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# Behaviour of female common cuckoos, *Cuculus canorus*, in the vicinity of host nests before and during egg laying: a radiotelemetry study

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We radiotracked 13 common cuckoo females in the southeastern part of the Czech Republic. Seven females laid eggs in the nests of reed warblers, *Acrocephalus scirpaceus*, sedge warblers, *A. schoenobaenus*, and marsh warblers, *A. palustris*. We observed 53 nest visits, of which 26 involved egg laying. Cuckoos spent significantly more time within 50 m of the host nest on the laying day than on the 5 prelaying days. The vantage point used when parasitizing or visiting a nest was on average four times further from the nest than the closest possible vantage point, but there was a positive correlation between these two distances. Cuckoos spent on average 20 min observing host nests from their vantage points before they visited a nest. Comparison of cuckoos' visits to host nests with and without egg laying revealed no significant differences in the duration of visits or in other measures of behaviour. There was significant variation in behaviour between cuckoos, particularly in the time of day when eggs were laid in host nests. This variation can be attributed to the strong, but not absolute, host and habitat specificity of individuals.

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The interactions between avian brood parasites and their hosts have been subject to much interest during recent years because this is a very suitable model system for studying coevolution (Rothstein & Robinson 1998). The parasitic adaptations for fooling the hosts and the evolution of defence mechanisms among hosts have led to an evolutionary arms race (Davies 2000). In this arms race, an important adaptation among parasites is to evolve improved abilities to locate host nests that are at a suitable stage for parasitism, and without giving the hosts any cue that their nests are at risk of being parasitized. However, few systematic observations have been made of such parasite behaviour. There is a need for such data because they will contribute to the knowledge of an important parasite adaptation and thereby to a better understanding of general problems in the evolution of brood parasitism and host defences. We addressed these problems by investigating the nest-searching behaviour of the common cuckoo.

The females of brood parasites usually search for host nests secretively (Norman & Robertson 1975; Wyllie 1981), and in the common cuckoo, no cooperation between males and females is assumed (Wyllie 1981). In approaching potential host nests, the importance of trees as suitable viewpoints has been stressed (Alvarez 1993; Øien et al. 1996; Moskát & Honza 2000).

In the Palaearctic region, the common cuckoo is the most frequent brood parasite. During the course of evolution, the cuckoo has radiated into several different strains, the so-called gentes, and each gens is thought to be specialized on one particular host species (Baker 1942; Lack 1968; Wyllie 1981; Brooke & Davies 1988). Host specialization among cuckoo females has been demonstrated through radiotelemetry studies (Wyllie 1981; Dröscher 1988; Nakamura & Miyazawa 1997; Vogl

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et al. 2002), and Gibbs et al. (2000) showed that there are genetic differences between cuckoo gentes. Analyses of cuckoo eggs in European museums suggest, however, that cuckoos are not as strict specialists as is commonly believed, because their eggs often show poor mimicry with the hosts' eggs (Moksnes & Røskaft 1995). Nevertheless, host preference in cuckoos may operate without being manifested in 'perfect' egg mimicry races (Edvardsen et al. 2001; Honza et al. 2001).

Before laying, the female cuckoo perches at a suitable viewpoint and waits for the host pair to leave their nest, usually in the afternoon (Lack 1968; Wyllie 1981; Alvarez 1993; Øien et al. 1996; Moskát & Honza 2000). This strategy is adaptive, because the rejection rate of cuckoo eggs is higher when hosts have noticed the cuckoo's presence at their nest (experimental evidence: Davies & Brooke 1988; Moksnes & Røskaft 1989; field observations: Moksnes et al. 2000). The speed of egg laying has been regarded as high in cuckoos and therefore has been interpreted as an adaptation to brood parasitism (Chance 1922; Davies & Brooke 1988; Sealy et al.1995). However, video recordings of cuckoos in the act of parasitizing showed that birds laying in reed warbler, *Acrocephalus scirpaceus*, nests in the Czech Republic spent, on average, 41 s (maximum 138 s) at the host nest during laying (Moksnes et al. 2000).

We studied cuckoo behaviour in the egg-laying period by tracking radiotagged females from 1995 to 1998 in southern Moravia, in the Czech Republic. We focused on the behaviour of females before laying visits and during visits without laying to host nests, including (1) the time a female cuckoo spent near the target nest during the 5 days before laying, (2) the distance from the nest where she sat before entering, (3) the time she spent at this vantage point and (4) the time she spent at the nest when just visiting and when parasitizing it. We analysed the data in relation to habitat characteristics, host species and individual cuckoo females and discuss the results in the context of hypotheses that aim to explain how female cuckoos find host nests.

## METHODS

### Study Area and Field Work

We studied the common cuckoo during four breeding seasons (1995–1998) from early May to mid July. Our study area, consisting of reed, herb and bush vegetation surrounding commercially used fish ponds and adjacent forest, was near Hodonín (45°51′N and 17°04′E) in the Czech Republic. We distinguished two vegetation types found at pond edges. 'Reeds' consisted of reed beds, *Phragmites australis*, mixed with up to 20% herbs, and reedmace, *Typha angustifolia*. 'Herbs' consisted of a variety of herbaceous plants with a high percentage (>60%) of *Solidago canadensis* and nettles, *Urtica dioica*, and with a maximum of 20% reed. The banks of ponds were in many places overgrown with shrubs, with a number of fully grown, usually solitary, trees. The forests surrounding the ponds were managed for timber production and contained a mixture of oak, *Quercus* spp., stands of various ages, robinia, *Robinia pseudoacacia,* and pine, *Pinus sylvestris*. Host nests were checked for the presence of cuckoo eggs by a systematic survey in reeds and herbs (Øien et al. 1998).

### Radiotracking

We tried to trap female cuckoos on most days between early May and late June with mist nets (6 × 10 m) and playbacks of female and male song or calls. Sixteen trapped females were marked with an aluminium ring and coloured wing tag (1.5 × 2.5 cm) and equipped with a radiotransmitter weighing 2.5 g (about 2.5% of the bird's weight), which we attached to the central tail feather. Instant glue and nylon threads were used, with the antenna attached with a thread to the quill of the same feather. No adverse effect of the tag or transmitter was observed. Since the transmitters were attached only to the central tail feather, all of them were lost during moulting. We subsequently located 13 of these females by radiotelemetry (Table 1). In two cases, we were able to recapture and identify individual birds by their rings after their return from the wintering grounds the next calendar year.

According to Moksnes et al. (2000), cuckoo females in the study area lay between 1400 and 2000 hours. This general pattern supports that reported by Wyllie (1981), who presented data for 120 females. In 1995–1997, we therefore tracked individual females during this time of day. However, in 1998, we observed one female laying eggs before noon. We therefore started tracking this female at 0900 hours. When observing a focal female, we exercised caution to minimize disturbance. Movements and positions of females were drawn on maps (scale 1:10 000) and were recorded continuously on audiocassette or paper. Seven of the 13 telemetry females were observed to visit host nests, both with and without laying (Table 1).

A potential nest visit was assumed when a focal female flew straight from its vantage point down to the reeds or herbs, where she disappeared for a short time before flying away. Immediately after the female had disappeared, the observer checked the nest or searched for the nest if it had not already been found. In 26 cases, a nest was found with a cuckoo egg in it. There is a theoretical possibility that the cuckoo egg could have been laid by another female, but because we had identified and frequently checked most of the nests of the reed warbler and great reed warbler, *A. arundinaceus*, in the area, we regard this source of error as negligible for these two species. If a host nest was found without a cuckoo egg inside, we interpreted the cuckoo's behaviour as a nest visit without laying. However, on some occasions when we observed females in the vegetation, we were unable to find a host nest. The time spent by the cuckoo at the vantage point before descending to the vegetation was noted as a measure of the time she potentially spent watching the nest. We never observed cuckoos using a series of perches, so we regard this definition as adequate. The distance between the vantage point and the nest, recorded with an accuracy of 1 m, was measured as the

**Table 1.** Trapping date, tracking period and duration, time of day and number of nest visits with and without laying eggs, and host species used by radiotagged female cuckoos

| Cuckoo (identification number/year) | Trapping date | Tracking period | Tracking duration (min) | Time of day when visiting host nests | | Host species visits | Host species layings |
|---|---|---|---|---|---|---|---|
| | | | | Eggs not laid | Eggs laid | | |
| 1/95 | 20 May 1995 | 1–12 June | 2916 | | | | |
| 3/95 | 26 May 1995 | 27 May–24 June | 8335 | 1640, 1757 | 1623, 1500 | 2m | 2m |
| 5/95 | 1 June 1995 | 2–12 June | 2998 | 1725, 1650, 1452, 1740 | 1604, 1705 | 2r, 1m, 1g | 1m, 1r |
| 10/95 | 18 June 1995 | 20–28 June | 1886 | | | | |
| 2/96 | 9 May 1996 | 10–11 May | 480 | | | | |
| 11/96 | 11 June 1996 | 15 May–3 July | 5359 | 1758 | 1956, 1642, 1902, 1906, 1759, 1922 | 1m | 6m |
| 12/96 | 13 June 1996 | 14–27 June | 2607 | | | | |
| 14/96 | 14 June 1996 | 15–22 June | 2474 | 1630, 1739, 1757 | 1830 | 3r | 1r |
| 2/97 | 16 May 1997 | 16 June–4 July | 12 154 | 1740, 1822, 1604 | 1856, 1746, 1934, 1707, 1821, 1846, 1706, 1512 | 2r, 1s | 6r, 2s |
| 5/97 | 23 May 1997 | 28 May–5 July | 15 062 | 1640, 1745, 2020, 2040, 1517, 1639, 1842, 1730, 1920 | 1747, 1230 | 6m, 2r, 1s | 2m |
| 8/97 | 28 May 1997 | 29–31 May | 132 | | | | |
| 3/98 | 25 May 1998 | 1–27 June | 6397 | 1310, 1922, 1640, 1658, 1210 | 1226, 1416, 1651, 1012, 1031 | 5s | 5s |
| 4/98 | 27 May 1998 | 1–6 June | 1675 | | | | |

m=marsh warbler, r=reed warbler, s=sedge warbler, g=great reed warbler.

**Table 2.** Number of observations of female cuckoos laying an egg in a host nest or visiting a nest without laying relative to the hosts breeding cycle

| Stage in host breeding cycle | Visits with laying | Visits without laying |
|---|---|---|
| No nest found | — | 14 |
| Before laying | — | 7 |
| During laying | 26 | 15 |
| Late incubation/hatching | — | 4 |
| Unknown stage | — | 1 |

distance on the ground between where the cuckoo sat and the host nest. We also measured the distance on the ground between the nest and the closest possible vantage point, which we defined as the nearest shrub or tree that was more than 5 m high. The time (s) that the cuckoo spent at the nest was measured from when the cuckoo entered the host's nest habitat to when it reappeared to leave the nest area. We justify this definition as follows. (1) The distance between where cuckoos were seen entering the vegetation and the host nest was only about 0.5 m in herb habitat and about 1–2 m in reeds (all observations were done in easily surveyed habitat for a human observer); (2) videorecordings in the study area have shown that cuckoos fly directly to the nest (Moksnes et al. 2000). According to Wyllie (1981), cuckoos usually hide within 50 m of host nests before swooping down to lay in them. Øien et al. (1996) indicated an even shorter distance. We therefore continuously recorded the activity of the focal cuckoo (identified by radio frequency) within a radius of 50 m on the egg-laying day and 5 prelaying days.

Four potential host species bred in the area; reed warblers, marsh warblers, *A. palustris*, sedge warblers, *A. schoenobaenus*, and great reed warblers. The subjects visited all four species, but laid their eggs in the nests of only the first three species (Table 1).

Because most of the data in this study are not normally distributed, mainly nonparametric, two-tailed, statistics are used.

## RESULTS

We recorded 27 nest visits without laying and 26 egg layings of seven cuckoo females (Tables 1, 2). Four of seven females visited (without laying) only one host species, and the others visited two or three host species. Laying at two different host species was observed in two cuckoo females. All 26 parasitic layings occurred during the host's laying period. Seven of the 27 visits without laying occurred during nest building or before eggs had been laid in the host nest, most visits were recorded during the laying period, and four visits occurred during the host's late incubation. For one nest visit without laying, the stage was unknown. Four of the cuckoo females were observed in the vegetation where we were unable to find a nest. This 'nest-searching' behaviour was observed 14 times altogether in both habitats (Table 2).

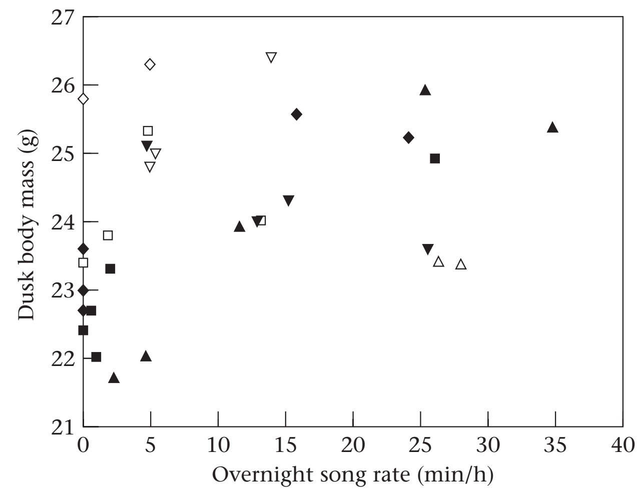


**Figure 1.** Box and whiskers plots of the time (min) that female cuckoos spent within 50 m of the nests they chose for laying. Day 0 is the laying day, day 1 is the day before laying, and day 5 is 5 days before laying. The box represents the interquartile range, which contains the 50% values. The whiskers are lines that extend from the box to the highest and lowest values, excluding outliers. Outliers (asterisks) are values between 1.5 and 3 box lengths from the upper or lower edge of the box. A line across the box indicates the median.

### Time Spent Near Host Nests

We analysed the median time cuckoo females spent within 50 m of the parasitized nest on the laying day (day zero) and for 5 days before laying. On the laying days, cuckoo females spent significantly more time near the parasitized nest than during the 5 days before laying (median test: $\chi^2_5$=36.4, *N*=84, *P*<0.001; Fig. 1). When we omitted the data from the laying day from the analysis, the median time spent by cuckoo females within 50 m of the parasitized nest did not differ during the 5 days before laying (median test: $\chi^2_4$=5.27, *N*=59, NS; Fig. 1).

### Distance Between Nest and Vantage Points

The distance between the vantage point and host nest was similar when cuckoo females laid an egg and visited a host nest without laying (Table 3). The median distance between the nearest possible vantage point and the visited nest was 5.0 m ($q_1$=3.0 m, $q_3$=14.0 m, *N*=44) in both cases, which was significantly closer than to the vantage point actually used (pooled data for layings and visits, median test: $\chi^2_1$=24.7, *N*=86, *P*<0.001). There was a significant positive correlation between the nearest possible vantage point and the vantage point actually used by a female cuckoo ($r_{37}$=0.369, *P*=0.021). This correlation was significant even when controlling for whether cuckoos were laying or not (partial correlation: $r_p$=0.380, *N*=36, *P*=0.019), different habitats (partial correlation: $r_p$=0.326, *N*=36, *P*=0.045), host species (partial correlation: $r_p$=0.346, *N*=36, *P*=0.034) or individual

**Table 3.** Medians for different characteristics during nest visits with and without laying by cuckoo females (binomial distribution test)

| | Nest visits | | |
|---|---|---|---|
| | Without laying (*N*) | With laying (*N*) | *P* |
| Distance between nest and vantage point (m) | 21 (6) | 28 (7) | 0.688 |
| Time at vantage points (min) | 21 (7) | 45 (7) | 0.125 |
| Time of day when laying or nest visits occurred (hours) | 1708 (7) | 1624 (7) | 1.000 |
| Time spent at nest (s) | 17 (7) | 26 (6) | 0.668 |

female cuckoos (partial correlation: $r_p$=0.402, $N$=36, $P$=0.012).

A factorial general linear model (GLM) analysis revealed that only the variable individual female cuckoo explained a significant part of the variation in distance to the vantage point actually used before laying (adjusted $r^2$=0.332, corrected model $F_{1,10}$=2.89, $P$=0.013; effect of female cuckoo: $P$=0.008). The variables laying or visiting ($P$=0.803), nearest possible vantage point (grouped data: $P$=0.133), habitat ($P$=0.548) or host species ($P$=0.483) had no significant effect on the explanation of this variation.

## Time at Vantage Points

The time that cuckoo females spent at their vantage points before nest visits with and without laying was not significantly different (Table 3). There was no significant correlation between the distance from the nest to the vantage point used by a female cuckoo and the time she spent at this point ($r = -0.060$). We found no significant difference between the median time used at the vantage point in the two habitats reeds and herbs (median test: $\chi^2_1$=0.00, $N$=52), between the time used at the vantage point at the nest of the different host species (median test: $\chi^2_2$=2.23, $N$=53) and between the time used at the vantage point by different cuckoo females (median test: $\chi^2_6$=6.82, $N$=53).

A GLM analysis revealed that none of the above variables analysed together significantly explained the variation in time spent at the vantage point before laying (adjusted $r^2 = -0.040$, corrected model $F_{1,9}$=0.78, $P$=0.633).

## Time of Day and Time at Nest

The median time of day for egg laying and visits to host nests by females without laying did not differ statistically (Table 3). The time of day when nests were visited by female cuckoos (data for visits with and without laying were pooled; Table 1) differed significantly between habitats (median: herbs: 1651 hours, reeds: 1821 hours; median test: $\chi^2_1$=5.96, $N$=52, $P$=0.015), between host species (median: marsh warbler: 1745 hours, reed warbler: 1746 hours; sedge warbler: 1610 hours; median test: $\chi^2_3$=8.10, $N$=53, $P$=0.044) and between individual females (median test: $\chi^2_6$=17.4, $N$=53, $P$=0.008). A GLM analysis revealed that only the differences between individual females significantly explained the variation in the time of day of nest visits (adjusted $r^2$=0.342, corrected model $F_{1,9}$=3.94, $P$=0.001; effect of female cuckoo: $P$=0.039); there was a nonsignificant trend for habitat to have some effect as well ($P$=0.074).

There was no significant difference between the median times spent at host nests by female cuckoos in different habitats (nest visits with and without laying pooled; median test: $\chi^2_1$=0.45, $N$=43), at different host nests (median test: $\chi^2_2$=0.64, $N$=43) and by different females (median test: $\chi^2_6$=2.89, $N$=43). However, a GLM analysis revealed that there was a significant effect for the female cuckoos. Our results significantly explained the variation in time spent at nests when laying or just visiting (adjusted $r^2$=0.341, corrected model $F_{1,9}$=3.93, $P$=0.001; effect of female cuckoo: $P$=0.039), while there was a nonsignificant trend for habitat to have some effect as well ($P$=0.074).

# DISCUSSION

We found no differences between the behaviour of females when laying an egg in a host nest or when just visiting a nest, which supports the results of Moksnes et al. (2000). Visiting females frequently eat host eggs at the nest (Moksnes et al. 2000), but alternatively they might just check the status of a nest. Females occasionally visited nests late in the incubation period, which has been observed also in the brown-headed cowbird, *Molothrus ater* (Scott et al. 1992). Such visits could be interpreted as predatory behaviour (Davies & Brooke 1988; Hauber 2000).

## Time Spent Near Host Nests

As mentioned above, Wyllie (1981) suggested that cuckoos parasitizing reed warblers usually occupied hidden positions within 50 m of the parasitized host nests. The cuckoo females in the present study spent significantly more time, around 20 min, within this distance from the host nest on the laying day than on the 5 previous days. Our general impression was that they did not show much interest in host nests during the 5 days prior to laying. This behaviour may indicate that the cuckoo already knew the location and status of the nest from the host's building period. However, it could also mean that in some cases females had to spend extra time relocating the nest in the vegetation. Another explanation for spending around 20 min at the vantage point could be that they waited to be ready to lay or for the optimal moment in relation to the host's behaviour.

The hypothesis that brood parasites use the activity of hosts during nest building to locate nests is supported by data both for the cuckoo (Chance 1922, 1940; Jourdain 1925; Gärtner 1981, 1982; Wyllie 1981; Teuschl et al. 1998) and for the brown-headed cowbird (Clotfelter 1998; Banks & Martin 2001; see also Robinson & Robinson 2001). This hypothesis is also supported by our observations of female cuckoos searching in the laying habitats and visiting nests during the building stage before any eggs were laid. Nest building by hosts is normally finished about 5 days before nest parasitism by cuckoos. Our results indicate that cuckoo females on their laying days watched the host behaviour more closely, perhaps waiting for an opportunity to lay without being seen by the host. However, Moksnes et al. (2000) showed by videorecordings that cuckoos parasitizing reed warblers in our study area did not time their laying visits to periods when the host was absent from its nest, as had been suggested (Wyllie 1981; Davies & Brooke 1988; see also Neudorf & Sealy 1994). Moksnes et al. (2000) suggested that, in dense reed vegetation with a high density of nests, it could be difficult for egg-laying cuckoos to assess whether the host was present in the vicinity of the nest. There were no indications of such behaviour from cuckoos against other host species in the area.

The fact that the cuckoo females in this study spent little time near the nest the day before laying (Fig. 1) also supports the view that they already knew the location of the nest. The cuckoo lays an egg every second day, and if she was short of host nests, she might also use this day for searching in addition to feeding. Consistent with this hypothesis is that the egg-laying areas around the ponds in our study were near the feeding areas, mainly in adjacent oak woodland. However, there is no empirical evidence to support this possibility. The proportion of time cuckoo females spent in egg-laying habitat was significantly greater on laying days than on nonlaying days in the study area (Vogl et al. 2002).

## Distance Between Nest and Vantage Point

It has been generally assumed that brood parasites locate host nests by observing host activity from concealed vantage points in trees (e.g. Chance 1940; Banks & Martin 2001). One should therefore expect that nests close to trees are more vulnerable to parasitism than nests further away from trees. This 'perch-proximity hypothesis' has been covincingly supported for both cuckoo hosts (Alvarez 1993; Øien et al. 1996; Moskát & Honza 2000) and brown-headed cowbird hosts (Clotfelter 1998; Larison et al. 1998; Hauber & Russo 2000). The result from the present study, that cuckoo females did not use the closest possible vantage point before approaching a host nest, could at first seem to contradict the 'perch-proximity hypothesis'. The distance to the vantage point actually used by female cuckoos was almost four times further from the nest than was the closest possible one.

However, a simpler explanation may be that, even if the closest vantage points were used by the parasite during nest location in the building period, the parasite may find it optimal to watch the nest from further away on the laying day. By this behaviour, the cuckoo females may avoid being detected or attacked by the hosts. This is supported by the fact that most of the vantage points were concealed tree branches which give protection against both aggressive hosts and predators. The majority of host species are aggressive towards the cuckoo (Moksnes et al. 1990), for example, great reed warblers, which are frequently used hosts in the area, may injure or kill egg-laying cuckoos (Molnar 1944). Some host species also reject cuckoo eggs at a higher rate when they have observed a cuckoo near their nests (Davies & Brooke 1988; Moksnes & Røskaft 1989).

## Time of Day and Time at Nest

Common cuckoos typically lay their eggs in the afternoon, mainly between 1400 hours and dusk (Wyllie 1981; Davies 2000), in contrast to their hosts, which tend to lay in the early morning. This typical pattern of afternoon laying by cuckoos in reed warbler nests in the area of the present study has been documented by Moksnes et al. (2000) who also discussed the parasitic adaptations behind the evolution of this pattern (see also Davies 2000). However, laying in the afternoon is not a general strategy across parasite species. Many interspecific brood parasites, such as the brown-headed cowbird (Neudorf & Sealy 1994), the pied crested cuckoo, *Clamator jacobinus* (Gaston 1976), the Horsfield's bronze-cuckoo, *Chrysococcyx basalis*, and the shining bronze-cuckoo, *Ch. lucidus*, in Australia (Brooker et al. 1988) lay in the morning.

The variation in laying behaviour in the present study was best explained by variation between females. This was especially clear for the time of day when laying. Since the females showed a high, although not absolute, degree of host specificity, this variation resulted in a significant difference between the host species in the time of day when they were visited by cuckoos, and also between the two habitats herbs and reeds. The surprising result that some layings occurred before noon was due to the female that parasitized sedge warblers. Her five layings occurred between 1012 and 1416 hours. Such early laying has rarely been observed. Wyllie (1981) found that only five (4.2%) of 120 females laid before 1400 hours and 2 (1.7%) before 1200 hours. The other six radiotracked females in the present study mainly laid in the afternoon and otherwise visited nests as expected. Therefore, we do not consider it likely that layings by these females should have remained undetected, as we started tracking after 1400 hours.

It takes brood parasites only a few seconds to lay an egg in a host's nest (Chance 1922, 1940; Hann 1941; Seel 1973; Brooker et al. 1988; Sealy et al. 1995). Sealy et al. (1995) summarized the main adaptations underlying quick laying in brood parasites: (1) rapid laying reduces the chance that the host will injure or kill the parasite; (2)

by laying eggs rapidly parasites may avoid drawing attention to the nest; (3) rapid laying may reduce the chance of the host preventing the parasite laying in its nest; (4) female parasites that lay without being seen by the host may increase the probability that their parasitic eggs will be accepted. With video recordings, Moksnes et al. (2000) showed that cuckoos in our study area stayed on average 41 s at reed warbler nests when laying. Although this average is longer, it is not significantly different from the average of 26 s recorded in the present study (Mann–Whitney $U$ test: $Z=-1.22$, $N_1=14$, $N_2=6$, $P=0.222$). For nest visits without laying, Moksnes et al. (2000) reported an average of 28 s per visit, which is also longer but not significantly different from the 17 s of our radiotagged females (Mann–Whitney $U$ test: $Z=-1.00$, $N_1=N_2=7$, $P=0.317$). The duration of these stays at the host nest is considerably longer than those previously reported (mostly around 10 s or less; Chance 1940; Wyllie 1981; Davies & Brooke 1988). The method that we used (see Methods) could potentially overestimate the time at the nest compared with other studies. However, videorecordings of cuckoo egg laying in the area (Moksnes et al. 2000) support our results.

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## References

**Alvarez, F.** 1993. Proximity of trees facilitates parasitism by cuckoos *Cuculus canorus* on rufous warblers *Cercotrichas galactotes*. *Ibis*, **135,** 331.

**Baker, E. C. S.** 1942. *Cuckoo Problems*. London: Whitherby.

**Banks, A. J. & Martin, T. E.** 2001. Host activity and the risk of nest parasitism by brown-headed cowbirds. *Behavioral Ecology*, **12,** 31–40.

**Brooke, M. de L. & Davies, N. B.** 1988. Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature*, **335,** 630–632.

**Brooker, M. G., Brooker, L. C. & Rowley, I.** 1988. Egg deposition by the bronze-cuckoos *Chrysococcyx basalis* and *Ch. lucidus*. *Emu*, **88,** 107–109.

**Chance, E. P.** 1922. *The Cuckoo's Secret*. London: Sidgwick & Jackson.

**Chance, E. P.** 1940. *The Truth About the Cuckoo*. London: Country Life.

**Clotfelter, E. D.** 1998. What cues do brown-headed cowbirds use to locate red-winged blackbird host nests? *Animal Behaviour*, **55,** 1181–1189.

**Davies, N. B.** 2000. *Cuckoos, Cowbirds and other Cheats*. London: Poyser.

**Davies, N. B. & Brooke, M. de L.** 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. *Animal Behaviour*, **36,** 262–284.

**Dröscher, L.** 1988. A study on radio-tracking of the European cuckoo (*Cuculus canorus canorus*). In: *Proceedings of the 100th International Deutsche Ornithologen-Gesellschaft Meeting* (Ed. by R. van den Elzen, K.-L. Schuchmann & K. Schmidt-Koenig), pp. 187–193. Bonn: Deutsche Ornithologen-Gesselschaft.

**Edvardsen, E., Moksnes, A., Røskaft, E., Øien, I. & Honza, M.** 2001. Egg mimicry in cuckoos parasitizing four sympatric species of *Acrocephalus* warblers. *Condor*, **103,** 829–837.

**Gärtner, K.** 1981. Das Wegnehmen von Wirtsvögeleiern durch den Kukuck *Cuculus canorus*. *Ornithologische Mitteilungen*, **33,** 115–131.

**Gärtner, K.** 1982. Zur Ablehnung von Eiern und Jungen des Kuckucks (*Cuculus canorus*) durch die Wirtsvögel: Beobachtungen und experimentelle Untersuchungen am Sumpfrohrsänger (*Acrocephalus palustris*). *Vogelwelt*, **103,** 201–224.

**Gaston, A. J.** 1976. Brood parasitism by the pied crested cuckoo *Clamator jacobinus*. *Journal of Animal Ecology*, **45,** 331–345.

**Gibbs, H. C., Sorenson, M. D., Marchetti, K., Brooke, M. de L., Davies, N. B. & Nakamura, H.** 2000. Genetic evidence for female host-specific races of the common cuckoo. *Nature*, **407,** 183–186.

**Hann, H. W.** 1941. The cowbird at the nest. *Wilson Bulletin*, **53,** 211–221.

**Hauber, M. E.** 2000. Nest predation and cowbird parasitism in song sparrows. *Journal of Field Ornithology*, **71,** 389–398.

**Hauber, M. E. & Russo, S. A.** 2000. Perch proximity correlates with higher rates of cowbird parasitism of ground nesting song sparrows. *Wilson Bulletin*, **112,** 150–153.

**Honza, M., Moksnes, A., Røskaft, E. & Stokke, B. G.** 2001. How are different common cuckoo *Cuculus canorus* egg morphs maintained? An evaluation of different hypotheses. *Ardea*, **89,** 341–352.

**Jourdain, F. C. R.** 1925. A study of parasitism in the cuckoos. *Proceedings of the Zoological Society, London*, **1925,** 639–667.

**Lack, D.** 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen.

**Larison, B., Laymon, S. A., Williams, P. L. & Smith, T. B.** 1998. Song sparrows vs. cowbird brood parasites: impacts of forest structure and nest-site selection. *Condor*, **100,** 93–101.

**Moksnes, A. & Røskaft, E.** 1989. Adaptations of meadow pipits to parasitism by the common cuckoo. *Behavioral Ecology and Sociobiology*, **24,** 25–30.

**Moksnes, A. & Røskaft, E.** 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,** 625–648.

**Moksnes, A., Røskaft, E., Braa, A. T., Korsnes, L., Lampe, H. M. & Pedersen, H. C.** 1990. Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. *Behaviour*, **116,** 64–89.

**Moksnes, A., Røskaft, E., Hagen, L. G., Honza, M., Mørk, C. & Olsen, P. H.** 2000. Common cuckoo *Cuculus canorus* and host behaviour at reed warbler *Acrocephalus scirpaceus* nests. *Ibis*, **142,** 247–258.

**Molnar, B.** 1944. The cuckoo in the Hungarian plain. *Aquila, Budapest*, **51,** 100–112.

**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.

**Nakamura, H. & Miyazawa, Y.** 1997. Movements, space use and social organisation of radiotracked common cuckoos during the breeding season in Japan. *Japanese Journal of Ornithology*, **46,** 23–54.

**Neudorf, D. L. & Sealy, S. G.** 1994. Sunrise nest attentiveness in cowbird hosts. *Condor*, **96,** 162–169.

**Norman, R. F. & Robertson, R. J.** 1975. Nest searching behaviour in the brown-headed cowbird. *Auk*, **92,** 610–611.

**Øien, I. J., Honza, M., Moksnes, A. & Røskaft, E.** 1996. The risk of parasitism in relation to the distance from reed warbler nests to cuckoo perches. *Journal of Animal Ecology*, **65,** 147–153.

**Øien, I. J., Moksnes, A., Røskaft, E. & Honza, M.** 1998. Costs of cuckoo *Cuculus canorus* parasitism to reed warblers Acrocephalus scirpaceus. *Journal of Avian Biology*, **29,** 209–215.

**Robinson, W. D. & Robinson, T. R.** 2001. Is host activity necessary to elicit brood parasitism by cowbirds? *Ethology, Ecology and Evolution*, **13,** 161–171.

**Rothstein, S. I. & Robinson, S. K. (Ed.)** 1998. *Parasitic Birds and Their Hosts: Studies in Coevolution*. New York: Oxford University Press.

**Scott, D. M., Weatherhead, P. J. & Ankney, C. D.** 1992. Egg-eating by female brown-headed cowbirds. *Condor*, **94,** 579–584.

**Sealy, S. G., Neudorf, D. L. & Hill, D. P.** 1995. Rapid laying by brown-headed cowbirds *Molothrus ater* and other parasitic birds. *Ibis*, **137,** 76–84.

**Seel, D. C.** 1973. Egg-laying by the cuckoo. *British Birds*, **66,** 528–535.

**Teuschl, Y., Taborsky, B. & Taborsky, M.** 1998. How do cuckoos find their nests? The role of habitat imprinting. *Animal Behaviour*, **56,** 1425–1433.

**Vogl, W., Taborsky, M., Taborsky, B., Teusch, Y. & Honza, M.** 2002. Cuckoo females preferentially use specific habitats when searching for host nests. *Animal Behaviour*, **64,** 843–850.

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