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Are tits really unsuitable hosts for the Common Cuckoo?

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Avian brood parasites exploit hosts that have accessible nests and a soft insect diet. Common Cuckoo (*Cuculus canorus*) hosts were traditionally classified as suitable if both parameters were fulfilled or unsuitable if one, or both, were not. In line with this view, hole-nesting tits (Paridae) have become a text-book example of unsuitable Cuckoo hosts. Our extensive literature search for Cuckoo eggs hatched and chicks raised by hosts revealed 16 Cuckoo nestlings in Great Tit (*Parus major*) nests, 2 nestlings and 2 fledglings in Blue Tits (*Cyanistes caeruleus*), and 1 nestling in a Crested Tit (*Lophophanes cristatus*) nest. Our own data from natural observations and cross-fostering experiments concur with literature data that Great Tits are able to rear Cuckoo chicks to fledging. The natural observations involve the first known cases where a bird species became parasitized as a by-product of nest usurpation (take-over). Surprisingly, Cuckoo chicks raised by Great Tits grew better than Cuckoo chicks raised by common hosts, even alongside host own chicks. The frequency of Cuckoo parasitism in tits may be underestimated by studying tits in artificial nest-boxes with small entrances that prevent Cuckoos from laying and/or fledging. Results support a view that host suitability is not a categorical parameter (host suitable or unsuitable) but a continuous phenomenon. Understanding the diversity of parameters that determine host selection by Cuckoos is limited, because studies on Cuckoo chick diet, growth, and survival in most hosts are rare. Therefore any data are valuable and provide indispensable material for future meta-analyses.

1. Introduction

Brood parasitism rates by Common Cuckoos (*Cuculus canorus*; hereafter: Cuckoo) vary dramatically both within (Stokke *et al.* 2008) and between host species (Kleven *et al.* 2004, Grim *et al.* 2011). It is traditionally believed that potential host species can escape brood parasitism by using inaccessible nest sites (Røskaft *et al.* 2002) and/or having a diet that is unsuitable for parasites (Seel & Davis 1981).

However, recent studies cast multiple doubts on these traditional views. For example, even purely insectivorous hosts that were traditionally considered "suitable" Cuckoo fosterers may be in fact unsuitable as exemplified by 100% Cuckoo chick mortality in the nests of the Verditer Flycatcher (*Eumyias thalassinus*). The flycatcher feeds nestlings with insects just like other Cuckoo hosts (Grim & Honza 1997) but, as opposed to recent Cuckoo hosts, only those with hard exoskeletons (Yang *et al.* 2013). In contrast, a diet consisting of mostly non-insect items may in fact be suitable for the Cuckoo. Parasitic Cuckoo chicks that are fed predominantly with earthworms and molluscs (in the nests of the Song Thrush, *Turdus philomelos*) grew even better than those fed mostly insects (in the nests of Reed Warblers, *Acrocephalus scirpaceus*; Grim 2006a). Martín-Gálvez *et al.* (2005) found high proportion of grapes (~17%) in the diet fed to Cuckoo chicks by Rufous Bush Robins (*Cercotrichas galactotes*). Seel & Davis (1981) reported Cuckoo chicks fledging successfully from nests of seed-eating Greenfinches (*Carduelis chloris*).

An emerging view is that host suitability is a result of various parameters and their interactions (Grim *et al.* 2011). For example, nest cup design facilitating or preventing Cuckoo chick eviction behaviour (Anderson *et al*. 2009, Grim *et al.* 2009a,b), host willingness to feed foreign nestlings (Grim *et al.* 2011), or the specific composition of the diet that hosts bring to the chicks (Yang *et al.* 2013). However, our understanding of the diversity of these parameters is in its infancy, mostly because of a scarcity of studies on Cuckoo chick diet, growth and survival in hosts other than the Reed Warbler that is the single most frequently studied host. Therefore, here we combine an extensive literature review and empirical data on the performance of Cuckoo chicks in the nests of tits (Paridae) which are traditionally given as the textbook example of unsuitable Cuckoo hosts (Davies 2000).

2. Material and methods

2.1. Literature review

To identify cases of tits (Paridae) fostering a Cuckoo chick, we primarily used our extensive database of published information on Cuckoo chicks raised by various hosts (>5,000 data points). Additionally, we searched for relevant terms ((cuckoo* OR Cuculus) AND (Parus/Cyanistes/Periparus/Poecile/Lophophanes OR tit*)) in the ISI Web of Knowledge, SCOPUS, Zoological Record, the Cuculiformes bibliography by Erritzøe (2000) and its addenda (http://www.birdresearch.dk/?page_id=143) as well as the Czech ornithological bibliography (http://www.biblioteka.cz).

We specifically focused on Cuckoo chicks and not eggs because the eggs found were typically removed from host nests (for museum collections, see Moksnes & Røskaft 1995) or not followed afterwards, and thus do not provide any information about whether or how well tits are able to rear Cuckoo chicks. Here we review all cases of tit nests where Cuckoo eggs hatched. Still, we briefly discuss some cases of Cuckoo eggs found in tit nests within the Results.

Additional data were collected from extensive communication with ornithologists from various countries within the breeding distribution of the Cuckoo. We believe that this effort provided a balanced overview about any germane published or unpublished information. It is reasonable to expect that cases of tits rearing Cuckoo chicks are generally viewed as peculiar, and therefore were most likely published. Indeed, we obtained numerous unpublished records of many hosts rearing Cuckoos, but none of those included any tits.

2.2. Fieldwork

We conducted fieldwork in forests nearby Ruokolahti (61°24’N, 28°37’E) in south-eastern Finland from May to July 2005 and 2013. The study sites were cultivated pine (*Pinus sylvestris*) forests. We employed 400 nest-boxes designed to be of similar size to natural Redstart (*Phoenicurus phoenicurus*) cavities (for dimensions see Rutila *et al.* 2002). At the start of the breeding season, we regularly checked all nest-boxes at 2–3 week intervals. We checked active nests several times per week.

In the Great Tit (*Parus major*), we observed two nests naturally parasitized by the Cuckoo; however, only one Cuckoo chick successfully hatched (hereafter: natural Cuckoo chick). Additionally, we experimentally parasitized two Great Tit nests (hereafter: experimental Cuckoo chicks). One of these experimental Cuckoo chicks did not survive due to inclement weather (Great Tit and Redstart chicks in several nests died in the same period of very cold and rainy weather; thus, this

Cuckoo death was clearly not a result of chick discrimination, cf. Grim 2006b, 2011). We measured the mass (precision = 0.1 g) of all Cuckoo and Great Tit chicks (until their eviction or fledging) with a digital balance a minimum of every second day (often daily).

The natural Cuckoo chick was also video-recorded daily from the age of 12 days using an HD digital video camera Panasonic HDC-HS80EP attached and hidden within the roof of a custom-built nest-box. The time of all video-recordings ranged between 15:30 and 20:00 (EEST), except for the 28th July when we recorded from 9:30 to 11:00. Each recording lasted between 0:40–4:00 hours (average = 2:00 hours).

2.3. Statistical analyses

From video recordings we estimated feeding rates (number of feedings per hour) for each chick every day and obtained data on prey size and quality (broad categories at family or higher taxonomical levels). We assessed size of prey relative to adult fosterer bill length (1 = smaller, 2 = similar, 3 = larger).

We used a linear mixed model to compare feeding rates between the Cuckoo and the Great Tit chick. The model included "day" (nominal: nine days) as a random effect and "chick mass" (continuous) and "chick species" (nominal: Cuckoo vs. Great Tit) as fixed predictors. In this model the response variable was "feeding rate" (continuous: number of feedings per hour per chick).

To compare diet composition between the Cuckoo and the Great Tit chicks we used a generalized linear mixed model (GLMM; the Poisson family with log link), with the "count of prey items" as the response variable. In contrast to the chi-square goodness of fit test, the GLMM allows for random effects and continuous predictors and takes into account different sample sizes between subjects. This model contained "day" (nominal; nine days) as a random effect, and as predictors with fixed effects "chick mass" (continuous), "chick species" (nominal: Cuckoo vs. Great Tit), "prey type" (nominal: seven taxonomical categories; Table 1) and the interaction between "chick species" and "prey type". Results of simple goodness of fit (i.e., without covariates) and GLMM were similar (only GLMM results are shown).

Table 1. Percentage of prey type delivered by parents to a Cuckoo chick (n = 127 items) and a Great Tit chick (n = 29 items) that hatched in the same nest. Data are from a naturally parasitized nest where a Great Tit pair usurped an active Redstart nest. Note that sample sizes differ from those for feeding rates and prey sizes (see below) because in some cases it was not possible to estimate prey type reliably.

Prey type	Cuckoo (%)	Great Tit (%)
Lepidoptera larvae indet.	47	38
Arachnidae	26	38
Noctuidae	18	14
Diptera	2	3
Syrphidae	2	3
Pupae indet.	2	3
Coleoptera	2	–

All statistical analyses were conducted using R 2.15.2 (R Development Core Team 2012). All values are given as mean ± SE.

3. Results

3.1. Literature data

Overall, our extensive literature search revealed that 16 Cuckoo chicks hatched from naturally laid Cuckoo eggs in 13 nests of the Great Tit (i.e., including two multiply parasitized nests, see below). In addition, Cuckoo chicks naturally hatched in two Blue Tit (*Cyanistes caeruleus*) and one Crested Tit (*Lophophanes cristatus*) nest. Additionally, two Cuckoo fledglings fed by Blue Tits were reported. No cases of Cuckoo chicks were detected in other tit genera (*Poecile, Periparus*) whose breeding ranges overlap with that of the Cuckoo.

Most records of Cuckoo chicks raised by tits were reported in the Great Tit (Šír 1883, Puhlmann 1914, Kroutil 1965, Homoki Nagy 1978, Dolenc 1990). In most of these cases no data were given on Cuckoo eviction or fledging success. However, in four cases the authors explicitly reported that the Cuckoo chick fledged (Puhlmann 1914, Homoki Nagy 1978, Dolenc 1990). Interestingly, in all these cases the nest was shared by Cuckoo and

Fig. 1. A Great Tit feeding a 14-d old Cuckoo chick and an 11-d old own nestling. The nest was originally occupied by Redstarts (one of the evicted original host eggs can be seen next to the nest box wall) and was later usurped by Great Tits that thus became parasitized. Both chicks successfully fledged. To our knowledge, this is the first documented case of such a "second-hand" brood parasitism.

host chicks for at least some time. In Hungary, a Cuckoo did not evict any Great Tit eggs or chicks and it shared the nest with nine host chicks; both the Cuckoo and all host chicks successfully fledged (Homoki Nagy 1978). In Croatia, three Cuckoo eggs hatched in one multiply parasitized Great Tit nest, the Cuckoo(s) evicted all nine host eggs before they hatched, but finally only a single Cuckoo remained in the nest, evicting the other two Cuckoos that died below the nest and the fate of the nest was not reported (Dolenc 1990). In Germany, a single Cuckoo chick in one nest and two Cuckoo chicks in another nest shared their respective nests with host chicks (brood sizes not given) and both mixed broods successfully fledged (Puhlmann 1914).

In addition to the 16 natural cases of Cuckoo parasitism in the Great Tit, there are three other studies that experimentally cross-fostered Cuckoo chicks into Great Tit nests (Vilks 1973, Löhrl 1979, Varga 1994). In Germany, a Cuckoo egg found below an overturned Blackcap (*Sylvia atricapilla*) nest was transferred to a Great Tit clutch, from which a 3-day old Cuckoo chick was later removed and subsequently bred in captivity (Löhrl 1979). However, both in Latvia (Vilks 1973) and Hungary (Varga 1994), the Cuckoo chick successfully fledged but authors did not give any information on the fate of host eggs or chicks.

The Blue Tit has also been reported several times as a fosterer of Cuckoo chicks. Šír (1883) reported a Cuckoo chick that occupied a Blue Tit nest that was within a hole in a tree stump. Scheenstra (1964, 1965) found a Cuckoo alongside Blue Tit chicks in a nest-box; he transferred four host chicks to another nest-box, and the Cuckoo could fledge only after the roof of the original nest-box was opened by the observer. Müller (1889) and Moltoni (1951) reported that Blue Tits fed a fledged Cuckoo in the Czech Republic and Italy, respectively.

The Crested Tit was reported as a cuckoo host only once (Poll 1927). In this case, the Cuckoo chick shared a nest (located in a tree hole) with five young Crested Tits. After host chicks fledged, the host parents only attended their own fledglings. Although the Cuckoo chick decreased its mass due to fosterer neglect, it managed to fledge successfully.

In addition, there are several cases of Cuckoo eggs found in the Great Tit in Europe (single Cuckoo eggs from the UK, Denmark and Poland, Makatsch 1955; two eggs from the UK, Baker 1942) and three cases in India (Baker 1942). Baker (1942) also found a Cuckoo egg in a clutch of the Yellow-cheeked Tit (*Parus spilonotus*). The Coal Tit (*Periparus ater*) is only listed (together with the Great Tit) as a Cuckoo host in Italy without any additional details by Moltoni (1951). Similarly, Knorre *et al.* (1986) mention the Coal Tit as a

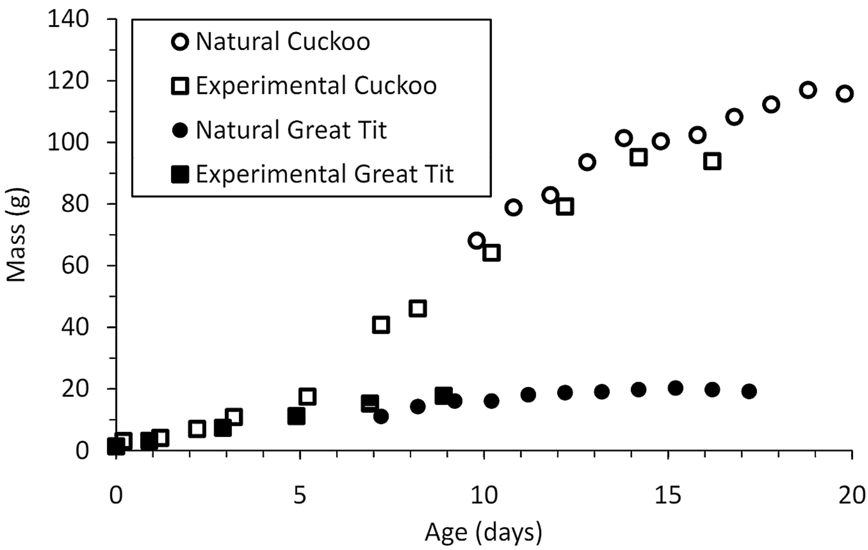

Fig. 2. Chick growth in two Great Tit nests. The "natural" nest was originally built by Redstarts but after being parasitized by the Cuckoo the nest was usurped by a Great Tit pair. The "experimental" nest was established by cross-fostering a freshly hatched Cuckoo chick from a Redstart nest into a Great Tit nest, which was the most synchronous out of the available pool of Great Tit nests. In both the natural and experimental nest Cuckoos did not evict all host eggs/chicks and were raised alongside a Great Tit chick (see Results). Data points were slightly horizontally displaced to decrease their overlap.

Cuckoo host in Thuringia, Germany and Sunkel (1926) mentioned the Blue Tit as a rare host in Hessen, Germany.

3.2. Natural secondary parasitism cases

In the first parasitism case that we detected, on 8th June 2007 the nest-box contained four Redstart eggs and one Cuckoo egg lying outside of the nest cup on the nest material (all the eggs were cold and the Cuckoo egg was moved by JR into the nest cup). On 9th June the nest contained five Redstart eggs and a Cuckoo egg. On 22nd June the nest contained six cold Redstart eggs and a Cuckoo egg covered with nest material (moss with some fur) commonly used by Great Tit. On 27th June the nest contained three Great Tit eggs, six Redstart eggs and a Cuckoo egg. On 2nd July the nest contained 11 Great Tit eggs, six Redstart eggs and a Cuckoo egg. On 12th July the Great Tit was brooding and eggshell pieces (species not determined) were scattered around nest cup. On 27th July the nest contained ten Great Tit chicks. Thus, the Cuckoo egg either did not hatch at all or the Cuckoo chick died within first eight days after hatching and was removed by the hosts.

In the second parasitism case, on 19th June 2013 the nest contained one Redstart egg and one Cuckoo egg (the eggs were cold and no Redstart was observed nearby). On 4th July the nest contained a single Redstart egg, a single Cuckoo egg, and eight Great Tit eggs. On 12th July the Great Tit was brooding but the nest contents were not checked (to avoid disturbing the incubating parent). On 18th July the nest contained one young Cuckoo chick, one young Great Tit chick and one Redstart egg was evicted outside the nest cup (Fig. 1). The Cuckoo chick thus apparently evicted the Redstart egg before it hatched (the egg remained within the nest-box outside the nest cup till the Cuckoo chick fledged). The Cuckoo also successfully evicted six out of eight Great Tit eggs or chicks: one egg remained in the nest lining and the other one hatched and was raised alongside the Cuckoo.

In the second parasitism case we suggest that the Great Tit pair most likely usurped the nest im-

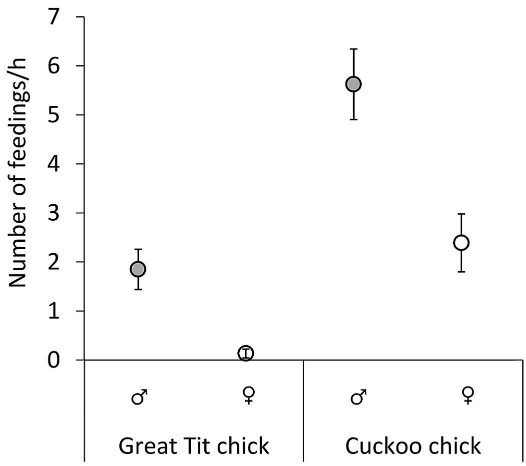

Fig. 3. Feeding rates for each chick (number of feedings per hour averaged across nine daily averages; mean ± SE; raw data) for a Cuckoo (at age 12–20 days) and a Great Tit (at age of 9–17 days) chick fed by Great Tit male (♂ = grey circles) and female (♀ = open circles). Data are from the naturally parasitized nest where a Great Tit pair usurped an active Redstart nest.

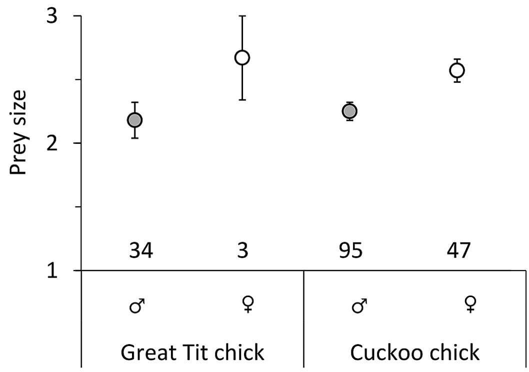

Fig. 4. Variability in prey size (mean ± SE) delivered by each fosterer/parent sex (♂ = grey circles, ♀ = white circles) to the Cuckoo and the Great Tit chick, respectively. Number of delivered prey items is shown above the x-axis. Data from the naturally parasitized nest where a Great Tit pair usurped an active Redstart nest.

mediately after the first nest check on 19^{th} June and started to lay on 20^{th} June. Assuming a single egg laid per day (Haftorn 1981, Perrins 2008) we estimate the day of Great Tit clutch completion was 27^{th} June. Great Tits start to incubate on the day that the last egg is laid (Haftorn 1981). Incubation of the Cuckoo egg typically lasts 11.6 days (Wyllie 1981), thus the Cuckoo chick most likely hatched on 8^{th} July (hatching day = 0). Assuming this hatching day, the chick would be 10 days old when we weighed it for the first time (18^{th} July). Its mass (68.1 g) was very similar (considering natural variation in mass of same-aged Cuckoo chicks, Grim 2006a) to the mass (64.2 g) of another 10-day old Cuckoo chick that was raised in another Great Tit nest (see next section). We knew the exact age of the latter chick because we cross-fostered it from a Redstart nest into a Great Tit nest immediately after hatching. This mass comparison and remarkably similar pre-fledging growth of both Cuckoo chicks in Great Tit nests (Fig. 2) suggests that this estimated date of hatching is precise.

During all nest checks (n = 11) the Great Tit chick was hidden below the wings or flanks of the much bigger Cuckoo chick and was not visible without removing the Cuckoo chick. Both the Cuckoo and the Great Tit fledged on 29^{th} July, estimated age of the Cuckoo chick being 20 days and that of the Great Tit chick 18 days. The fledging period we recorded is the same as that reported by Homoki Nagy (1978). This also corresponds to average fledging time of Cuckoo chicks in Redstart nests recorded within the same study area (20.5 ± 0.48 days; range 18–24; n = 18).

Video-recording of chick provisioning at the nest showed that the fosterers fed the Cuckoo chick (feeding frequency: 7.4 ± 0.6 feeds per hour) more often than the Great Tit chick (2.0 ± 0.5; $F_{1,13}$ = 9.43, p = 0.009; Fig. 3) controlling statistically for chick mass. Both the Cuckoo and the Great Tit chick were fed more often by the male fosterer (paired t-test; Cuckoo: t_8 = 3.40, p = 0.009; Great Tit: t_8 = 4.04, p = 0.004; Fig. 3).

Prey size did not differ between the Cuckoo (n = 142 prey items) and the Great Tit chick (n = 37 prey items; Mann-Whitney Test, W = 2866.5, p = 0.35; Fig. 4). Composition of prey type did not differ between the Cuckoo and the Great Tit chick ($F_{6,110}$ = 0.43, p = 0.86; Table 1) taking chick mass into account.

Post-fledging feeding rates were observed (by TG from a hide) for 6 hours (till the Cuckoo chick flew far away from the nest; the Great Tit chick remained in the nest throughout this period). First post-fledging feeding of the Cuckoo took place only 2.5 hours after fledging and the Great Tit chick was fed twice during this period. Overall, the

Cuckoo received in total six feedings during the six hours (five large caterpillars and one butterfly imago). The Great Tit chick received in total four feedings during the same six hours (id of the prey was unclear due to the position of the hide in relation to the nest box). The Cuckoo chick sat passively and only occasionally and weakly produced host-absent begging calls (sensu Šicha *et al.* 2007). When begging in the presence of fosterers, the Cuckoo always showed asymmetrical wing-shake begging (sensu Grim 2008).

3.3. Experimental cross-fostering parasitism cases

The first Cuckoo chick hatched in a Redstart nest on 11th June 2013 from an egg sized 21.5 × 16.4 mm and was immediately cross-fostered into the most synchronous available Great Tit nest. We did not video-record the nest but regularly observed both male and female Great Tits attending the nest. When the chick was seven days old (18th June), two Great Tit eggs hatched. The Cuckoo co-habited the nest with both Great Tits for two days; on 20th June it managed to evict the smaller of the two Great Tit nestlings. The Cuckoo co-habited the nest with the remaining Great Tit chick until 28th June when the nest was attacked by a predator (based on predator tracks most likely the Pine Marten *Martes martes*). The predator removed the Cuckoo (aged 17 days, i.e., shortly before fledging) but the Great Tit chick survived and remained in the nest, being hidden under the disturbed nest material. However, the nest was abandoned the day after the predation event.

The second Cuckoo chick was cross-fostered from a Redstart nest box into another Great Tit nest in 2013. The chick grew normally during the first three days post-hatch. However, an abrupt change in weather (decreased temperature, heavy rains) led to decreased food supply and to the nest cup lining getting wet. The Cuckoo died when it was 5 days old. Other Redstarts and large Cuckoo chicks died in the study site during the same period (penultimate week of July 2013), therefore it is likely that this Cuckoo chick would have grown normally, as other Cuckoo chicks in Great Tit nests (as suggested by its standard growth before the weather changed).

4. Discussion

Our extensive literature search showed that although Great Tits are rarely parasitized by the Cuckoo, they can successfully fledge the brood parasite. However, there are multiple reasons to expect that literature data underestimate Cuckoo parasitism rates in tits. Virtually all recent studies of tits used artificial nest-boxes with small entrance holes (Lambrechts *et al.* 2010). In contrast, natural tit nests often have larger entrances but are hard to find and therefore are rarely studied (reviewed in Wesołowski 2007). The most frequently used natural holes excavated by Great Spotted Woodpeckers (*Dendrocopos major*) have entrance diameters of 5–6 cm (Perrins & Cramp 1998) whereas standard tit nest boxes are often much smaller (as small as 2.6 cm, Lambrechts *et al*. 2010). One of the major cuckoo host in Scandinavia is the Redstart which frequently uses tree holes originally excavated by woodpeckers. Nest-box entrance diameter in the present study was 6–7 cm (Rutila *et al*. 2002) which did not prevent cuckoos from frequently laying into Redstart nests. In addition, tits also frequently use alternative breeding sites, such as ground nests, nests in rock crevices, between branches or even in old thrush *Turdus* nests (Glutz von Blotzheim 1993). Thus, natural tit cavities seem to be much more accessible to Cuckoos than artificial nest-boxes. This physical/logistic constraint might have contributed to low rates of Cuckoo parasitism reported in recent studies. On the other hand, European populations of tits typically accept almost all foreign eggs (Davies & Brooke 1989, Kempenaers 1995) which suggests that they have not evolved any anti-cuckoo defences (Davies 2000). However, egg rejection decisions in Cuckoo hosts are typically highly plastic, and may disappear within several years after Cuckoos stop parasitizing a particular population (e.g., Thorogood & Davies 2013). Thus, current absence of both parasitism and adaptive responses to experimental parasitism may not be conclusive in deciding whether there were any host-parasite interactions in the past (see below).

These considerations would predict that parasitism rates and, consequently, foreign egg rejection rates by tits should be higher in areas where (i) tits breed in holes with larger entrances, and/or (ii) where small bodied cuckoos (e.g., genus *Chryso-*

coccyx in East Asia) may enter even in holes with small entrances. Indeed, a recent large-scale study (Liang *et al*., in review) found high egg rejection rates in Asian tit populations and a positive correlation between local parasitism risk and egg rejection rates. Further, (iii) tits may specifically prefer breeding holes with small entrances as a counter-adaptation against predators, Cuckoos or both. Indeed, data from previous studies and also our study site suggest that tits preferentially occupy nest-boxes with small entrances, and this forces Redstarts to occupy nest-boxes with large entrance and this leaves them vulnerable to Cuckoo parasitism (e.g., van Balen *et al*. 1982). We suggest that future studies should target tit populations in areas where (i) alternative suitable cuckoo hosts are rare/absent, and tits (ii) breed in natural large-entrance cavities. In areas where it is not possible to find small holes, the risks (and costs) of cuckoo parasitism may increase, leading to an evolution of anti-cuckoo adaptations in tits.

The egg-laying period of the Great Tit usually starts from late-April depending on the geographic position and local conditions, with later laying dates (mid-May) in Northern Europe (Perrins & Cramp 1998). The Cuckoo egg laying period lasts from mid-April to mid-July, with the main egg laying period from May to June (Perrins & Cramp 1998). Hence, in some regions the first clutches of the Great Tit may be ahead of the Cuckoo egg-laying period, but generally there is an extensive overlap in breeding seasons of the two species, especially in northern Europe. Thus, the Great Tit is a potential host of the Cuckoo based on the seasonal timing of egg laying.

Importantly, both literature and our data clearly show that tits are able to successfully rear a Cuckoo chick till fledging. Here, we add a new case of a successful natural Cuckoo parasitism of the Great Tit in south-eastern Finland. In this case, a nest originally belonging to a Redstart pair was parasitized by the Cuckoo and then the already parasitized nest was usurped by the Great Tit. Nest usurpation itself is unsurprising because various secondary cavity nesters compete for suitable breeding places. These fierce interspecific interactions can result in nest usurpation which may even cause death of the owner or intruder (e.g., Mackenzie 1950, Merilä & Wiggins 1995). Normally, the usurper which is a stronger competitor expels the owner, removes the nesting material and eggs or builds a new nest over the original nest (JR unpubl. observations). In some cases, however, (some of) the eggs of the predecessor may be incubated alongside the usurper's eggs resulting in mixed broods between different species reared by the usurper (e.g., Tietze & Klodwig 2009, Suzuki & Tsuchiya 2010). Exceptionally, parents of both species may care for the mixed brood (Sundkvist 1979, Robinson *et al.* 2005). Great and Blue Tits regularly produce mixed broods when the socially subordinate Blue Tits initiate clutches that are subsequently usurped by the later nesting Great Tits which are dominant (Ammann 1949, Weinzierl 1961, Slagsvold 1998). Rarely, mixed broods between Great Tits and other species have been reported (Amman 1949, Schmidt 1956, Weinzierl 1961, Curry-Lindahl 1963, Löhrl 1964, Michocki 1971). Sometimes Redstart nestlings cohabit a nest with Great Tit chicks being fed by the tit parents (Ammann 1949, Mackenzie 1954). Our cases would hence not be that exceptional if the usurped nests did not contain a Cuckoo egg which in one case was successfully incubated by the Great Tit. To our knowledge, these are the first known cases where a bird species became parasitized as a by-product of nest usurpation (Fig. 1). Thus, usurpation of a previously parasitized nest may represent a so far not considered cost of nest usurpation.

Observations of Cuckoo chicks fledging together with host nestlings (e.g., Malchevsky 1954, this study) even without any detriment to the parasite growth are exciting. They show that competition with host nestlings is not always detrimental to Cuckoo chicks as suggested by previous studies which were mostly experimental (Soler 2002, Martín-Gálvez *et al.* 2005, Hauber & Moskát 2008, Grim *et al.* 2009b). The natural Cuckoo chick in the present study achieved a noticeably higher mass at fledging (116 g; the experimental Cuckoo weighed 94 g at the age of 16 days when measured for the last time) than is typical for the most common hosts, reed warblers (~70 g; Grim 2006a), or for even larger hosts, great reed warblers (~88 g; Kleven *et al.* 1999). Also the Great Tit chick reached above the average fledging mass (~19 g vs. ~16 g; see, e.g., Naef-Daenzer *et al.* 2001).

In the present study the Great Tit chick cohabiting with the Cuckoo (both in the natural and the cross-fostered nest) was invisible because it was hidden below the Cuckoo nestling during all nest checks. Thus, it is possible that some cases of cohabitation between the Cuckoo and a host chick may not have been noticed if researchers did not handle the Cuckoo chick.

Tits lay large clutches and when weather conditions are favorable they can raise large broods (Ahola *et al.* 2009). This host ability may compensate the challenging nest environment experienced by the Cuckoo chicks when they try to evict host eggs (Anderson *et al*. 2009, Grim *et al*. 2009a) and compete with any non-evicted host chicks (Grim *et al*. 2009b). The narrow nest entrance constitutes an insurmountable constraint for the large bodied Cuckoo nestling (Peiter 1892, Stevanović *et al.* 1989). Thus, the apparent rarity of Cuckoo parasitism in tits may be, at least partly, explained by logistic research constraints – the use of artificial small-entrance nest-boxes (Lambrechts *et al.* 2010) and neglect of natural nesting cavities (Wesołowski 2007) which may sometimes be large enough for the Cuckoo female to lay and for the Cuckoo chick to fledge (see above).

Great Tits also cover their clutches throughout the laying period with nest material (e.g., Haftorn 1981). The functional role of this behavior remains unclear (Haftorn & Slagsvold 1995). Interestingly, Loukola *et al*. (2014) showed experimentally that Great Tits increased egg covering in the presence of a Pied Flycatcher (*Ficedula hypoleuca*), suggesting that tits hide clutch information cues used by flycatchers in their habitat and nest-site selection decisions to prevent subsequent costs to Great Tits in terms of interspecific competition. We hypothesize that in addition to improving nest microclimate, reducing the risk of nest predation (Haftorn & Slagsvold 1995) or information parasitism (Loukola *et al*. 2014), the nest cup covering may also serve as an anti-cuckoo adaptation. Specifically, this behavior may deter visiting Cuckoo females from parasitizing tit nests that are seemingly empty. This novel hypothesis predicts that nest covering should be more prevalent in species/populations of tits (or any other passerines) that are sympatric with Cuckoos and have accessible nests for brood parasites.

Although our sample sizes are small (but still similar to many recent Cuckoo chick studies, reviewed in Grim 2006b, 2011), we argue that our conclusions are robust. Our main conclusion, that the Great Tit can successfully raise the Cuckoo chick till fledging, concurs with data from other five geographically isolated sites across Europe (Puhlmann 1914, Vilks 1973, Homoki Nagy 1978, Dolenc 1990, Varga 1994). Both in our and previous studies, natural and experimental Cuckoo chicks grew well and fledged successfully. All these studies were conducted independently in several separated study sites (n = 6 including our work) and clearly indicate that the Great Tit can successfully raise the Cuckoo chick till fledging. Therefore from the provisioning point of view, the Great Tit is a suitable Cuckoo host.

The two Cuckoo chicks in our study grew at the same rate. This is consistent with other findings, which show that Cuckoo chick growth rate is very consistent within host species (Grim 2006a; TG own unpubl. data). We recorded the fledging period of 20 days (for the non-predated natural Cuckoo) which is identical to that reported by Homoki Nagy (1978). Although larger sample sizes will be needed to check the generality of these findings, the results of similar studies (i.e., cross-fostering chicks into nests of a different species) are highly consistent and clear-cut: experimental chicks either survive in 100% cases, or die in 100% cases (Grim 2006a, Grim *et al.* 2011, Yang *et al.* 2013).

In conclusion, our data support the recent view (De Mársico & Reboreda 2008, Grim *et al.* 2011) that host suitability is better considered a continuous phenomenon instead of traditional categorical parameter (host suitable or unsuitable). Both data from the literature and our own observations suggest that under particular circumstances species that were considered "typical" unsuitable hosts can actually be suitable for the Cuckoo.

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Ovatko tiaiset oikeasti sopimattomia käen isänniksi?

Avopesijät ja pehmeitä hyönteisiä ravinnokseen käyttävät linnut ovat loispesijöiden yleisesti suosimia isäntälajeja. Perinteisesti käelle (*Cuculus canorus*) sopiviksi isänniksi on luokiteltu lajit, joilla molemmat näistä ehdoista täyttyvät ja sopimattomiksi lajit, joilla toinen tai molemmat kriteerit eivät toteudu. Vallitsevan käsityksen mukaisesti kolopesijöinä tunnetut tiaiset (Paridae) ovat malliesimerkkejä käelle sopimattomista isännistä. Perusteellisessa kirjallisuusselvityksessämme etsimme tapauksia, joissa käen muna on kuoriutunut ja poikanen kasvanut isännän pesässä. Paljastui, että 16 käen pesäpoikasta oli kasvanut talitiaisen (*Parus major*) pesissä, 2 pesäpoikasta ja 2 lentopoikasta sinitiaisen (*Cyanistes caeruleus*) ja yksi pesäpoikanen töyhtötiaisen (*Lophophanes cristatus*) pesässä.

Oma aineistomme, perustuen havaintoihin ja poikasten siirtokokeisiin, todistaa myös talitiaisen kykenevän kasvattamaan käen poikasen pesästä lähtöikään. Havaintomme käsittävät myös ensimmäiset tunnetut tapaukset, joissa lintulaji on altistunut loisinnalle pesänvaltauksen seurauksena. Yllättäen talitiaisten ruokkimat käenpoikaset kasvoivat paremmin, jopa tiaisen omien poikasten joukossa, kuin yleisempien isäntälajien pesissä. Tiaisten loisinta-aste aliarvioidaan helposti, koska tutkimuksissa käytetään pönttöjä, joiden lentoaukko on liian pieni käen onnistuneelle loismuninnalle tai poikasen menestyksekkääseen pesästä poistumiseen.

Tuloksemme tukevat viimeaikaisia näkemyksiä siitä, että isännän sopivuus on paremmin kuvattavissa jatkuvana muuttujana, kuin kategorisena muuttujana (isäntä sopiva tai sopimaton). Käen isännänvalintaan vaikuttavien tekijöiden ymmärtäminen on puutteellista, koska tutkimukset käen poikasen ravinnosta, kasvusta ja eloonjäännistä ovat vähäisiä. Siksi kaikki aineisto on todella arvokasta ja tuo korvaamatonta lisämateriaalia tuleville meta-analyyseille.

References

Ahola, M., Laaksonen, T., Eeva, T. & Lehikoinen, E. 2009: Great Tits lay increasingly smaller clutches than selected for: a study of climate- and density-related changes in reproductive traits. — Journal of Animal Ecology 78: 1298–130.

Ammann, F. 1949: Junge Kohlmeisen (*Parus major*) und Blaumeisen (*Parus caeruleus*) im gleichen Nest. — Der Ornithologische Beobachter 46: 187–190. (In German)

Anderson, M. G., Moskát, C., Bán, M., Grim, T., Cassey, P. & Hauber, M. E. 2009: Egg eviction imposes a recoverable cost of virulence in chicks of a brood parasite. — PLoS ONE 4: e7725.

Curry-Lindahl, K. 1963: Våra Fåglar i Norden, IV. — Bokförlaget Natur och Kultur, Stockholm. (In Swedish)

Davies, N. B. 2000: Cuckoos, Cowbirds and Other Cheats. — T & AD Poyser, London.

Davies, N. B. & Brooke, M. L. 1989: An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. — Journal of Animal Ecology 58: 225–236.

De Mársico, M. C. & Reboreda, J. C. 2008: Differential reproductive success favours strong host preference in a highly specialized brood parasite. — Proceedings of the Royal Society B 275: 2499–2506.

Dolenc, Z. 1990: The young Cuckoo in the Great Tit nest. — Troglodytes 3: 18.

Erritzøe, J. 2000: Working Bibliography of Cuckoos and Turacos of the World. — J. Erritzoe, Christiansfeld.

Glutz von Blotzheim, U. N. & Bauer, K. M. 1993: Handbuch der Vögel Mitteleuropas. Vol. 13. — Aula, Wiesbaden.

Grim, T. 2006a: Cuckoo growth performance in parasitized and unused hosts: not only host size matters. — Behavioral Ecology and Sociobiology 60: 716–723.

Grim, T. 2006b: The evolution of nestling discrimination by hosts of parasitic birds: why is rejection so rare? — Evolutionary Ecology Research 8: 785–802.

Grim, T. 2008: Wing-shaking and wing-patch as nestling begging strategies: their importance and evolutionary origins. Journal of Ethology 26: 9–15.

Grim, T. 2011: Ejecting chick cheats: a changing paradigm? Frontiers in Zoology 8: 14.

Grim, T. & Honza, M. 1997: Differences in parental care of Reed Warbler (*Acrocephalus scirpaceus*) to its own nestlings and parasitic Cuckoo (*Cuculus canorus*) chicks. — Folia Zoologica 46*:* 135–142.

Grim, T., Rutila, J., Cassey, P. & Hauber, M. E. 2009a: The cost of virulence: an experimental study of egg eviction by brood parasitic chicks. — Behavioral Ecology 20: 1138–1146.

Grim, T., Rutila, J., Cassey, P. & Hauber, M. E. 2009b: Experimentally constrained virulence is costly for Common Cuckoo chicks. — Ethology 115: 14–22.

Grim, T., Samaš, P., Moskát, C., Kleven, O., Honza, M., Moksnes, A., Røskaft, E. & Stokke, B. G. 2011: Constraints on host choice: why do parasitic birds rarely exploit some common potential hosts? — Journal of Animal Ecology 80: 508–518.

Haftorn, S. 1981: Incubation during the egg-laying period in relation to clutch-size and other aspects of reproduction in the Great Tit *Parus major*. — Ornis Scandinavica 12: 169–185.

Haftorn, S. & Slagsvold, T. 1995: Egg covering in birds: description of the behaviour in tits (*Parus* spp.) and a test of hypotheses of its function. — Cinclus 18: 85–106.

Hauber, M. E. & Moskát, C. 2008: Shared parental care is costly for nestlings of Common Cuckoos and their Great Reed Warbler hosts. — Behavioral Ecology 19: 79–86.

Homoki-Nagy, I. Jr. 1977/1978: Kuckuck (*Cuculus canorus*) unter Kohlmeisenjungen (*Parus major*) aufgezogen. — Aquila 84: 106: 113. (In German)

Kempenaers, B., R. Pinxten & Eens M. 1995: Intraspecific brood parasitism in two tit *Parus* species: occurrence and responses to experimental parasitism. — Journal of Avian Biology 26: 114–120.

Kleven, O., Moksnes, A., Røskaft, E. & Honza, M. 1999: Host species affects the growth rate of Cuckoo (*Cuculus canorus*) chicks. — Behavioral Ecology and Sociobiology 47: 41–46.

Kleven, O., Moksnes, A., Røskaft, E., Rudolfsen, G., Stokke, B. G. & Honza, M. 2004: Breeding success of Common Cuckoos *Cuculus canorus* parasitising four sympatric species of *Acrocephalus* warblers. — Journal of Avian Biology 35: 394–398.

Knorre, D. von, Grün, G., Günther, R. & Schmidt, K. 1986: Die Vogelwelt Thüringens. — VEB Gustav Fischer Verlag, Jena.

Kroutil, O. 1965: O kukačce – *Cuculus canorus* L. — Živa 13: 233–235. (in Czech)

Lambrechts, M. M. *et al.* (55 coauthors) 2010: The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. — Acta Ornithologica 45: 1–26.

Löhrl, H. 1964: Mischgelege, Doppelgelege und verlegte Eier bei Höhlenbrütern (Gattung *Parus, Ficedula*). — Vogelwelt 85: 182–188. (In German)

Löhrl, H. 1979: Untersuchungen am Kuckuck, *Cuculus canorus* (Biologie, Ethologie und Morphologie). — Journal für Ornithologie 120: 139–173. (In German)

Loukola, O. J., Laaksonen, T., Seppänen, J.-T. & Forsman, J. T. 2014: Active hiding of social information from information-parasites. — BMC Evolutionary Biology 14: 32.

Mackenzie, J. M. D. 1950: Competition for nest-sites among hole-breeding birds. — British Birds 43: 184–185.

Mackenzie, J. M. D. 1954: Redstarts reared in tits' nests. — Scottish Naturalist 66: 146–154.

Makatsch, W. 1937: Der Brutparasitismus in der Vogelwelt. — Quelle & Meyer, Leipzig. (In German)

Makatsch, W. 1955: Der Brutparasitismus in der Vogelwelt. — Neumann Verlag, Radebeul. (In German)

Malchevsky, A. S. 1954: O vzaimootnosheniyakh kukushki (*Cuculus canorus*) i gorikhvostki (*Phoenicurus phoenicurus*) v period ikh razmnozheniya. — Vestnik Leningradskogo Universiteta 7: 3–18. (In Russian)

Martín-Gálvez, D., Soler, M., Soler, J. J., Martín-Vivaldi, M. & Palomino, J. J. 2005: Food acquisition by Common Cuckoo chicks in Rufous Bush Robin nests and the advantage of eviction behaviour. — Animal Behaviour 70: 1313–1321.

Merilä, J. & Wiggins, D.A. 1995: Interspecific competition for nest holes causes adult mortality in the Collared Flycatcher. — Condor 97: 445–450.

Michocki, J. 1971: Lęg mieszany bogatki (*Parus major*) i szpaka (*Sturnus vulgaris*). — Notatki Ornitologiczne 12: 78. (In Polish)

Moltoni, E. 1951: Le specie di uccelli nel cui nido vengono deposte in Italia le uova dal Cuculo. —Rivista Italiana di Ornitologia 21: 75–78. (In Italian)

Müller, C. 1889: Das Auffüttern junger Kuckucke. — Jäger-Zeitung für Böhmen und Mähren 5: 144. (In German)

Naef-Daenzer, B., Widmer, F. & Nuber, M. 2001: Differential post-fledging survival of Great and Coal Tits in relation to their condition and fledging date. — Journal of Animal Ecology 70: 730–738.

Peiter, W. 1892: Ornithologisches aus dem Hocherzgebirge. — Schwalbe 16: 31–32. (In German)

Perrins, C. M. 2008: Eggs, egg formation and the timing of breeding. — Ibis 138: 2–15. Oxford University Press, Oxford.

Perrins, C. & Cramp, S. 1998: The Complete Birds of the Western Palearctic on CD-ROM.

Poll, P. I. 1927: Die Vogelwelt von Metten und seiner Umgebung. — Verhandlungen der Ornithologischen Gesellschaft in Bayern 17: 376–411. (In German)

Puhlmann, E. 1914: Die Kuckuckswiege. — Ornithologische Monatsschrift 39: 232–234. (In German)

R Development Core Team. 2012: R: A Language and Environment for Statistical Computing. — R Foundation for Statistical Computing, Vienna, Austria.

Robinson, P. A., Norris, A. R. & Martin, K. 2005: Interspecific nest sharing by Red-breasted Nuthatch and Mountain Chickadee. — Wilson Bulletin 117: 400–402.

Røskaft, E., Moksnes, A., Stokke, B. G., Bičík, V. & Moskát, C. 2002: Aggression to dummy Cuckoos by potential European Cuckoo hosts. — Behaviour 139: 613–628.

Rutila, J., Latja, R. & Koskela, K. 2002: The Common Cuckoo *Cuculus canorus* and its cavity nesting host, the Redstart *Phoenicurus phoenicurus*: a peculiar cuckoo-host system? — Journal of Avian Biology 33: 413–419.

Scheenstra, W. 1964: Koekoeksjong in nest van Pimpelmees. — Het Vogeljaar 12: 338. (In Dutch)
Scheenstra, W. 1965: Koekoeksjong (*Cuculus canorus*) in nest van een Pimpelmees (*Parus caeruleus*). — Limosa 38: 87. (In Dutch)
Schmidt, E. 1956: Mischgelege von Kohlmeise (*Parus major*) und Trauerschnäpper (*Muscicapa hypoleuca*). — Ornithologische Mitteilungen 8: 35. (In German)
Seel, D. C. & Davis, P. R. K. 1981: Cuckoos reared by unusual hosts in Britain. — Bird Study 28: 242–243.
Šicha, V., Procházka, P. & Honza, M. 2007: Hopeless solicitation? Host-absent vocalization in the common cuckoo has no effect on feeding rate of reed warblers. Journal of Ethology 25: 147–152.
Šír, V. 1883: Kukačka. — Listy českého spolku pro ochranu ptactva v Praze 3: 7–13, 17–25, 34–36. (In Czech)
Slagsvold, T. 1998: On the origin and rarity of interspecific nest parasitism in birds. — American Naturalist 152: 264–272.
Soler, J. J., Møller, A. P. & Soler, M. 1999: A comparative study of host selection in the European Cuckoo. — Oecologia 118: 265–276.
Soler, M. 2002: Breeding strategy and begging intensity: influences on food delivery by parents and host selection by parasitic cuckoos. — In The Evolution of Begging (ed. Wright, J. & Leonard, M.L.): 413–427. Kluwer, Dordrecht.
Stevanović, A., Rašajski, J. & Gavrilov, T. 1989: Mimetičke karakteristike jaja i gnezdeći parazitizam obične kukavice (*Cuculus canorus* L.) u nekim krajevima Vojvodine. — Glasnik prirodnjačkog muzeja u Beogradu 43/44: 35–46. (In Serbian)
Stokke, B. G., Hafstad, I., Rudolfsen, G., Bargain, B., Beier, J., Campas, D. B., Dyrcz, A., Honza, M., Leisler, B., Pap, P. L., Patapavičius, R., Procházka, P., Schulze-Hagen, K., Thomas, R., Moksnes, A., Møller, A. P., Røskaft, E. & Soler, M. 2008: Host density predicts presence of Cuckoo parasitism in Reed Warblers. — Oikos 116: 913–922.
Sundkvist, H. 1979: Häckning av svartvit flugsnappare och rödstjärt i samma holk. — Vår Fågelvärld 38: 106. (In Swedish)
Sunkel, W. 1926: Die Vogelfauna von Hessen. — J. Braun Verlag, Eschwege. (In German)
Suzuki, T. N. & Tsuchiya, Y. 2010: Feeding a foreign chick: a case of a mixed brood of two tit species. — Wilson Journal of Ornithology 122: 618–620.
Tietze, D. T. & Klodwig, U. 2009: Tannenmeisen (*Parus ater*) ziehen Waldbaumläufer (*Certhia familiaris*) mit auf. — Ornithologischer Anzeiger 48: 150–154. (In German)
Thorogood, R. & Davies, N. B. 2013: Reed warbler hosts fine-tune their defences to track three decades of cuckoo decline. — Evolution 67: 3545–3555.
van Balen, J. H., Booy, C. J. H., Franeker J. A., Osieck, E. R. 1982: Studies on hole-nesting birds in natural nest sites. 1. Availability and occupation of natural nest-sites. — Ardea 70: 1–24.
Varga, F. 1994: Cuckoo observations around the source of the river Zagyva. — F. Varga, Salgótarján.
Vilks, K. 1973: Dažas ziņas par dzeguzi *Cuculus canorus* in Latvija. — Zooloģijas Muzeja Raksti 9: 7–14. (In Latvian)
Weinzierl, H. 1961: Mischgelege von Kohl- und Blaumeisen (*Parus major* und *P. caeruleus*). — Vogelwelt 82: 187–189. (In German)
Wesołowski, T. 2007: Lessons from long-term hole-nester studies in a primeval temperate forest. — Journal of Ornithology 148: S395–S405.
Wyllie, I. 1981: The Cuckoo. — Batsford, London.
Yang, C., Stokke, B.G., Antonov, A., Cai, Y., Shi, S., Moksnes, A., Røskaft, E., Møller, A. P., Liang, W. & Grim, T. 2013: Host selection in parasitic birds: are open-cup nesting insectivorous passerines always suitable Cuckoo hosts? — Journal of Avian Biology 44: 216–220.