

The Wilson Journal of Ornithology 130(2):536–542, 2018

Postfledging behavior of the Common Cuckoo (*Cuculus canorus*) attended by the Chaffinch (*Fringilla coelebs*): a comprehensive approach to study the least-known stage of brood parasite–host coevolution

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ABSTRACT—In contrast to the thoroughly studied incubation and nestling periods, the postfledging period of the Common Cuckoo (*Cuculus canorus*) remains virtually unknown. Here, we report detailed observations of a cuckoo fledgling attended by a male Chaffinch (*Fringilla coelebs*). Molecular data (nuclear DNA) showed the fledgling was a male belonging to the *Cuculus c. canorus*/*C. saturatus* clade while mitochondrial DNA data confirmed that it did not belong to blue egg gens that parasitizes Redstarts (*Phoenicurus phoenicurus*), which is the most common local host and the only regular Common Cuckoo host. During one week of observations, feeding rates did not change, body mass decreased (by 10%), and wing length increased (by 16%). Video recordings showed that the provided diet consisted mostly of larvae and that the fledgling also self-fed on lichens. A radio transmitter fitted on the fledgling revealed that daily movement distances ranged from 0 to 650 m and significantly increased with age. We suggest that future studies should focus on the postfledging period in brood parasite young because this stage currently represents a major gap in our understanding of parasite–host arms races. Received 22 December 2016. Accepted 15 April 2017.

Key words: arms race, brood parasitism, coevolution, *Cuculus canorus*, fledgling, *Fringilla coelebs*, telemetry.

Comportamiento postemancipatorio del cuco *Cuculus canorus* criado por el pinzón *Fringilla coelebs*: un enfoque completo para el estudio de la etapa menos conocida de la coevolución entre parásitos de puesta y sus hospederos

RESUMEN (Spanish)—En contraste con los bien estudiados periodos de incubación y permanencia en el nido, el periodo postemancipatorio del cuco *Cuculus canorus* permanece virtualmente desconocido. Aquí reportamos observaciones detalladas de un cuco volantón criado por un macho del pinzón *Fringilla coelebs*. Los datos moleculares (DNA nuclear) nos muestran que el volantón era un macho que pertenecía al clado *C. c. canorus*/*C. saturatus*, mientras que su DNA mitocondrial confirma que no pertenece al grupo de huevos azules que parasita al colirrojo *Phoenicurus phoenicurus*, que es el hospedero más común localmente y el único hospedero regular de *C. canorus*. Durante una semana de observaciones, la tasa de alimentación no cambió, la masa corporal decreció (un 10%) y la longitud de las alas se

incrementó (un 16%). Las grabaciones en video mostraron que la dieta provista consiste principalmente de larvas y que el volantón también se alimentó por sí mismo de líquenes. Al fijar un radiotransmisor en el volantón, se reveló que las distancias de movimientos diarios varían de 0 a 650 m e incrementan significativamente con la edad. Sugerimos que futuros estudios se enfoquen en el periodo postemancipatorio de las crías de parásitos de puesta, dado que esta etapa representa un vacío mayúsculo en nuestro entendimiento de la competencia entre parásitos y hospederos.

Palabras clave: Coevolución, competencia, *Cuculus canorus*, *Fringilla coelebs*, parasitismo de puesta, telemetría, volantón.

Interactions between brood parasites, such as Common Cuckoos (*Cuculus canorus*), and their hosts present an intensely studied model system of coevolutionary arms races. Most studies on Common Cuckoos have focused on egg and nestling stages (e.g., Davies 2000, Stokke et al. 2004, Grim et al. 2011); by contrast, almost nothing is known about the postfledging period (Wyllie 1981) and migration from breeding to wintering grounds (Vega et al. 2016). The only detailed data on the duration of postfledging care were reported by Wyllie (1981). Therefore, the postfledging period remains the least-known stage of brood parasite–host interactions, and even anecdotal observations can improve our understanding of cuckoo–host coevolution (e.g., Seel and Davis 1981, Knysh 2000, Grim 2008a). The current rarity of studies of parasite fledglings (De Mársico et al. 2012) parallels a previous rarity of studies of parasite nestlings (Grim 2007a); recent studies revealed that cases of nestling discrimination by hosts can, contrary to traditional claims, be quite common (e.g., Grim 2006, 2007b; Sato et al. 2015; reviewed in Grim 2017). This finding has fundamentally changed our view of host–parasite arms races (reviewed in Grim 2017) because additional lines of defenses (e.g., nestling discrimination in addition to egg discrimination or aggression towards adult parasites) affect fitness

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and evolutionary trajectories of both parasites and hosts (Britton et al. 2007). The same principle applies to interactions at the postfledging stage when fledgling discrimination can occur (De Mársico et al. 2012). Thus, ignoring the postfledging stage can dramatically bias estimates of parasite fitness. For example, successfully fledged Common Cuckoo chicks from mixed broods (i.e., cuckoos sharing the nest with host nestlings that the cuckoo chick did not manage to evict; Grim et al. 2009) suffer total mortality soon after fledging (Grim and Rutila 2017).

Here, we provide detailed observations, supported by molecular and telemetry techniques, of a fledgling Common Cuckoo provisioned by a Chaffinch (*Fringilla coelebs*). Chaffinches and the closely related Bramblings (*Fringilla montifringilla*) were involved in intense coevolution with cuckoos, as evidenced by their excellent abilities to reject foreign eggs (Braa et al. 1992, Stokke et al. 2004, Vikan et al. 2011). Many cases of Common Cuckoo eggs found in *Fringilla* nests were reported during 20th century (Malchevsky 1960, 1987; Moksnes and Røskaft 1995). Our literature review revealed nearly 100 records of Common Cuckoo nestlings and fledglings reared by Chaffinches in Russia (Promptov 1941; Malchevsky 1960, 1987), Ukraine (Knysh 2000), the Czech Republic (Šír 1883, Richter 1933, Kroutil 1965), and the United Kingdom (Seel and Davis 1981). Unfortunately, all these sources only reported the observational records and provided no additional data on the biology of Common Cuckoo chicks.

Methods

During our project on relationships between Common Cuckoos and Redstarts (*Phoenicurus phoenicurus*; Samaš et al. 2016), we found a Common Cuckoo fledgling fed by a male Chaffinch on 18 July 2014, at 1230 h (EEST). The cuckoo was hidden in a 4 m tall tree (the Norway spruce, *Picea abies*) in the middle of a mature Scotch pine (*Pinus sylvestris*) forest (61°22'N, 28°32'E). The cuckoo fledgling perched on a branch ~0.5 m above ground and begged. The fledgling was unable to fly, thus we were able to catch it by hand. We banded the fledgling with a metal ring of the Finnish Ornithological Society

(B-66643). We took a blood sample from a wing vein (15 µL) and stored it in 96% ethanol toward later determination of the fledgling's sex (following Griffiths et al. 1998) and gens (i.e., ecological race; Davies 2000) using a COI marker (following Fossøy et al. 2016).

Between 18 July and 23 July 2014, we were able to re-catch the cuckoo and take body measurements once daily. We measured the fledgling's body mass with a portable electronic balance (precision 0.1 g), its tarsus length ("maximum" tarsus length, following figure 4.5a in Sutherland et al. 2004; precision 0.01 mm), wing length (following figure 4.4 in Sutherland et al. 2004; precision 1 mm), bill length (distance measured from the tip of the bill to the distal-most point of the fleshy fold of the rictal flange, precision 0.01 mm; Grim and Honza 2001), and bill width (distance measured between the bilateral fleshy folds of the rictal flange, precision 0.01 mm; Grim and Honza 2001).

We commenced video recording of the fledgling immediately after noticing it was attended by a male Chaffinch. Video recording took place from 18 July to 26 July 2014 between 0630 and 2400 h and lasted 3–8 h per day, 5 h on average. We employed video cameras to record feeding events without disturbing the birds (we also observed a female Chaffinch feeding 4 Chaffinch fledglings nearby; however, this female was never recorded feeding the cuckoo fledgling). Recordings were obtained with an HD digital video camera (Panasonic HDC-HS80EP) mounted on a tree trunk overlooking the location of the fledgling. To minimize disturbance, the camera was hidden in wooden box (figure 2b in Samaš et al. 2016) and placed ~10 m from the fledgling. The camera view covered the cuckoo's position and the surrounding branches to account for potential short movements of the fledgling.

From the video footage, we calculated the feeding rate as the number of feedings per hour (Soler et al. 2014) and identified prey types down to order level (see also Grim et al. 2014). As a result of changing weather conditions, orientation and position of the fledgling, and the angle at which the Chaffinch male was feeding, we were sometimes unable to determine prey identity with certainty. We estimated dominance as $D = \text{number of items of a respective order} / \text{total number of items} \times 100$, and frequency as $F = \text{number of feeding}$

Table 1. Composition of food delivered to the Common Cuckoo fledgling by a male Chaffinch. Total number of food items was 232 (from 165 video-recorded feeding events). D = dominance, F = frequency. See methods for details.

Prey type	D (% of items)	F (% of feeding events)
Lepidoptera and Hymenoptera larvae	58.6	55.8
Lepidoptera imago	3.0	4.2
Orthoptera	2.2	3.0
Araneida	1.3	1.8
Diptera	0.4	0.6
Unidentified	34.5	48.5

events in which items of the respective order appeared/total number of feeding events \times 100 (Table 1). Because of their strong similarity, larvae of Lepidoptera and Hymenoptera were counted as one prey type. The number of items is higher than the number of feeding events because the fosterer often provided several items per feeding. Graphical sonograms of the fledgling's begging calls were obtained by uploading calls into Xeno-canto database (www.xeno-canto.org) as XC347199 (begging call in the absence of the Chaffinch male) and XC347200 (begging call with Chaffinch male present).

Following the methods of Nakamura and Miyazawa (1997) and Diemer et al. (2014), we attached a glue-mounted transmitter PIP3 Ag393 (Biotrack Ltd) to the back feathers of the fledgling to monitor its movement and behavior. The transmitter included a 15 cm long wire antenna and weighed 2.1 g (we used the same transmitters to radio track Common Cuckoos fledged from Redstart nests). We glued this transmitter to clipped back feathers with cyanoacrylate (Super Glue; Diemer et al. 2014). Transmitter loss was expected with molting (Diemer et al. 2014), which occurs in young Common Cuckoos prior to migration (Verheyen 1950, Stresemann and Stresemann 1961, Rohwer and Broms 2013). The detection ranges of the PIP3 tag were 200–600 m (ground to ground) and 500–1200 m (above ground).

We always commenced tracking at the location of the last visual contact with the cuckoo and used a portable 4 MHz Sika receiver with a hand-held Lintec flexible 3-element Yagi antenna (138 MHz) to capture the signal and retrack the cuckoo. After we established first visual contact with the cuckoo,

we recorded its GPS position in the mobile application Locus Map Version 2.10.1 (precision 2–6 m) to measure daily movement distances. We recorded the height and type of its shelter (always a tree) and fledgling height above ground (precision 0.5 m). When our presence or capture attempts caused the fledgling to flush from its shelter, we also recorded the type of movement it used (hopping/flying), the distance it flew, and the number of flying bouts (precision 1 m in all cases). We denoted the day we tagged the fledgling as day 0. We conducted radio tracking daily until we first noticed signs of the cuckoo fledgling's independence (i.e., absence of fledgling's begging, no feeding, and no alarm calls from the Chaffinch male) and then tracked the cuckoo every second day for another 10 d after it became independent.

Values are reported as mean (SD). All analyses were conducted in STATISTICA 12 (StatSoft Inc. 2013).

Results

Nuclear DNA analysis showed that the Common Cuckoo fledgling was a male. The COI mitochondrial DNA marker showed that the individual belonged to the *C. c. canorus/C. saturatus* clade.

Video recordings showed that prey belonged to several invertebrate orders (Table 1). Surprisingly, from the second day of observations onward, the fledgling was self-feeding on lichens from branches (Supplementary material video: <https://www.youtube.com/watch?v=EGg5fpmvIs>). The consumed fragments of lichen measured $\sim 0.5 \times 0.5$ cm (maximum 2×1 cm; reconstructed through the known size of the Common Cuckoo's bill) and were usually consumed when the Chaffinch was not present ($n = 21$ self-feedings). Feeding frequency by the male Chaffinch was 6 (4) feeds per hour (median = 5, range = 1–19, $n = 29$ h) and did not correlate with fledgling age (daily means: $r_s = 0.64$, $P = 0.12$).

When the Chaffinch male was not present, the Common Cuckoo emitted a host-absent begging call (Šicha et al. 2007) about 0.1 s in duration and 4–8 kHz in frequency, repeated in 1 call/s intervals (Fig. 1a). After the Chaffinch male appeared, the fledgling changed the structure of the call to the standard begging call (Grim 2008a) with a

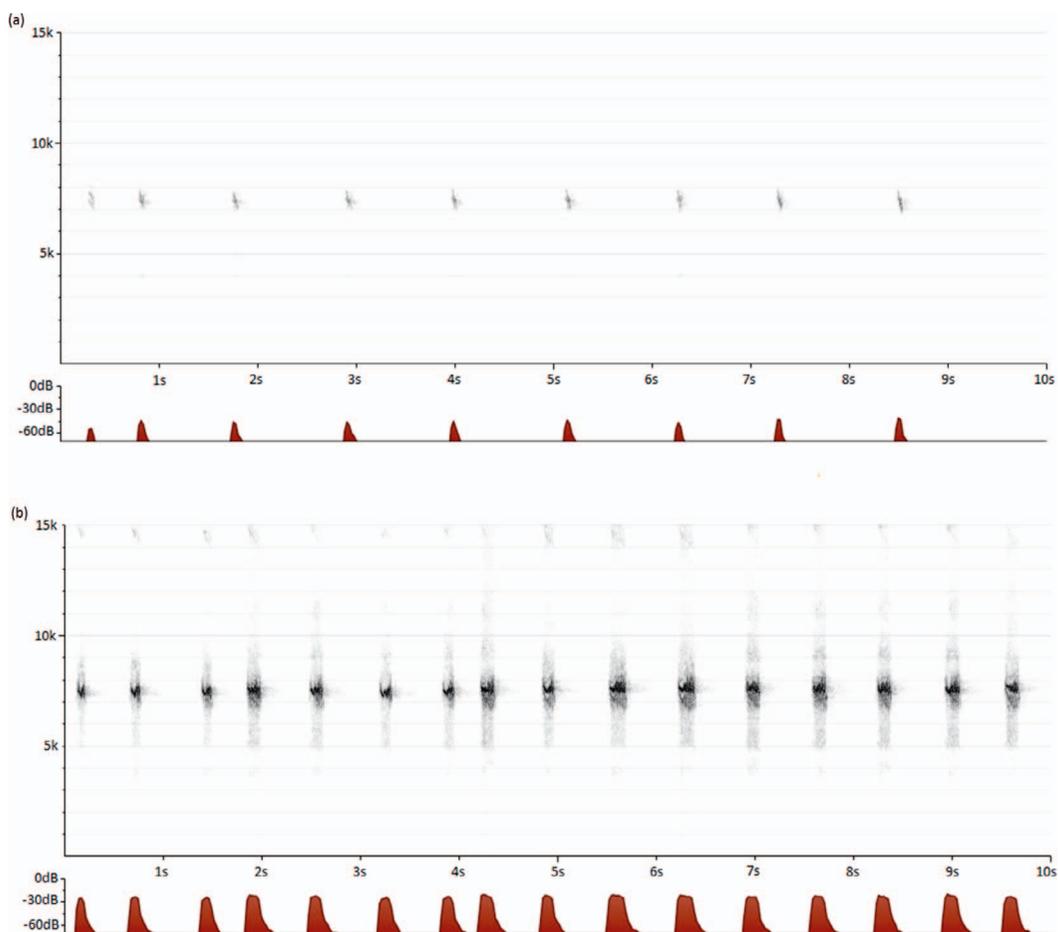


Figure 1. Sonograms of begging calls of the fledgling Common Cuckoo in (a) the absence of the Chaffinch male (Xeno-canto id: XC347199) and (b) during presence of the Chaffinch male (Xeno-canto id: XC347200). The sonograms were created using Xeno-canto website and the background noise (wind) was cleaned.

duration of about 0.1–0.2 s and a frequency of 5–15 kHz, which was repeated at a rate of ~ 2 calls/s (Fig. 1b).

During feeding, the Common Cuckoo always raised and shook its wing in the direction of the arriving Chaffinch if the fosterer was arriving from right or left side (68%, $n = 144$; asymmetrical wing-shake begging; Grim 2008b). When the Chaffinch arrived from the front (32%), the fledgling shook both its wings (Fig. 2).

In the flightless stage (first 3 d from day 0, starting 18 July), the Common Cuckoo remained in the same tree and at a constant height of ~ 0.5 m above ground level. On 21 July, we found the cuckoo perched on a 4 m tall spruce tree, 0.5 m above ground, at a distance of 40 m from its

original position. It spent the next day in the new shelter as well at the same height of 0.5 m above ground level. We first observed the cuckoo in flight on 23 July when we flushed it from a 3 m tall spruce on which it perched ~ 1 m above ground level. This spruce was located at a 40 m distance from the previous day's last recorded position, and the cuckoo flew about 50 m before it landed. This observation occurred on the last day when the cuckoo perched < 2 m high and also the last occasion on which we managed to catch and measure the bird. In this 6 d period, daily measurements revealed that body mass changed from 73.2 to 66.1 g, tarsus length from 25.8 to 25.7 mm, wing length from 122 to 142 mm, bill length from 22.8 to 24.5 mm, and bill width from



Figure 2. The fledgling of the Common Cuckoo shaking both wings while being fed by the Chaffinch male. Photo credit: Z. Tyller.

16.7 to 17.5 mm. In this period, body mass (68.7 [2.85] g, median = 68.1 g, range = 66–73.2 g, $n = 6$) decreased significantly with fledgling age ($r_s = -0.83$, $P = 0.042$), while tarsus length (25.8 [0.17] mm, median = 25.8 mm, range = 25.52–26.01 mm, $n = 6$) did not ($r_s = -0.14$, $P = 0.79$). Wing-length (132 [7.95] mm, median = 132 mm, range = 122–142 mm, $n = 6$) increased with fledgling age ($r_s = 1.00$, $P < 0.001$). Bill-length (24.0 [0.68] mm, median = 24.3 mm, range = 22.8–24.6 mm, $n = 4$) and bill-width (17.3 [0.30] mm, median = 17.4 mm, range = 16.7–1.75, $n = 4$) did not change with fledgling age ($r_s = 0.80$, $P = 0.20$; and $r_s = 0.80$, $P = 0.20$, respectively).

After the flightless period, we continued to track the Common Cuckoo fledgling daily until we first noticed its independence on 2 August (15 d from tagging). We then tracked the cuckoo down at least every second day until 13 August (26 d from tagging). We recorded 15 GPS positions of the cuckoo fledgling. The daily movement distances varied from 0 to 650 m (127.5 [195.4] m, median = 65 m, $n = 14$ distances from the previous position) and increased significantly with fledgling age ($r_s = 0.81$, $P < 0.001$). The height of the trees selected by the cuckoo as shelters (9.2 [5.0] m, median = 8 m, range = 3–15 m, $n = 15$) increased with fledgling age ($r_s = 0.83$, $P < 0.001$). The height of the fledgling's position above ground level (4.5 [4.1] m, median = 4 m, range = 0.5–12 m, $n = 15$) positively correlated with both fledgling age ($r_s = 0.94$, $P < 0.001$) and with shelter height

($r_s = 0.86$, $P < 0.001$). The length of the cuckoo's flight after being disturbed by us (61.4 [47.1] m, median = 50 m, range = 20–150 m, $n = 7$) increased with fledgling age ($r_s = 0.56$, $P = 0.038$), but the number of flying movements during particular observations (3.6 [1.8], median = 3, range = 1–6, $n = 7$) did not correlate with fledgling age ($r_s = 0.49$, $P = 0.74$).

Discussion

Although the Chaffinch is one of the best rejecters of Common Cuckoo eggs (e.g., Braa et al. 1992), our and previous data (discussed earlier) confirm that this species is a suitable Common Cuckoo host that can raise the Common Cuckoo to independence. Notably, the Common Cuckoo fledgling reported herein was able to achieve independence despite being reared by only a single Chaffinch foster parent. Molecular analyses excluded the blue egg gens as the affinity of the Common Cuckoo fledgling (the blue egg gens is the only cuckoo gens that can be recognized genetically; Fossøy et al. 2016). This information confirms that the Common Cuckoo fledgling was not originally raised by the Redstart, the most common (Samaš et al. 2016) and sole regular Common Cuckoo host (Grim et al. 2014) in our study area, and later adopted by the Chaffinch male. To our knowledge, this is the first observation where the phylogenetic identity of a brood parasite fledgling was confirmed genetically and potential adoption excluded (cf. Sealy and Lorenzana 1997). We believe that future studies would benefit from using molecular data to strengthen their conclusions. In addition, this evidence and independent observations of a Common Cuckoo fledgling fostered by a Chaffinch in 2016 (we were unable to follow this fledgling) confirm that Chaffinches may regularly act as local hosts of cuckoos in our study area.

The most commonly recorded dietary components were larvae of Lepidoptera and Hymenoptera, which agrees with the diet fed to Common Cuckoo fledglings by Redstarts in our study area (Grim et al. 2017). Such an insect-dominated diet is also typical for Common Cuckoo nestlings (Grim and Honza 2001). Our observation of the Common Cuckoo fledgling self-feeding on non-animal diet (i.e., lichens obtained from branches) is

therefore noteworthy and has not previously been reported. The consumption of lichens was clearly visible on the recordings (Supplementary video), but the video resolution was insufficient to exclude the potential presence of small insects on the surface of the lichens. Furthermore, self-feeding on lichens was only observed during absence of the Chaffinch male, suggesting that it represented foraging behavior (see “exploratory pecking” described by Woodward 1983) and not simply bored play. Observed wing-shaking patterns were similar to those of Common Cuckoos raised by other hosts (Grim 2008b).

The only available data on Common Cuckoo fledglings show that those attended by Reed Warblers (*Acrocephalus scirpaceus*; Wyllie 1981) and Redstarts (MK, unpubl. data) remain flightless during only 0–3 d postfledge. This finding, combined with the fact that on the day of first encountering the Common Cuckoo fledgling its body mass and wing length were in the typical range for Redstart-provisioned cuckoos at fledging (Grim and Samaš 2016; MK, unpubl. data), suggests that we commenced observations of the cuckoo shortly after it fledged.

Our data on fledgling growth, daily movement distances, and fledgling behavior are impossible to compare with equivalent records because no such detailed observations of Common Cuckoo fledglings were ever published from any host species (literature search). We can only compare age at independence: 15 d in the Chaffinch nest vs. 16 d on average in Reed Warbler nests (table 32 in Wyllie 1981). Common Cuckoo fledglings in Reed Warbler nests left the nest after 17 d on average, first flew at 19 days old (i.e., 2 d after fledging), and became independent 33 d after hatching (table 32 in Wyllie 1981).

Despite the anecdotal nature of our observations, no previous study provided such detailed data on the postfledging period in any host of the Common Cuckoo. Specifically, our comprehensive approach included molecular analyses, video recording of host provisioning and fledgling begging behavior, sonogram analysis, diet composition analysis, postfledging daily movement measurements, and growth measurements. Our study for the first time demonstrates it is methodologically feasible to obtain detailed data on the postfledging period in the Common Cuckoo and calls for further study. Because Common

Cuckoo chick parameters are highly specific per host species (e.g., chick growth data show high statistical repeatability across various hosts; Grim and Samaš 2016), even anecdotal observations can provide useful samples (e.g., Grim 2008a). Additional datasets equivalent to the data presented here could inform meta-analyses and lead to new insights into the least-studied stage of brood parasite–host coevolution.

Acknowledgments

We are grateful to the Czech Science Foundation (P506/12/2404), Human Frontier Science Program (RGY83/2012), and the Internal Grant Agency of Palacký University (IGA_PrF_2016_017 and IGA_PrF_2017_023) for funding. We thank J. Haikola, J. Rutila, and P. Samaš for field assistance. F. Fossøy conducted all molecular analyses. P. Procházka helped with the extensive literature search. D. Hanley and D. Voeten corrected the language.

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