When should Common Cuckoos *Cuculus canorus* lay their eggs in host nests?

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Capsule Brood parasitic Common Cuckoo *Cuculus canorus* chicks hatch earlier than the nestlings of their Great Reed Warbler *Acrocephalus arundinaceus* hosts, but hatching priority is less certain when cuckoo eggs are laid after the onset of host incubation.

Aim To reveal by field observations what the optimal stage is for cuckoos to lay their eggs in relation to the host laying cycle to ensure prior hatching of the parasitic chicks.

Methods We monitored the hatching of cuckoo chicks in relation to the hosts' laying stage at which the cuckoo eggs appeared and also monitored host incubation behaviour.

Results Great Reed Warblers incubated more on day 5 after the host's onset of laying relative to day 3. All cuckoo eggs hatched earlier than hosts when they were laid prior to the onset of host incubation (day 4). Cuckoo eggs also maintained hatching priority in about 2/3 of the nests when laid on days 5-6.

Conclusions Most cuckoo eggs are laid prior to the onset of host incubation, and this, together with other adaptive mechanisms, ensures the prior hatching of cuckoo eggs. Cuckoo eggs laid after incubation lose the advantage of prior hatching in clutch in ca. 30% of nests.

INTRODUCTION

Avian incubation is a critical factor for successful reproduction, and the optimal incubation strategies and tactics to ensure maximal reproductive outputs are complex (Tomás 2015). For example, predation threat to the nest may affect the incubation rhythm of parent(s) (Pozgayová et al. 2009, Kovarik & Pavel 2011). Optimal incubation has unique importance in avian brood parasitism, where brood parasites lay their eggs in the nests of their hosts, and leave the cost of incubation and chick provisioning to foster parents (Davies 2000). Nestlings of the Common Cuckoo *Cuculus canorus*, an obligate brood parasite, are typically raised alone in the nest, because the young hatchling cuckoo evicts all eggs and/or hatchlings from the nest within its first 2-3 days of life (Honza et al. 2007, Anderson et al. 2009). Incorrect timing of laying the parasitic egg into the host nest at the incorrect time may cause failure of the parasitic egg to hatch (McMaster & Sealy 1998, Strausberger 1998, Hauber 2003); or, in the case of the cuckoo chick, it may not be able to evict its host nestmates, causing cohabitation in the mixed brood (Petrescu

& Béres 1997, Grim et al. 2011). Older host nestlings may suppress the begging success and the development of the cuckoo young, and cause the death of the brood parasite nestling (Molnár 1939, Rutila 2002, Grim et al. 2009a).

Birkhead et al. (2011) revealed that the mechanism that aids the cuckoo chick to hatch early in songbird nests is pre-laying internal incubation. The incubation of the cuckoo eggs begins while still inside the female cuckoos' oviduct where it is retained for 31hr (Birkhead et al. 2011). Other mechanisms, including energy reserves in cuckoo eggs that are lower than in the eggs of their hosts, may also facilitate the pattern of cuckoo embryos to hatch earlier (Igic et al. 2015). Unlike several other host-parasite systems (Mermoz & Reboreda 1999, De Mársico & Reboreda 2008), there is a lack of high-quality observational data on the impact of whether and how early hatching is manifested in cuckoo parasitism; namely, how consistent is it that the cuckoo eggs hatch first within parasitized clutches? Consequently, we hypothesize that cuckoos' adaptations to parasitism enable cuckoo eggs to hatch early in Great Reed Warblers' *Acrocephalus arundinaceus* clutches, so we predict that cuckoo eggs hatch first in a parasitized clutch, independent of when was it parasitized during the laying stage. Alternatively, we hypothesize that cuckoos could not adapt perfectly to hosts in ensuring the earliest hatching of the cuckoo eggs in Great Reed Warbler clutches. We predict variable success in early hatching of the parasitic eggs depending on a key date within the period of egg laying. In this case we hypothesize that the key date is the date of onset of incubation by the host. From prior knowledge (Uzun et al. 2014) we predict that incubation starts on the day when the fourth egg is laid by Great Reed Warblers.

MATERIALS AND METHODS

We monitored the hatching of cuckoo eggs in relation to the time of parasitic egg laying in 2013-2015, in the surroundings of Apaj (47°07'N; 19°06'E), ca. 50 km south of Budapest, Hungary. In this area Great Reed Warblers breed in narrow (2-4 m) reed beds growing on both sides of irrigation channels, where these channels form a dense network. In this area, Common Cuckoos frequently parasitize Great Reed Warblers with > 50% of the nests annually containing one or more cuckoo eggs (Moskát & Honza 2002, Zölei et al. 2015). We also reviewed our field notes regarding the fate of cuckoo eggs from previous years (1998-2012) while monitoring naturally parasitized nests at this long-term study site. The Great Reed Warbler is a high-quality host for the cuckoo, as cuckoo chicks grew faster and fledged with higher weight from nests of Great Reed Warblers than from that of the smaller Reed Warblers (*Acrcocephalus scirpaceus*) (Kleven et al. 1999). Previous studies showed that the Great Reed Warbler possessed some ability to adapt its incubation by shifting its laying date in response to climate change (Dyrcz & Halupka 2009).

We selected only cases of parasitism where the history was fully known, i.e. typically when the nest was found during the building stage and monitored daily. Cuckoo eggs were individually identified with a "+" sign or with small numbers to reveal any potential multiple parasitism. Because the probability of parasitism is highest in the pre-egg and early stages of laying (when the nest contains 0-3 host eggs, Moskát & Honza 2002), the number of cases of parasitism were not sufficiently high for statistical analyses of cuckoo egg hatching time for the 4-6 host eggs / nest stages. For this reason, we increased the sample size in this category by placing a cuckoo egg in non-parasitized host clutches, where the parasitic egg was freshly-laid and collected from multiply parasitized nests or nests containing only one cuckoo egg. The Great

Reed Warbler is an especially suitable host species for studying cuckoo egg hatching as the cuckoo and great reed warbler eggs' volumes are similar (Hargitai et al. 2011), so differences in egg sizes within a clutch would not effect warming and heat resistance of the eggs, although there may be an effect of shape which is different between this parasite and host (Bán et al. 2011).

We analyzed which factors affected the hatching sequence in a parasitized clutch by binary logistic regression analysis, using SPSS ver. 17. Priority of cuckoo hatching was regarded as a binary response variable (1 = cuckoo hatched first, 0 = Great Reed Warbler hatched first). This was tested against clutch size, laying date (Julian date), and timing of parasitism (from 0 to 6) as independent variates. We also tested the effect of natural vs. experimentally introduced cuckoo eggs in the nest as a binary factor. No interaction among terms was detected as significant.

We recorded the start of incubation at a subset of unparasitized Great Reed Warbler nests using two Brinno TLC200 time-lapse cameras that were housed in a green-painted waterproof case and placed on a tripod. These cameras ran continuously for several days, but they switched off automatically at nightfall (ca. between 21 h and 05h). Typically, video monitoring started during the evening of the day when the second host egg was laid, ran continuously for the next three days (we used these three days for analyses), and was terminated on the morning after this three-day period. The following recording options were chosen: time interval of 5 sec, avi frame rate of 15 FPS, and output resolution of 720P. By this method, we collected data when hosts were sitting on the nest on the 3rd, 4th, and 5th day after the onset of laying (by definition, day = 1 when the 1st host egg was laid). On occasion, cuckoo eggs were laid 1-2 days preceding the onset of host egg laying (days -1 and 0). We monitored the 3-5 day period after Uzun et al.

(2014) revealed with a small sample (n = 5) that Great Reed Warblers in Turkey rarely sat on the nest on day 3, but regularly incubated on day 5. Day 4 was an intermediate stage, where some incubation onset occurred. Their finding was independent of clutch size (3-6 eggs). When cuckoos lay, they typically remove one host egg from the clutch (Moskát and Honza 2002), so the number of eggs in the nest does not change. The only exception is when cuckoos lay one or two days earlier than the initiation of egg laying by the host, when they cannot remove any host egg (Moskát & Honza 2002, Moskát and Hauber 2007). In total, we monitored ten nests, although three of them could not be used because they were destroyed by predation early in incubation.

Hatching rate of the cuckoo eggs in the natural and experimental parasitism proved to be highly similar (natural parasitism: 19 hatched, 1 not hatched; experimental parasitism: 12 hatched, 1 not hatched; Fisher's exact test, two-tailed, $P > 0.999$). We omitted two cases of natural parasitism where Great Reed Warblers hatched first, because further monitoring of whether the cuckoo eggs hatched was not possible.

RESULTS

Our monitoring of nests with the time-lapse cameras revealed that Great Reed Warblers increased the amount of time spent on the eggs from day 3 to day 5 (Fig. 1). The difference between days 3 and 4, as well as between days 3 and 5 proved to be significant (Wilcoxon test, both for d3-4 and d3-5: $Z = -2.366$, $n = 7$, $P = 0.018$), but not for categories days 4 and 5 ($Z = -676$, $n = 7$, $P = 0.499$). These results confirm the patterns reported by Uzun et al. (2014) in that some incubation in Great Reed Warblers started on day 4 and regular incubation started on day 5.

Binary regression analysis revealed that the only term that affected hatching priority of cuckoos was the timing of parasitism ($\chi^2 = 6.827$, df = 1, P = 0.009; model: $\chi^2 = 22.951$, df = 4, P < 0.001, McFadden rho = 0.512). When cuckoos parasitized host nests before the onset of incubation, host eggs never hatched prior to the cuckoo egg. In turn, once Great Reed Warblers started incubation on day 4, there was a significantly higher chance that host eggs hatched first (Mann-Whitney $U_{44,23} = 352.0$, P < 0.001). Accordingly, when cuckoo eggs were laid on days 5 and 6, the host eggs preceded hatching relative to the cuckoos in about one-third of the nests (Fig. 2). Other potential factors did not affect hatching priority (clutch size: $\chi^2 = 2.153$, df = 1, P = 0.142; laying date: $\chi^2 = 2.833$, df = 1, P = 0.092; type of parasitism (natural/experimental): χ^2= 1.069, df = 1, P = 0.301). However, assuming that after the onset of incubation (day 4) all eggs in the nest have the same chance of hatching first, cuckoo eggs still hatched above the random expectation (1/(total clutch size)) even in nests when parasitism took place on days 4-6 (Wilcoxon test: Z = -3.392, n = 23, P = 0.001).

Cuckoo eggs spent 11.63 ± 0.97 (mean ± sd) days in a host nest before hatching when measured from the onset of incubation; this was the equivalent of 12.85 ± 1.39 days when measured from the time of parasitism. Early laying of cuckoo eggs in host nests, i.e. one day before onset of the host laying its first egg, yielded a 100% hatching rate of cuckoo eggs (n = 9). We identified four other cases when cuckoo eggs were laid even earlier, two (n = 3) or three (n = 1) days before the onset of the host's laying. Cuckoo chicks also hatched from all (100%) of these earlier-laid eggs, despite staying 4-6 days in the nest until incubation started. In turn, cuckoo eggs laid after the onset of incubation (day 4) had a hatching rate of (65%) and spent less time in nests than cuckoo eggs laid before or on the day of incubation starts (before: 13.39 days ± 1.24; after: 11.53 days ± 0.61, Mann-Whitney $U_{43.19}$ = 69.500, $P < 0.001$).

DISCUSSION

We observed that the cuckoo eggs frequently, but not always, hatched first in Great Reed Warbler nests. The unique phenomenon called internal incubation (Birkhead et al. 2011), together with other adaptations, may ensure the early hatching of the obligate brood parasitic cuckoo chicks relative to host eggs when the cuckoo egg is laid before the onset of incubation (day 4). When the cuckoo egg was laid after this key date, the fate of the cuckoo egg was less predictable, but still more likely to hatch than any one of the host eggs. In seven nests, the host chicks hatched first, and in three of these nests the parasite chick hatched later, with one cuckoo chick by one day later, and two other cuckoo chicks by two days later. Two of these later-hatched cuckoo chicks successfully evicted all host nestlings by one and two days after their hatching, respectively (the third nest was depredated). If the young cuckoo chick cannot evict host eggs or nestlings within 3 days after hatching, the fate of the cuckoo chick will be less predictable. Specifically, an experimental study revealed severe and mutual chick competition among Great Reed Warbler and cuckoo chicks with the age of at least 5 days. Moskát and Hauber (2010) revealed cohabitating cuckoo and host nestlings (n = 12) often pushed either the host (83%) or the cuckoo chicks (17%) accidentally.

Our results support the adaptive value of the internal incubation of cuckoo eggs (Birkhead et al. 2011). This mechanism aids the earlier hatching of cuckoo eggs when parasitism takes place in the early laying stage, when the nest contained 0-3 host eggs, but it also allows for earlier hatching by the parasite, although with less efficiency, when cuckoo eggs are laid on the 4th to 6th day after the onset of laying. This is in agreement with our video observations that Great Reed Warblers started incubation on the day when the 4th or 5th host egg was laid.

In brood parasitism, both the parasitic and the host populations show several forms of coevolutionary adaptations (Davies 2000, Schulze-Hagen et al. 2009). On the parasite's side, internal incubation seems to be an adaptation of cuckoos for brood parasitism by laying pre-incubated eggs (Birkhead et al. 2011). However, this gives an advantage of only about one day for the brood parasite, so we could expect some counter-adaptation on the host side. Our results suggest that an earlier onset of incubation by the host could potentially reduce the priority hatchability of some cuckoo eggs, which are laid after this time point. However, most cuckoos lay during the 0-3 host egg stage (Moskát & Honza 2002), during which cuckoo eggs always hatch first according to the present data. As Great Reed Warblers typically lay 4-6 eggs, this host likely cannot adapt to an extremely early onset of incubation, which might threaten the hatching success of their own subsequently laid eggs, or might cause extremely asynchronous hatching (Tonra et al. 2008). In our study area, multiple parasitism by cuckoos of the same host nest is frequent (Moskát & Honza 2002, Moskát et al. 2006, Zölei et al. 2015), so an early date of onset of incubation would be even less effective. Consequently, multiple parasitism on different dates may increase the chance that at least one of the cuckoo eggs are laid before onset of incubation, which increases the chance that the hosts will raise a cuckoo chick instead of their own nestlings. Our results suggest that the time of onset of incubation plays a key role in influencing whether the parasitic egg hatches first, although this effect is far from perfect. Consequently, an early date of onset of incubation may decrease and a late date may increase the chance of prior hatching by the cuckoo eggs. Cuckoos are frequently attacked by hosts during egg laying or visits to potential host nests, as was revealed in a similar, but smaller species (the Reed Warbler *Acrocephalus scirpaceus*) (Davies & Brooke 1988, Moksnes et al. 2000). Although there is no parallel study on the laying habits of the Great Reed Warbler, this host also attacks cuckoos aggressively (e.g. Bártol et al. 2002), which may cause the death of the laying cuckoo female by drowning it in the reed bed (Molnár 1944). The chance for heavy attacks or such accidents is much higher after incubation has started (c.f. Moksnes et al. 2000). Although different types of maternal effects are responsible for the hatching success of Great Reed Warbler eggs (Knape et al. 2008), hosts lose all their parental investment in their eggs when the cuckoo chick hatches first and survives in the nest after evicting all host eggs and nestmates (Anderson et al. 2009). Moreover, later hatching of the cuckoo eggs does not mean necessarily the loss of the cuckoo chicks, as a one-two day delay in hatching simply means that the cuckoo chick evicts host hatchlings from the nest rather than host eggs (Hauber and Moskát 2008, Grim et al. 2009b, Geltsch et al. 2012). Finally, a longer hatching asynchrony, which typically causes the death of the later hatched cuckoo chick, is extremely rare (Molnár 1939). Thus, our results did not reveal any effective response by Great Reed Warblers to the adaptation of the cuckoos to internally incubate the parasitic egg prior to laying.

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Legend to figures

Fig. 1 Box-plots of time spent on nest by Great Reed Warblers on the third, fourth and fifth day after onset of laying (expressed in min/hour; box-and-whisker plots show median, minimum and maximum values, and quartiles).

Fig. 2 Hatching rate of Common Cuckoo eggs in relation to time of parasitism. The horizontal axis shows when the cuckoo egg was laid into the nest. (0 = laid into an empty nest, i.e. one day before onset of laying, 1 = the day when the first host egg was laid (the onset of laying), 2 = the nest contained two host eggs, etc.) (*/NS shows the significant/not significant difference at P = 0.05, obtained by the Wilcoxon signed rank test. See Results for exact numerical values of the tests.)

Fig. 1

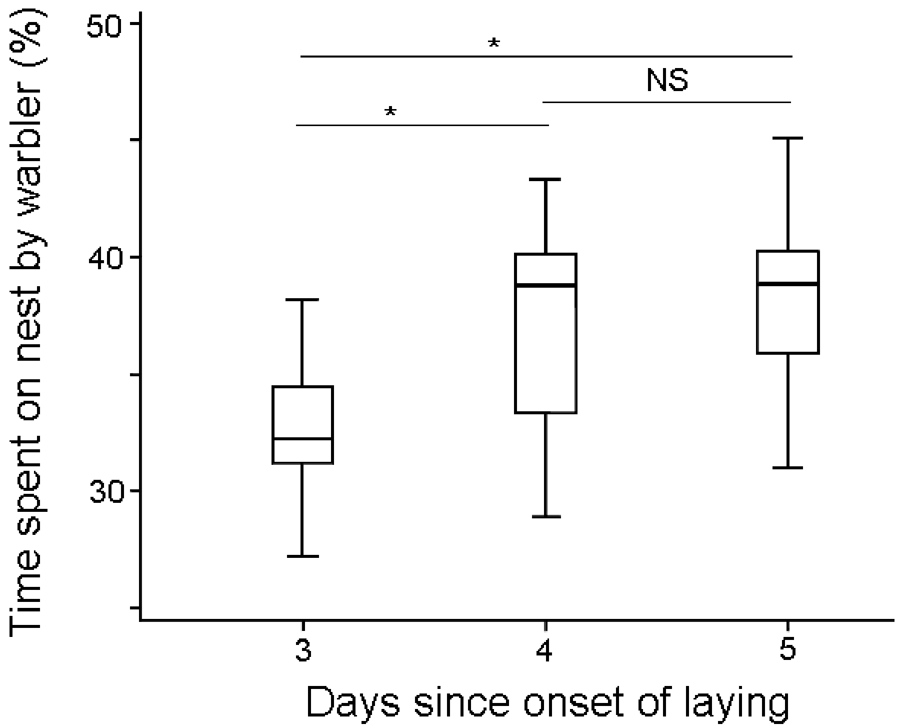
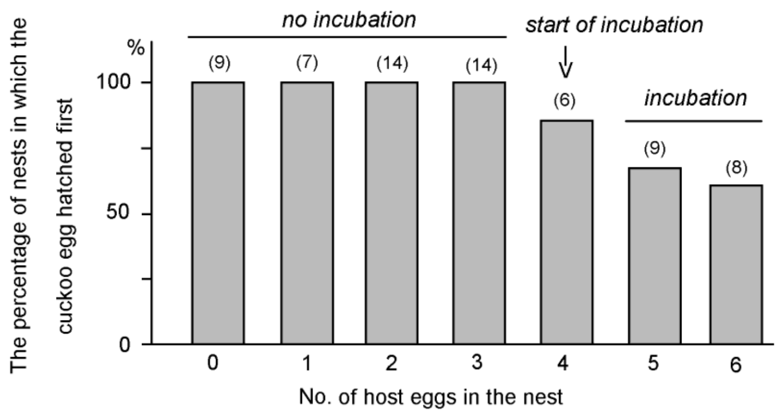

50
40
30
*
NS
*
3
4
5
Time spent on nest by warbler (%)
Days since onset of laying

Fig. 2


no incubation
start of incubation
incubation
%
100
50
0
(9)
(7)
(14)
(14)
(6)
(9)
(8)
0
1
2
3
4
5
6
No. of host eggs in the nest
The percentage of nests in which the
cuckoo egg hatched first