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Caught on camera: circumstantial evidence for fatal mobbing of an avian brood parasite by a host

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Abstract. Hosts have evolved a multiplicity of defensive responses against avian brood parasites. One of them is mobbing behaviour which often includes direct contact attacks. These aggressive strikes may not only distract the parasites but may also be fatal to them, as documented by cases of dead brood parasite females found near host nests. Here, we present the first video-recording of a great reed warbler (*Acrocephalus arundinaceus*) host whose vigorous nest defence appears to directly lead to the death of a female common cuckoo (*Cuculus canorus*). We suggest that the chance of parasite death probably rises with the presence of unfavourable factors, such as water below the nest. Our observation supports previous suggestions that hosts may pose a lethal danger to their parasites.

Key words: ornithology, behavioural ecology, brood parasitism, nest defence, killing, video evidence

Interspecific brood parasites exploit the parental care of other species (Spottiswoode et al. 2012). Obligatory brood parasitism, when parasites always use hosts for rearing their young, has been observed in both invertebrates and vertebrates. For example, among invertebrates, such parasites (often referred to as social parasites, kleptoparasites or inquilines) have evolved in bees (Bogusch & Straka 2012), wasps (Cervo 2006) and ants (Mori et al. 2001), but also in lycaenid butterflies (Als et al. 2004), beetles (Trumbo 1994), aphids (Wang et al. 2008) and arachnids (Boulton & Polis 2002, Tizo-Pedroso & Del-Claro 2014). Among vertebrates, brood parasites have evolved mostly in birds (Soler 2017), but a rare example has also been described in a fish (Sato 1986, Reichard 2019).

Brood parasitism negatively affects host fitness because the host often loses all their progeny. Therefore, hosts have evolved a variety of defensive adaptations. One of these adaptations is aggressiveness directed against parasitizing females. Among insects, aggressive hosts may successfully drive a parasitic queen away, but conflicts can also escalate into a fight between host and parasite which may lead to the death of the parasite (Bogusch et al. 2006). Avian hosts can also fiercely defend their nests: they chase, mob and often attack the parasitic female by tearing out feathers and pecking the head and body (Gloag et al. 2013, Jelínek et al. 2020) in an attempt to impede the parasite from entering their nest and preventing her from laying an egg. There are several indirect pieces of evidence that these host attacks can occasionally result in the death of the parasite, with instances when parasitic females (Molnár 1944, Janisch 1948, Moyer 1980, Loflin 1982, Lorber 1985, Gloag et al. 2013) or even males

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(Loflin 1982) have been found dead under host nests. Although rare, this phenomenon has been observed, but never recorded, *in situ* (Yoshino 1999, Jackson & Kyne 2010, Mérő & Žuljević 2014). Here, we present the first video-recording of an avian host attack that lead to the death of the brood parasite attempting to parasitize a nest, supporting previous observations.

During the breeding season (May-June 2019), we video-recorded nests of great reed warbler (*Acrocephalus arundinaceus*) (hereafter GRW) hosts continuously during their egg-laying stage. Fieldwork was conducted in the South Moravian region of the Czech Republic, in a fish rearing area between Hodonín (48°51′ N, 17°07′ E) and Mutěnice (48°54′ N, 17°02′ E) where this host is heavily parasitized (Honza et al. 2020) by the common cuckoo (*Cuculus canorus*; hereafter cuckoo). In total, we recorded 64 visits of cuckoo females at 32 host nests (39 visits resulted in egg-laying). In 26 of these laying visits, we observed host mobbing behaviour and at 20 of them the mobbing included direct attacks on the cuckoo. Thus, aggressiveness directed against cuckoos is common by this host.

On the morning of May 17th, we found a freshly dead cuckoo female floating on the water surface approximately 20 m from a GRW nest (Fig. 1A) that was continuously video-recorded. After analysing the video-recording from this nest, we found the moment (video 1) when the cuckoo female visited the nest on May 16th at 19:03. During this visit, the cuckoo sat at the rim of the nest and immediately

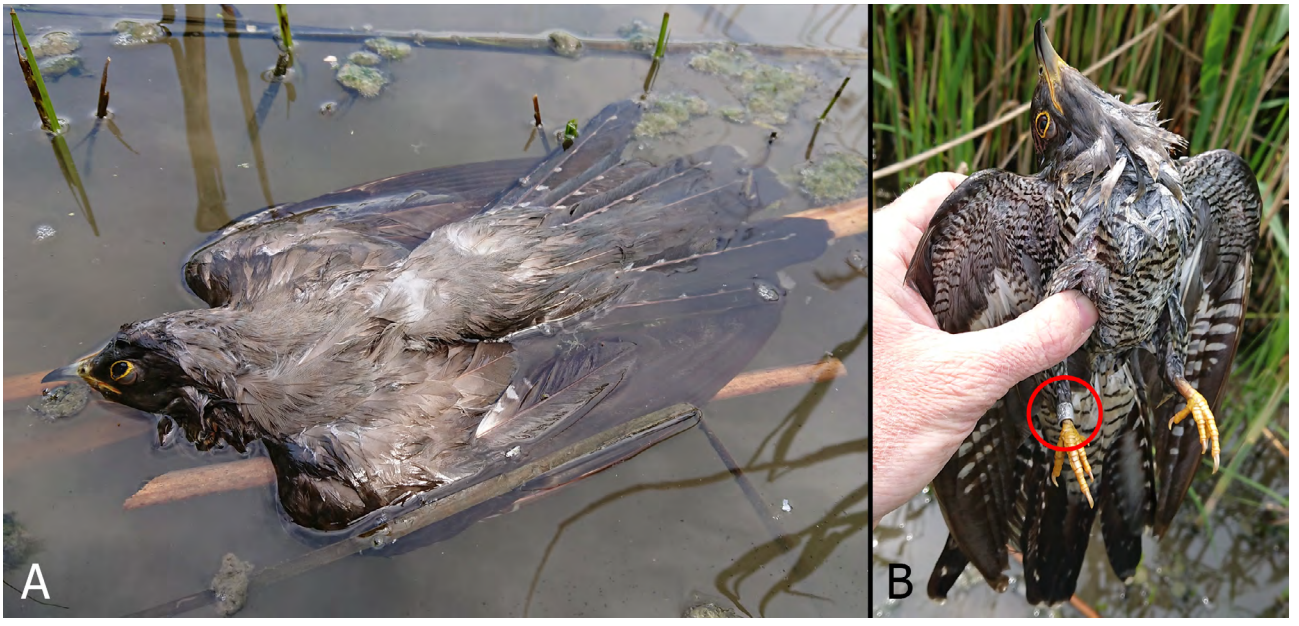

Fig. 1. Female cuckoo (ring no. GA 4235) found dead in the water with several feathers plucked out of her head but without any other obvious wounds (A) ca. 20 m from a great reed warbler nest on May 17, 2019. This bird was ringed (B) as a nestling and reared by great reed warblers in June 2010 in the same fish rearing area, (photos Petr Procházka).

Fig. 2. Screenshots from the video-recording in which a female common cuckoo was knocked down from the nest by the great reed warbler female. The nest contained three host eggs and the cuckoo removed one of them during the attacks by the host female. The female cuckoo did not lay her own egg. The second frame shows that the cuckoo had a ring on her right tarsus (in the red circle). For the whole video, see supplementary online material.

took one of three host eggs in her beak. During egg removal, the host female initiated an attack on the cuckoo female by landing on her back and immediately knocking her down from the nest. Following this incident, the cuckoo was out of view since our camera captured only a small area around the nest (Fig. 2). However, vigorously shaking reeds were visible for several minutes more, with both GRW hosts remaining near, but mostly below, the nest. When the reed stopped shaking (19:11), the GRW female, evidently disturbed, appeared at the nest several times and before finally resuming normal behaviour after about 20 minutes following the initial intrusion by the cuckoo. Since there was about a meter of water below the nest, we speculate that the shaking of reeds following the host's attack was a result of the cuckoo trying to escape from the water. However, we consider it probable that the host birds continued to attack the cuckoo while she was trapped in the water, similarly to that observed by Mérő & Žuljević (2014) in the same host-parasite system in Serbia.

For identification of individual hosts in the field, we use unique combinations of colour rings and a metal ring. However, as we ring cuckoos only occasionally, and only with one metal ring, it was not possible to identify the cuckoo in the current video reliably. Nevertheless, there are convincing reasons to indicate that the cuckoo captured on video was the same one we found dead in the water on the following day. First, the dead cuckoo was found near the nest where we video-recorded the incident (distance ca. 20 m) and there was no other active GRW nest in the proximity. Second, the condition of the dead cuckoo (freshly dead without any signs of decomposition; Fig. 1) corresponded to the timing of the filmed incident. Third, both the dead cuckoo and the video-recorded cuckoo females were a grey colour morph. Finally, both cuckoos had a metal ring on the right tarsus (Fig. 1B and Fig. 2). Interestingly, the dead cuckoo was ringed as a nestling that had been reared by GRWs in June 2010 in the same area in which it subsequently died. Together with another rufous cuckoo female mentioned by Koleček et al. (2019), this information provides rare evidence that cuckoo females parasitize the same host species that reared them.

Such extreme outcomes of host-parasite interactions are probably rare in the GRW since we have studied this system for more than 20 years and have encountered dead cuckoos only twice previously. The other dead female cuckoo, also found below a GRW nest, probably died in late May or early June 2018 (GRW breeding period) because we found it at an advanced stage of decomposition on June 9, 2018. This dead cuckoo was ringed in the same area in 2017 as an adult.

Our video-recordings from 2019 also suggest that cases when the parasite dies in response to host aggression occur only rarely. We observed that most cuckoos that come under host attack escape by flying upwards from the nest (13 of 20 cases). When cuckoos escape below the nest, they are at risk of drowning since GRWs usually breed above water. Although the GRW is one of the most aggressive hosts of the cuckoo (Moskát 2005, Požgayová et al. 2013, Jelínek et al. 2020), we propose that water below the nest is an important factor that may increases the likelihood that aggressive mobbing by the host results in the death of the cuckoo through drowning or hypothermia. While we were not able to determine the cause of death in the dead cuckoo, we ascertained that although the cuckoo had several plucked feathers on its head, there were no obvious wounds on the body. Drowning as a cause of death is also supported by the fact that dead female cuckoos have been mostly found (7 out of 8 cases) under GRW nests (Molnár 1944, Janisch 1948, Mérő & Žuljević 2014, this study, but see Yoshino 1999). However, it is important to note that this finding may also reflect a bias since cuckoo research has often focused on the GRW which is an important and heavily parasitized host in Europe (Trnka & Prokop 2011, Mérő et al. 2015, Zölei et al. 2015, Šulc et al. 2019).

Three other cases of dead brood parasites have been reported from other avian host–parasite systems; a shiny cowbird (*Molothrus bonariensis*) female was found impaled on a thorn below the nest of its chalk-browed mockingbird (*Mimus saturninus*) host in Argentina (Gloag et al. 2013); a lesser honeyguide (*Indicator minor*) female was found dead in the nest hole of a black-collared barbet (*Lybius torquatus*) host in Tanzania (Moyer 1980); and an eastern koel (*Eudynamys orientalis*) was observed to be killed by three little friarbirds (*Philemon citreogularis*) and a black butcherbird (*Melloria quoyi*) in Australia (Jackson & Kyne 2010). In the first two cases, the parasitic females had fully developed eggs in their oviducts, suggesting their parasitic intentions, but the eastern koel was in nonbreeding condition. In the first case, it is presumed that the cowbird

female was pushed onto the thorn by the weight of the attacking mockingbirds (Gloag et al. 2013). In the second case, the female honeyguide was in a battered condition with most of its tail feathers plucked out and its back bruised, suggesting a fight with the host (Moyer 1980). In the third case, a group of four birds of two species (probably both hosts) attacked the eastern koel. This high number of attackers might have reduced the chances of the parasite escaping. Since these parasite deaths are the only ones reported in these host-parasite systems, it is probable that they are also infrequent.

From the examples presented, it seems that the probability of parasite death rises with the presence of unfavourable factors, such as the occurrence of sharp thorns close to the nest, or when the parasite is trapped during host attacks. These are analogous to the occurrence of drowned cuckoos in water below host nests. Despite these circumstances, it clear that host aggression is the primary explanation for the death of parasites at host nests. Indeed, all reported cases occurred in hosts that actively defend their nests. Notably, we observed that at both nests where we found dead cuckoos, host GRW were unusually aggressive and even attacked researchers during daily nest checks. This behaviour is not typical in this species and may, therefore, represent an adaptive escalation of front-line defence against brood parasitism in a region of high rates of parasitism. Moreover, it has been observed that some well-armed hosts, such as the bull-headed shrike (*Lanius bucephalus*), may kill parasites directly (Yoshino 1999), implying a higher risk of parasitizing these hosts.

Although it does not seem that host mobbing can always prevent brood parasites from reaching a nest to parasitize it (Gloag et al. 2013, Jelínek et al. 2020), it has been shown that more aggressive individuals in a host population suffer lower brood parasitism (Fiorini et al. 2009, Welbergen & Davies 2009). Our video-recording, together with evidence from other published studies, illustrates that host aggressiveness has the potential for a fatal outcome for parasitic females. Furthermore, the nests where we found dead cuckoos subsequently stayed unparasitized and hosts raised their own chicks. This result suggests that host mobbing may effectively save hosts from parasitism and the fitness costs associated with rearing parasitic offspring.

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Supplementary online material

Video-recording (video 1) is available at (https://www.ivb.cz/wp-content/uploads/JVB-vol.-69-1-2020-Sulc-et-al.-video1.mp4).