string. We sewed these nests using needle and string to make them look similar in appearance to natural nests. We enlarged and reduced 36 nests in total for our nest experiments. We randomly selected one of the three types of nests and sewed them together with string (Fig. 1, group 2).

Experiments for attracting cuckoo parasitism

We searched systematically for naturally active Oriental reed warbler host nests and monitored reproductive activities of hosts daily. Observed nests were checked every day to confirm the first date of laying an egg. If these target nests were found to have one host egg, one set of the prepared combination of nests were tied to the reeds one meter away from this neighboring active nest, and two common quail (Coturnix coturnix) eggs were inserted into each of the three combinations of nests, respectively (Fig. 1). Here, we controlled that the two quail eggs stayed the same throughout the test period, avoiding that cuckoo females showed a preference bias towards variation in the number of eggs, and the large quail eggs had the advantage that warbler hosts cannot remove them, but the cuckoos can easily remove them.

To increase the risk of brood parasitism, we specifically tied the combination of nests higher (approximately 0.5 m) in the vegetation (the nest height hypothesis, Budnik et al. 2002; Patten and Reinking 2011) than the position of the active host nest. We made them easier to see from the angle of view (nest exposure hypothesis, Moskát and Honza 2000; Clarke et al. 2001), which allowed cuckoos to more easily choose a specific type of nest during parasitism. Cuckoos generally selected to lay their eggs in Oriental reed warbler nests (Yang et al. 2016a, 2017). Thus, we did not design control nests that simultaneously set up another combination of nests in a random direction and the same nest content and position, as there was little probability for cuckoo parasitism in nests without host activity (Yang et al. 2017).

All experimental and naturally active nests were monitored for up to 6 days to confirm cuckoo parasitism until completion of the clutch and start of incubation. All experimental nests were video recorded and checked once per day. Video devices were retrieved at dusk. For active warbler nests, we did not manipulate, but checked and monitored clutch size and cuckoo parasitism.

Statistical analyses

Binomial tests (two-tailed test) were used to test for a preference of nests during choice by cuckoos (Wang et al. 2021). Differences were considered significant at p < 0.05. Statistical analysis was conducted using IBM SPSS Version 22.0 (IBM Corp., Armonk, NY, USA), and unless otherwise specified, all results are presented as mean ± SD.

Results

The rate of nest parasitism as follows: group1 was 58% (21/36), group 2 was 70% (23/33) and group 3 was 54% (42/78), respectively. For group 1, the frequency of selection of the larger nests was 81% (17/21), and the preference for large nests was significant compared to small nests (Binomial test, p = 0.007; Fig. 2). For group 2, the frequency of selection of large nests was 78% (18/23) and the medium-sized nests was 22% (5/23), respectively (Fig. 2). The smaller nest was never parasitized (0%, 0/23). The parasitism rate of the larger nest was significantly higher than that of the medium-sized nest (Binomial test, p = 0.011; Fig. 2). For group 3, the frequency of selection of large nests (67%, 28/42) was significantly higher than that of the small sized nest (Binomial test, p = 0.044; Fig. 2).

There was no case of parasitism among naturally active warbler nests in all groups (0/36, 0/33, 0/42). Six cases of egg laying in large, medium and small nests are shown in Electronic Supplementary Materials Videos S1-S2 in group 1, and Videos S3-S4 in group 2 and Videos S5-S6 in group 3.

Discussion

The main finding of this study was that common cuckoos have the ability to distinguish different nest size, and prefer large host nests for parasitism when they have sufficiently many synchronous available nests. Our findings support the active selection hypothesis suggesting that cuckoos prefer to lay eggs in larger nests providing evidence for the ability to distinguish among host nests varying in size when monitoring available nests. In addition, the frequency of parasitism was higher than in previous studies of the same warbler population, which implies that host nests with a higher and exposed position would effectively increase the possibility of cuckoo parasitism (Yang et al. 2016a, 2017).

Nest size is an indicator of parental care, and it is a likely reason why cuckoos choose large host nests for parasitism. For example, magpie pairs with large nests provide higher quality of food for their nestlings compared to pairs with smaller cuckoo nests (de Neve et al. 2004). The great spotted cuckoo prefers to parasitize large magpie nests because nest owners of such nests can rear nestlings more successfully than control nests (Soler et al. 1995). The chicks in bigger nests great reed warbler (Acrocephalus arundinaceus) showed significantly lower falling-out rate (4 of 29) compared with those remained in smaller Eurasian...
reed warbler (*Acrocephalus scirpaceus*) nests (12 of 32), this study suggest that host nest size plays an important role in the suitability of host species and that smaller host nests may pose a high mortality risk to the relatively big cuckoo chicks (Honza et al. 2020). Nest size in the great reed warbler serves as a signal of female quality for investment in reproduction, because enlarged great reed warbler nests significantly increase male feeding effort (Trnka and Prokop 2011; Jelínek et al. 2016). However, no evidence supports the hypothesis that nest size affects the frequency of parasitism in the great reed warbler (Avilés et al. 2009; Jelínek et al. 2015). We showed that cuckoos laid their eggs in larger host nests suggesting that cuckoos have the ability to distinguish among different nest sizes. The combination of different types of experimental nests presented next to each other makes it feasible for cuckoos to choose a nest without consideration of distance, allowing a similar preference for different-sized nests, and the bigger ones were bias chosen. Perhaps this was the reason why our finding was different from the result of Jelínek et al. (2015), which they only provided one experimental nest for cuckoo parasitism; accordingly, the cuckoos have no choice when they come to lay eggs.

When cuckoos approach a combination of nests with a similar angle of view or height, they may be subject to physical constraints, such that it is easier to perch on and deposit eggs in larger rather than smaller nests. In such case, large nests should be easy to find and facilitate egg laying. Of course, this scenario depends on sufficiently many nests being available in the neighborhood. Ma et al. (2018) showed that isolated Oriental reed warbler host nests were more vulnerable to cuckoo parasitism far away from neighbors, cuckoo females having no other choice being forced to select the only isolated nest for parasitism. Our results show that parasitism frequency is higher than in the previous studies (Li et al. 2016a, b; Ma et al. 2018), the conspicuousness of host nests for the likelihood of being parasitized by the cuckoo are vulnerable (Patten and Reinking 2011; Clarke et al. 2001), that is, the higher and more exposed are host nests, the more effectively the increase in the probability of cuckoo parasitism, consistent with the nest height hypothesis (Budnik et al. 2002) and the nest exposure hypothesis (Moskát and Honza 2000; Patten and Reinking 2011).

There may be other reasons for why cuckoos prefer larger nests. For example, there might be a physical body constraint, because many small hosts may have evolved a small sized nest allowing for parasitism by small cuckoo parasites (e.g., Bianchi’s warbler *Seicercus valentine* vs. Asian emerald cuckoo *Chrysococcyx maculatus*) (for more examples, see Yang et al. 2012). The only evidence is that larger nests in many different species of birds lay larger clutches, and larger clutches being associated with higher quality nest owners (Møller et al. 2014). In this study, two large quail eggs in large nests may also better predict larger final clutch size, two large quail eggs in small nests where there is no free space for other eggs may indicate small size of a complete clutch. This could also result in a higher preference of cuckoos for larger experimental nests. Moreover, Wang et al.
revealed that cuckoos prefer to select the naturally active host nests with small clutch sizes for parasitism [e.g., 1–2 host eggs, 75% (183/245)], and the empirical study also supporting this result (78%, 25/33) (Wang et al. 2020b). In addition, a large clutch size (e.g., 5–6 eggs) also implies more space for cuckoo egg laying. Therefore, nest space may act as an important cue for cuckoo egg laying resulting in strong nest preferences.

In conclusion, the present study provided experimental evidence suggesting that cuckoos preferred to lay their eggs in larger host nests when they have more available nests for use at any given time. Furthermore, the conspicuousness of host nests caused by higher location and full exposure in the field resulting in more cuckoo parasitism, suggesting that host nest exposure could increase the risk of cuckoo parasitism.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10071-021-01574-5.

Acknowledgements We are grateful to Wenfeng Wang and Jianhua Ma from Zhalong National Nature Reserve for their help and cooperation. We thank Gangbin He, Huahua Zhao, Hanlin Yan, Tinggao Yang and Hailin Lu for their assistance with fieldwork.

Author contributions WL conceived and designed this project. LW and GH carried out field experiments. LW and CY performed data analyses. LW and APM were involved in discussion and revision of the manuscript. All authors read and approved the final manuscript.

Funding This work was supported by the National Natural Science Foundation of China (Nos. 31960105 to LW, 31772453 and 31970427 to WL).

Availability of data and materials Data used in this study are available in the electronic supplementary material.

Declarations

Conflict of interest The authors declare that they have no competing interest.

Ethical approval 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 (no. HNECEE-2012-003) and from Guizhou Normal University (no. GZNUCEE-2021-001).

References

Álvarez E, Barba E (2008) Nest quality in relation to adult bird condition and its impact on reproduction in great tits Parus major. Acta Ornithol 43:3–9

Antonov A, Stokke BG, Fossy F, Ranke PS, Liang W, Yang C, Moksnes A, Shykof J, Røskaft E (2012) Are cuckoos maximizing egg mimicry by selecting host individuals with better matching egg phenotypes? PLoS ONE 7:e31704

Avilés JM, Stokke BG, Moksnes A, Røskaft E, Asmål M, Möller AP (2006) Rapid increase in cuckoo egg matching in a recently parasitized reed warbler population. J Evol Biol 19:1901–1910

Avilés JM, Moskát C, Bán M, Hargitai R, Parejo D (2009) Common cuckoos (Cuculus canorus) do not rely on indicators of parental abilities when searching for host nests: the importance of host defenses. Auk 126:431–438

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

Cherry ML, Bennett AT, Moskát C (2007) Do cuckoos choose nests of great reed warblers on the basis of host egg appearance? J Evol Biol 20:1218–1222

Clarke AL, O’ien JJ, Honza M, Moksnes A, Røskaft E (2001) Factors affecting reed warbler risk of brood parasitism by the common cuckoo. Auk 118:534–538

de Brooke M, L, Davies NB, (1989) Provisioning of nestling cuckoos Cuculus canorus by reed warbler Acrocephalus schoenobaenus hosts. Ibis 131:250–256

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

de Neve L, Soler JJ, Soler M, Pérez-Contreras T (2004) Nest size predicts the effect of food supplementation to magpie nestlings on their immunocompetence: an experimental test of nest size indicating parental ability. Behav Ecol 15:1031–1036

Grim T, Tyller Z, Samaš P (2017) Unusual diet of brood parasitic nestlings and its fitness consequences. Auk 134:732–750

Hansell MH (2000) Bird nests and construction behaviour. Cambridge University Press, Cambridge

Hansell MH (2007) Built by animals. Oxford University Press, Oxford

Hauber ME (2007) Site selection and repeatability in brown-headed cowbird (Molothrus ater) parasitism of eastern phoebes (Sayornis phoebe) nests. Can J Zool 79:1518–1523

Heenan CB, Seymour RS (2011) Structural support, not insulation, is the primary driver for avian cup-shaped nest design. Proc R Soc B 278:2924–2929

Honza M, Capek M, Jelinek V, Šulc M (2020) Falling out of the host nest: an overlooked factor decreasing survival of brood parasitic chicks. J Avian Biol in Press. https://doi.org/10.1111/jav.02519

Honza M, Šulc M, Jelinek V, Požgayová M, Procházká P (2014) Brood parasitizes lay eggs matching the appearance of host clutches. Proc R Soc B 281:20132665

Jelinek V, Procházká P, Požgayová M, Honza M (2014) Common cuckoos Cuculus canorus change their nest-searching strategy according to the number of available host nests. Ibis 156:189–197

Jelinek V, Procházká P, Honza M (2015) Experimental enlargement of nest size does not increase risk of predation or brood parasitism in the great reed warbler Acrocephalus arundinaceus. Ibis 157:396–400

Jelinek V, Požgayová M, Honza M, Procházká P (2016) Nest as an extended phenotype signal of female quality in the great reed warbler. J Avian Biol 47:428–437

Li D, Ruan Y, Wang Y, Chang AK, Wan D, Zhang Z (2016a) Egg-spot matching in common cuckoo parasitism of the Oriental reed warbler: effects of host nest availability and egg rejection. Avian Res 7:21

Li D, Zhang Z, Grim T, Liang W, Stokke BG (2016b) Explaining variation in brood parasitism rates between potential host species with similar habitat requirements. Evol Ecol 30:905–923

Ma L, Yang C, Liu J, Zhang J, Liang W, Möller AP (2018) Costs of breeding far away from neighbors: Isolated host nests are more vulnerable to cuckoo parasitism. Behav Process 157:327–332
Molina-Morales M, Martínez JG, Avilés JM (2016) Criteria for host selection in a brood parasite vary depending on parasitism rate. Behav Ecol 27:1441–1448
Møller AP (2017) Fashion and out of fashion: Appearance and disappearance of a novel nest building innovation. Avian Res 8:14
Møller AP, Adriaensen F, Artemyev A, Banbura J, Barba E, Biard C et al (2014) Variation in clutch size in relation to nest size in birds. Ecol Evol 4:3583–3595
Moskát C, Honza M (2000) Effect of nest and nest site characteristics on the risk of cuckoo Cuculus canorus parasitism in the great reed warbler Acrocephalus arundinaceus. Ecography 23:335–341
Parejo D, Avilés JM (2007) Do avian brood parasites eavesdrop on heterospecific sexual signals revealing host quality? a review of the evidence. Anim Cogn 10:81–88
Patten MA, Reinking DL, Wolfe DH. Hierarchical cues in brood parasite nest selection. J Ornithol 152:521–532
Soler JJ, Cuervo JJ, Møller AP, de Lope F (1998) Nest building is a sexually selected behaviour in the barn swallow. Anim Behav 56:1435–1442
Soler JJ, Soler M, Møller AP, Martínez JG (1995) Does the great spotted cuckoo choose magpie hosts according to their parenting ability? Behav Ecol Soc 36:201–206
Soler M (2014) Long-term coevolution between avian brood parasites and their hosts. Biol Rev 89:688–704
Trnka A, Prokop P (2011) The use and function of snake skins in the nests of great reed warblers Acrocephalus arundinaceus. Ibis 153:627–630
Wang L, He G, Zhang Y, Ma J, Liang W (2021) Cryptic eggs are rejected less frequently by a cuckoo host. Anim Cogn. https://doi.org/10.1007/s10071-021-01507-2
Wang L, Yang C, He G, Liang W, Møller AP (2020a) Cuckoos use host egg number to choose host nests for parasitism. Proc R Soc B 287:20200343
Wang L, Zhong G, He G, Zhang Y, Liang W (2020b) Egg laying behavior of the common cuckoo (Cuculus canorus): data based on field video-recordings. Zool Res 41:458–464
Yang C, Liang W, Antonov A, Cai Y, Stokke BG, Fossøy F, Moksnes A, Røskaft E (2012) Diversity of parasitic cuckoos and their hosts in China. Chin Bird 3:9
Yang C, Wang L, Liang W, Møller AP (2016a) Egg recognition as antiparasitism defence in hosts does not select for laying of matching eggs in parasitic cuckoos. Anim Behav 122:177–181
Yang C, Wang L, Liang W, Møller AP (2016b) 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? Biol J Linn Soc 117:422–427
Yang C, Wang L, Liang W, Møller AP (2017) How cuckoos find and choose host nests for parasitism. Behav Ecol 28:859–865

**Publisher’s Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.