Cuckoo–Host Coevolutionary Interactions Across All Breeding Stages: Unusual Ecological Setting of a Cavity-Nesting Host

16

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Abstract

The great majority of brood parasitism studies focused on a single ontogenetic stage, typically egg stage, and on open-nesting hosts, especially those of the common cuckoo. Using extensive data from the cuckoo's only known regular cavity-nesting host, the common redstart, we highlight the importance of a comprehensive approach when all ontogenetic stages are studied. In contrast to open-nesting hosts, only minority of the cuckoo eggs are a threat to redstart hosts: most are laid outside the host nest cup and perish. Contrary to previous claims, we found that the impact of parasitism per host nest was virtually the same between this only regular cuckoo cavity-nesting host and a typical open-nesting host (the reed warbler): in both species, fitness of an average non-parasitized host nest was by an order of magnitude higher than fitness of an average parasitized host nest. This was partly because of uniquely low eviction success of cuckoo chicks and resulting cohabitation of parasite and host progeny in mixed broods. Data from post-fledging period, which remains the least known stage of parasite–host coevolution in any study system globally, were crucial because they showed that data from nestling period greatly overestimated cuckoo fitness. We suggest that metareplication of these approaches (i.e. integrative study of laying, incubation, nestling, fledgling and migration stages) across various parasite–host systems is the most important task for future coevolutionary studies in the context of brood parasite–host coevolution.

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16.1 Introduction

Just like in any field of science, studies of brood parasite–host coevolution focus on a few traditional model systems. Therefore they necessarily neglect other, consequently underused, models. Naturally, researchers also pay most attention to life stages that are methodologically easier to deal with. Therefore they inevitably create knowledge accumulation bias against other life stages.

Our aim in this contribution is twofold. First, we summarize literature data and our detailed field studies of parasite–host interactions in common redstarts (*Phoenicurus phoenicurus*, hereafter redstarts), the single documented regular cavity-nesting hosts of common cuckoos (*Cuculus canorus*, hereafter cuckoos) in Europe. We highlight the importance of extending research to less known brood parasite–host systems and specifically to those differing ecologically from typical (open nesting) hosts. Second, by addressing parasite–host interactions across all life stages, we illustrate how integrating data across life stages can improve our understanding of parasite–host arms races (Dawkins and Krebs 1979).

Redstart males are among the most colourful and attractive European birds, while females are drab. Such clear sexual dimorphism is unusual among cuckoo hosts and provides a clear logistic advantage over typical cuckoo hosts which are mostly monomorphic, given that it allows studying any parasite–host interactions at the level of individual sexes even without marking the birds (Grim et al. 2009a).

The redstart is the main cuckoo host in Finland (Haikola and Rutila 2008; Mikulica et al. 2017), and its congeners serve as cuckoo hosts in Asia (Yang et al. 2013, 2016). The redstart is a suitable cuckoo host since it feeds its chicks predominantly with invertebrate diet and it is fairly common. However, unlike other frequently used cuckoo hosts, the redstart is a cavity nester. Based on nest card records from the Helsinki Museum of Natural History, 50% of all the cuckoo eggs found in Finland (1931–2000) were in the redstart nests ($n = 127$; Rutila 2004).

Scientists classified cavity nesters as unsuitable cuckoo hosts (e.g. Davies and Brooke 1989), since many cavities are too small for the cuckoo female to lay its eggs effectively or the young cuckoo to fledge successfully. Löhrl (1979) showed that cavity entrances with diameters <50 mm are too small for young cuckoos to fledge. Redstarts however use a variety of different types of natural cavities and crevices, including those with large entrances (von Haartman 1969). This makes redstarts more vulnerable to cuckoo parasitism compared to strict cavity nesters (von Haartman 1981; Grim et al. 2014; Grim 2016; Liang et al. 2016).

Our study site is located in Ruokolahti, South Karelia in Southeast Finland (Samaš et al. 2016; hereafter, data provided without a bibliographic reference are unpublished results). All the results we present here are from several partly isolated study plots spread over the area of 25 × 7 km (Fig. 1, Samaš et al. 2016). This spatial metareplication decreases risks of pseudoreplicated sampling from the same females which is a common problem in typical studies which are based on spatial sampling 10–20 times smaller (details in Samaš et al. 2016). The population has been monitored over three decades (since 1983, J. Haikola, pers. comm.). All redstarts we studied bred in nest boxes with large entrances (60–80 mm, mostly 70 mm), which were created to reflect the situation in natural cavities (for details see Grim and Samaš 2016; Samaš et al. 2016).

Although country-wise parasitism rate is 3% (Rutila 2004), the parasitism rate in our study area is 33% (yearly variation: 17–50%), similarly to two other intensely studied populations in Joensuu (21%, yearly variation: 0–58%; Rutila et al. 2002) and Oulu (31%, yearly variation 13–47%; Thomson et al. 2016). This variation among sites is remarkably low compared to other hosts (for examples see Samaš et al. 2016). This may reflect very homogeneous breeding habitat of redstarts, i.e. rather open cultivated coniferous forests.

We have collected detailed data throughout the redstart and cuckoo breeding cycle from egg laying (Samaš et al. 2016), through incubation (Rutila et al. 2002), nestling (Grim and Samaš 2016) and post-fledgling periods (this chapter) to migration to wintering grounds (Vega et al. 2016). Further, we addressed questions at several levels of biological complexity, from chemical (Igic et al. 2012) and structural levels (including methods of material sciences; Igic et al. 2011), through molecular (Fossøy et al. 2016), to behavioural levels (Grim et al. 2009a, b). We also quantified fitness for parasites and hosts in respect to the constraints related to cavity nesting (this chapter). This has been done rarely with similar extent for any brood parasite–host system. We believe that such complex and comprehensive approach is beneficial because some conclusions (see below) could not be reached without integrating results from several life stages (as advocated by Grim 2007a and Grim et al. 2011) or levels of biological organization (Igic et al. 2012).

16.2 Laying Stage: Nest Design Constraints

Strikingly, from the 213 cuckoo eggs, that we have found over 11 intensely studied breeding seasons (2006–2016), only 36% were found inside the host nest cup (Samaš et al. 2016). The rest was found inside the nest box but at the nest rim (54%) or even on the ground under the nest box (5%) (Samaš et al. 2016). Some eggs were even found in incomplete nests (5%) (Samaš et al. 2016). Were these eggs ejected by hosts or are they the result of imperfect laying by female cuckoos?

We tested this hypothesis directly. For the first time, we video recorded a cavity-nesting hosts during the egg-laying period. Previously, the egg-laying behaviour of cuckoos has been reliably documented only rarely and only in open-nesting hosts (Wyllie 1981; Moksnes et al. 2000; Andou et al. 2005). We found that all eggs found outside the nest cup on the nest rim ($n = 12$) were mislaid by cuckoo females and did not result from redstart egg ejection. Redstarts ignored all cuckoo eggs, both those laid outside the nest cup (above) and those laid inside it ($n = 14$) (Samaš et al. 2016). The video recordings lasted for similar periods (mean = 5 days) after the cuckoo laid her egg as is the standard period used in experimental studies to score cuckoo host individuals as acceptors or rejecters (6 days; Moksnes et al. 1991; Grim et al. 2011).

16.3 Laying Stage: Host Front-Line Defences

Aggression against adult cuckoo represents the front line of host defences against brood parasitism. However, *Lanius* shrikes and the great reed warblers (*Acrocephalus arundinaceus*) are the only regular cuckoo hosts that were documented to harm adult parasites (Trnka and Grim 2013). Similarly to some other hosts (Moksnes et al. 2000), redstarts also showed low and ineffective nest defence, i.e. they were unable to chase laying cuckoo females away. Only at 15% nests ($n = 26$) redstart pairs showed any response against a cuckoo dummy (the dummy was placed at the top of the nest box during the egg-laying stage for 60 min). Responses included alarm calls and dives above the dummy. As a control, we exposed redstarts to a mistle thrush (*Turdus viscivorus*) dummy; none out of four tested pairs showed any response. Thus, redstarts seemed to recognize the cuckoo as an enemy but their responses were weak.

By video recording the cuckoo laying attempts, we directly estimated redstart aggression levels under natural conditions. Redstarts showed some responses towards female cuckoos, mainly giving alarm calls (at 17% of the video-recorded nests, $n = 46$). This proportion is virtually the same as that observed during dummy experiments, which suggests that dummy experiments well reflect the biological reality in this host species.

Overall, across host species, egg rejection rates and dummy aggression rates correlate positively (Moksnes et al. 1991). Low aggression combined with low egg rejection rates of natural parasite eggs (11% across 5 populations, all rejections by desertion; Samaš et al. 2016) in redstarts fits well these interspecific patterns.

16.4 Incubation Stage: Perfect Mimicry

Redstart-cuckoos strikingly differ from majority of other gentes of the common cuckoo in having immaculate eggs (but see Fuchs 1957; Yang et al. 2010). The redstart-cuckoo eggs are plain blue (Fig. 16.1a), only rarely (6%, $n = 54$ eggs) contain sparse and tiny rusty spots (Fig. 16.1b; see also Čapek 1896). Host redstart clutches (18%, $n = 110$) also contain rusty spots at variable proportion of eggs within a clutch (subsample of clutches with at least some spotted eggs: 17–100%, mean = 73%).

Blue cuckoo eggs represent a perfect match of host redstart eggs (Fig. 16.1a). This is irrespective of the assessment method, be it a naked human eye (Moksnes et al. 1995), spectrometry (Igic et al. 2012) or visual modelling (Avilés 2008). Surprisingly, Stoddard and Stevens (2011) reported no overlap in background egg colour of blue cuckoo and blue redstart eggs. What was the cause of this outlying result is unclear. Based on our personal field experience with natural freshly laid eggs (which were also used by Igic et al. 2012), we note that while the inset photo of

Fig. 16.1 (**a**) Immaculate blue cuckoo eggs represent one of the highest levels of mimicry achieved by any cuckoo host race (top right-hand side egg is the cuckoo's). (**b**) Rare eggs with rusty spots on plain blue background (a redstart egg is pictured; cuckoo eggs may show similar spots). (**c**) Cuckoo chick evicted two redstart chicks and one egg but currently still shares the nest with four redstart chicks and another egg. Photo credits: T. Grim

the redstart egg in Fig. 1 in Stoddard and Stevens (2011) looks typical, the redstart-cuckoo egg is aberrant and not representative as for both background colour and the presence of faint spots. Therefore we suspect that Stoddard and Stevens' (2011) conclusion on redstart-cuckoo mimicry is a by-product of using old museum eggs.

Although host redstarts possess cognitive abilities to eject nonmimetic experimental eggs, they never ejected any naturally laid cuckoo eggs at any of several study sites across Fennoscandia ($n = 330$ eggs from 4 populations; Samaš et al. 2016). This is not because redstarts would be puncture-ejecters, and increased thickness of cuckoo eggshells would prevent them to break the parasite eggs (Igic et al. 2011)—redstarts are grasp-ejecters as inferred indirectly from ejection of hard artificial models (Hauber et al. 2014; Dinets et al. 2015) and directly from video recordings (Samaš et al. 2016). This implies that it is indeed the parasite–host egg similarity which is responsible for complete absence of ejection of natural cuckoo eggs (see also Hanley et al. 2017). These lines of evidence and quantitatively very similar results (spectrometry, visual modelling) of Avilés (2008) and Igic et al. (2012) lead us to conclude that redstart-cuckoo eggs indeed do represent an example of perfect mimicry.

The uniqueness of the plain blue egg phenotype of redstart-cuckoos has a genetic basis (Fossøy et al. 2016). Cuckoo females that produce blue eggs form a ~2.6 Myr old monophyletic lineage as for both their mitochondrial DNA and W-chromosome DNA. In contrast, they do not differ from other gentes as for nuclear DNA which confirms that males mate irrespective of their female partner's genetic origin. These data also suggest that genes controlling blue egg colour are at female W chromosome.

Cuckoo eggs show perfect colour mimicry (Igic et al. 2012) thus pre-empting egg ejection as a viable host defence strategy (Thomson et al. 2016). This explains why the only redstart response to cuckoo parasitism is nest desertion (also in other populations; Rutila et al. 2006; Samaš et al. 2016). Specifically, in our study population, nest desertion rates in naturally parasitized nests were statistically significantly higher (19%, $n = 43$) than desertion rates in both naturally non-parasitized nests (6%, $n = 89$) and nests experimentally parasitized by us (1%, $n = 73$) (Samaš et al. 2016). This suggests that desertion is a specific defence against natural parasitism (but not a specific response to artificial parasitism, see above) and that a sight of a laying cuckoo female might be an important additional cue that alerts hosts and triggers their egg discrimination behaviour (see also Moksnes et al. 2000). However, experimental data are needed to test these suggestions directly.

How perfect colour mimicry could have evolved if the ejection rate of even nonmimetic eggs is only intermediate? Mimicry is not a result of current egg rejection rates but of past host egg discrimination (Davies 2000). If a parasite evolved perfect mimicry, then hosts that attempt to reject parasite eggs might suffer egg rejection costs and errors (Samas et al. 2014; Stokke et al. 2016) which leads to lower fitness of rejecter alleles and may translate into a decline of host anti-parasite adaptations (Davies 2000). Thus, at the egg stage, redstarts might have reached stage 4 in a coevolutionary sequence depicted by Davies (2000, p. 119), i.e. cuckoo egg mimicry that evolved due to *past* redstart egg rejection is now so precise that they force *current* redstarts to accept today's cuckoo eggs (Avilés et al. 2005).

However, this does not mean that redstart-cuckoo coevolution reached a dead end. The presence of rusty spots on some redstart eggs (Fig. 16.1b) may represent a new line of defence whereby hosts diverge from ancestral egg phenotypes (both their own and mimetic parasite) to facilitate egg recognition and rejection (as generally hypothesized before; Davies 2000). Preliminary analysis ($n = 47$ parasitized nests) did not find covariation between nest desertion (yes/no) and the presence (yes/no) of rusty spots on cuckoo eggs (Fisher's exact test: $p = 1.00$) or redstart eggs (Fisher's exact test: $p = 0.39$); however, only three nests in this dataset were deserted leading to low power of the analysis.

16.5 Nestling Stage: Unsuccessful Evictions and Mixed Broods

Before hatching, cuckoo and redstart eggs were incubated for very similar time periods (mean ± SD: 13.2 ± 0.2 and 13.7 ± 0.2, respectively, $n = 51$ clutches) (Samaš et al. 2016). This contrasts with typical cuckoo hosts where the cuckoo egg is incubated for 1–2 days shorter period than a host clutch (Davies 2000). Also in absolute terms, the incubation period of redstart-cuckoo eggs is unusually long (cf. 11.6 days in reed warbler nests; Wyllie 1981). This has fundamental consequences: every second cuckoo egg hatched on the same day or even later than redstart eggs. This unusual pattern, perhaps augmented by low concentrations of energy reserve lipids in cuckoo eggs (Igic et al. 2015) and nest cup design (see further), then translates into uniquely low success in killing host offspring by the cuckoo (Fig. 16.1c).

The hallmark of the common cuckoo biology is the instinct shown by the young parasite to evict its nestmates (Wyllie 1981). Cuckoo chicks virtually always succeed in pushing all host's eggs and nestlings over the nest rim, managing to quickly "clean" the nest of host offspring in the nests of open-cup breeding hosts (Honza et al. 2007 and references therein). The redstart-cuckoos represent a striking exception to this rule: redstart-cuckoo chicks often fail to evict some host progeny (20% under natural conditions; Samaš et al. 2016; Thomson et al. 2016), and the process of eviction is prolonged (even a week after hatching) and arduous (decreasing cuckoo chick growth by cc 25%; Grim et al. 2009b; see also Anderson et al. 2009). Such a prolonged eviction instinct in redstart-cuckoos might even be an adaptation against the cavity-nesting habits of its host: nest cup design (steep inner walls of redstart nests) decreases the chances that the cuckoo will succeed in its eviction attempts (Fig. 5 in Grim et al. 2009b; see also Honza et al. 2007; Grim et al. 2011). Therefore, we hypothesize that cuckoo individuals with prolonged eviction instinct might reach higher fitness than those whose eviction instinct dissipates earlier. However, the timing of eviction instinct dissipation remains unknown in all hosts other than the redstarts (because the data from other hosts were always observational; Honza et al. 2007) and should be tested experimentally in the future (as in Grim et al. 2009b).

Although in all cases the cuckoo has an open space where to push host offspring (typically the area between the nest cup and the front wall of the box), in some cases the nest cups are built just next to the rear wall of the box with little space to hold evicted eggs and chicks which may, after having been evicted, even fall back into the nest cup. Cuckoo chicks are blind for the most of the eviction period (Wyllie 1981) and seem to evict in random directions (but this was not tested so far). Thus, we hypothesize that the location of the nest cup relative to the box walls may affect cuckoo eviction success, growth and survival.

Although cavity nesting may bring some eviction costs that do not materialize in open nests (see above), it may prevent other costs associated with open nest design. In open-cup nests, cuckoo chicks sometimes evict themselves and die; although this happens rarely, the phenomenon was reported from several host species (Wyllie 1981). We video recorded a case when a cuckoo chick climbed out of the nest cup, crawled ca. 15 cm route across the nest box interior and finally climbed back into the nest cup (Grim et al. 2009b). Additionally, three cuckoo chicks (two in Finland, one in Czech Republic) repeatedly evicted themselves while evicting redstarts even though the observer returned them into the nest cup each time; all these self-evictors finally died, probably due to exhaustion and hypothermia (P. Samaš, M. Kysučan, pers. comm.). Thus, cavity nesting prevents self-eviction and may increase cuckoo survival prospects.

Surprisingly frequently (25%, $n = 44$ parasitized broods) we also recorded cases when an evicted redstart chick (or several chicks) fell back into the nest cup, even after spending hours in a distant part of the nest box, several cm from the rim of the nest cup (and therefore ignored by its parents). Such cases increased the workload for the cuckoo chick which was forced to evict the same individual host chicks repeatedly. In some cases, the cuckoo was unable to evict the returning host chick again and consequently shared the nest with it (experimentally manipulated nest sharing has a strong negative effects on cuckoo—but not redstart—growth and survival; Grim et al. 2009a).

Such complex temporal dynamics of brood composition in the nest cup are impossible in open-cup nests. One could speculate that cavity nest environment creates a potential for natural selection to favour more active host chicks (more crawling, even undirected one, would increase chances of accidentally climbing back into the nest cup) or even an ability in host chicks to eavesdrop on begging calls from the nest cup to find the way directly back into the only place where chicks are recognized as such by redstarts or any other passerines (Grim 2006c; see also p. 81 in Mikulica et al. 2017).

Although evicting cuckoo chicks suffer reduced growth during the eviction phase, they are able to compensate for this detrimental effect of their eviction efforts later (Anderson et al. 2009; Grim et al. 2009b). They increase their growth rate, perhaps via exaggerated begging (compared to solitary chicks, but this needs to be tested), and manage to reach similar fledging masses and success as solitary chicks (i.e. chicks that were relieved from the eviction costs experimentally; Grim et al. 2009a). Still, they fledge significantly later but the effect size is small (1 day later than solitary cuckoos). These plastic growth patterns do not seem to be a specific adaptation to cavity hosts as they were found in open-nesting hosts (Anderson et al. 2009; see also Geltsch et al. 2012).

Both observational (Rutila et al. 2002) and experimental data (Grim et al. 2009a) from redstart-cuckoos revealed that cuckoos are extremely poor competitors for parental care as it has also been showed in other host species (Martín-Gálvez et al. 2005; Grim 2006b; Hauber and Moskát 2008; Grim et al. 2011). Even a single cohabiting host chick inflicts massive negative effects on cuckoo chick growth (Geltsch et al. 2012). Cuckoos in mixed broods (i.e. sharing care with host chicks) show dramatically lower fledging masses (reaching only 74% mass of solitary cuckoos), delayed fledging (by 15% later than solitary cuckoos) and extremely poor survival till fledging (only 44% success of solitary cuckoos; estimates based on data from Grim et al. 2009a).

16.6 Nestling Stage: Behaviour, Host Provisioning and Unusual Diet

When begging, older cuckoo chicks perform asymmetrical wing shaking (Grim 2008): they raise single wing at a time and shiver it when fosterer arrives at the nest. Similarly to cuckoo chicks in reed warbler nests, preliminary observations show that also redstart-cuckoos wing shake only when fosterers are feeding them and mostly shake the wing towards the provisioning “parent” (see also Tyller et al. 2018). This suggests that asymmetrical wing shaking might be a species-level trait (i.e. not specific to a reed warbler-cuckoo gens where it was documented: Grim 2008) that is expressed in both open and cavity nests.

Avian chicks typically respond to parental alarm calls by reducing begging. Davies et al. (2006) showed that reed warbler-cuckoo chicks respond specifically to reed warbler alarms, and additionally to ceasing calling, the cuckoos show a specific response of gaping which might be a defensive action. In contrast, redstart-cuckoos (and even redstart chicks) do not respond to host alarm calls (Davies et al. 2006). The reason for this lack of responsiveness to parental alarm calls might be safe nesting site in cavities where predation rates are small compared to open-cup nests.

Redstart females generally invested more in the care for cuckoo chicks: compared to males, they provided ca. 50% more of their feedings to the cuckoo than to their own chicks in mixed broods (29% in females vs. 21% in males; Grim et al. 2009a; for a similar conclusion in a different cuckoo host see Požgayová et al. 2015). Both females and males increased proportions of their feeding to the parasite throughout the nestling period (Grim et al. 2009a). This suggests that both parents increased their provisioning in response to increasing body size ratio between the cuckoo vs. host chicks.

Cuckoo diet was rarely analysed in detail among cuckoo gentes with majority of the data confined to *Acrocephalus* warblers (Grim and Honza 2001 and references therein). Similarly to other hosts, we found that redstart-cuckoo chick diet is numerically dominated by insects and spiders (data from video recordings of hosts feeding redstart broods, $n = 87$ nests, and cuckoo nestlings, $n = 80$ nests; Grim et al. 2017). However, both redstart-cuckoos (at 11% of nests) and host's own broods (at 5% of nests), were also fed with berries. Previously, fruits were reported in the diet of cuckoo chicks only once (Martín-Gálvez et al. 2005). Both cuckoos (at 5% of nests) and host's own broods (at 7% of nests), were also fed with lizards, which were never before reported in the cuckoo nestling diet (Grim et al. 2017). Lizards were numerically rare ($<1\%$ of food items in both cuckoo vs. redstart chick diet), but their body size was ca. three orders of magnitude higher than any other items. Therefore, the mass dominance and, by implication, energy content of lizards were in fact much larger than mere numerical dominance would suggest.

This unique diet composition had fitness consequences for cuckoos: parasite, but not host chicks, fed with fruits and lizards had lower fledging masses (by 20% in both fruit- and lizard-fed cuckoos) and prolonged nestling periods (again by 20%). Although fledging success was not affected by diet composition (only invertebrate fed: 92%; also plant and vertebrate fed: 82%), the fledgling survival could still be decreased as a negative effect of lowered fledgling mass on post-fledging survival is the norm in birds (see also below). Thus, cuckoo chicks can digest plant and vertebrate material, but such unusual dietary components might cause ontogenetic stress (i.e. slower growth and delayed fledging). These results for the first time show that food composition may affect fitness of parasites not only at the host species level (Yang et al. 2013) but also at the level of individual host pairs. Although host diet selection most likely does not evolve as a specific anti-parasite defence in general (see discussion in Yang et al. 2013), it could be an important general life-history trait that affects brood parasite fitness (Grim et al. 2011).

Cuckoo chicks raised alone, i.e. after successfully evicting redstart progeny (thus not competing with host chicks), reached higher fledging masses (sometimes over 120 g; Grim et al. 2009a; Grim and Samaš 2016) than in any other host studied so far (reviewed in Grim 2006a). For example, at fledging a redstart-cuckoo can weigh twice as much as reed warbler-cuckoo (e.g. 60 g; Grim 2006a). This may be a consequence of cavity nesting: cavities protect chicks from inclement weather and partly release parents from the stressful influences of perceived predation risk (Zanette et al. 2011) (but not perceived parasitism risk, see Tolvanen et al. 2017). The length of the nestling period (20.6 ± 0.4 days, $n = 18$; Grim and Samaš 2016) was within the range (18–22 days) of previously reported values across cuckoos raised by 14 host species (reviewed in Grim 2006a; Grim and Samaš 2016). Additionally, the new redstart data support previous conclusions (Grim 2006a) that host species body mass does not influence either cuckoo chick fledging mass or age (Grim and Samaš 2016).

Longer nestling period of cuckoos (21 days) than redstarts (14 days) may lead to negative fitness consequences for the cuckoos. We detected two cases of mixed broods ($n = 16$) where both parents (or female, because males often stop to care for their brood before it fledges) focused on their own fledged brood and stopped to visit the nest where the cuckoo was still too young to fledge. Such cuckoo chicks perished due to starvation (Fig. 29.1c). It remains to be determined experimentally if such chick desertions are due to preprogrammed length of parental care in at least some redstart individuals (cf. Grim et al. 2003; Grim 2007b).

16.7 Fledgling Stage: Enigmatic in General

Although the post-fledging period and transition to independence are critical periods in the life of birds, these important aspects of parasite biology remain virtually unknown in any brood parasites (but see Soler et al. 2014 and references therein). In the common cuckoo, they have been studied only once. Wyllie (1981) reported that cuckoos fledged from reed warbler nests become able to fly clumsily 4–5 days after leaving the host nest and became independent on average 16 days after fledging. Host reed warbler fledglings reach independence earlier, after 10–14 days on average (Wyllie 1981). Data from a cuckoo chick attended by the chaffinch (*Fringilla coelebs*) showed quantitatively the same patterns (Tyller et al. 2018).

In contrast, our data (Kysučan et al., in prep.) show that at least some cuckoos fledged from redstart nests are able to fly immediately after departing from the nest (30%, $n = 10$) and can fly remarkably well—even directly up to forest canopy! This may be because some redstart-cuckoo chicks have a longer nestling period that allows cuckoos to mature more than in nests of other hosts (Grim and Samaš 2016). However, the majority (70%, $n = 10$) of the redstart-cuckoo fledglings observed by us mostly crawled in the herbaceous layer for the first 2–3 days after leaving the host nest and started to fly clumsily only afterwards. Surprisingly, radio tracking of young showed very similar lengths of post-fledging periods in both redstarts (18.5 ± 1.0 days, $n = 10$) and cuckoos (17.3 ± 0.8 days, $n = 10$).

Radio tracking of cuckoo fledglings revealed that post-fledging survival of cuckoo chicks that shared a nest with redstart chicks was 0% ($n = 5$; post-fledging survival to independence of cuckoos that were reared alone: 45%, $n = 11$; Kysučan et al. in prep.). This contrasts with the fledging success rates of cuckoos from experimental mixed broods (44%, $n = 9$; Grim et al. 2009a). Because all cuckoos that fledged from mixed broods seem to die within the first week after fledging (but see the low sample size), the nest sharing provides the strongest possible selection pressure on the maintenance of eviction instinct in cuckoo chicks in any host nests.

This finding also highlights the crucial importance of studying parasite–host interactions across all breeding stages (see Grim et al. 2011): without the data from post-fledging period, we (Grim et al. 2009a) severely underestimated the negative effects of cohabitation with host chicks for the parasite.

16.8 Post-independent Stage: Migrating Parasites

Satellite tracking (Vega et al. 2016) showed that first-year redstart-cuckoos initiate their migration the whole month after adults have already departed (means: August 14 vs. July 11). Young differed from adults in slower and less consistently directed movements after leaving the breeding grounds. Despite different directions and extensive crossings of the Baltic Sea (3 out of 5 fledglings) at the initiation of migration, the young independently arrived to similar wintering area in Angola ($n = 1$ fledgling surviving till arrival at wintering grounds).

The redstart-cuckoos thus provide the first direct evidence on migration route of any young common cuckoos and confirm for the first time that naïve parasites are able to reach correct wintering areas independently, solely via an innate migration programme (Vega et al. 2016). This may not hold in other brood parasites where there is a contact between adult parasites and their fledglings, creating a potential for joint migration of young and adult birds (Soler and Soler 1999).

16.9 Parasite Fitness: Little Effects of Cavity Nesting

Cavities have many disadvantages from the cuckoo's point of view. Two-thirds of cuckoo eggs are laid outside the nest cup and cannot produce a cuckoo chick. Eviction failures occurred at 20% of nests producing mixed broods. Cuckoo chicks that manage to fledge from mixed broods have no future, since they will die before they reach independence.

Surprisingly, cuckoos' reproductive success (no. of fledglings produced per egg laid) may not differ from that in common open-nesting hosts. Specifically, in our study population, the average reproductive success was 0.16. Similar reproductive success was reported in perhaps the most frequent (or at least most frequently studied) among cuckoo hosts, the reed warbler: 0.16 (Kleven et al. 2004). In other warblers, the cuckoo reproductive success varied from 0.04 to 0.30 (Kleven et al. 2004).

How is it possible that all the disadvantages of cavities do not translate into decreased fitness of the parasite? Cavities have also advantages: they protect the parasite chicks from inclement weather and predation. Redstarts, in contrast to typical cuckoo hosts, reject only minority of cuckoo eggs. These positive effects (from cuckoo's point of view) seem to balance the negative ones, resulting in virtually the same fitness of redstart-cuckoos compared to reed warbler-cuckoos.

16.10 Host Fitness: Reduced Costs of Parasitism?

Cavities have many advantages from the redstart's point of view, especially compared to open-nesting hosts. Only one third of cuckoo eggs end up inside the nest cup and produce a cuckoo chick; in contrast, in open-nesting hosts, all cuckoo eggs end up in the nest cup (Wyllie 1981; Moksnes et al. 2000; Andou et al. 2005; Mikulica et al. 2017). Only small proportion of cuckoo females (23%, *n* = 26) remove any redstart eggs prior to cuckoo's own laying, while egg removal is a rule in open-nesting hosts. Across populations, 15–45% of cuckoo chicks fail to kill all redstart progeny; in contrast, in open-nesting hosts, all host progeny dies due to cuckoo eviction (Davies 2000). In mixed redstart-cuckoo broods, at least some host's own chicks typically survive and fledge, while cuckoo chicks often die.

The cohabitation with a cuckoo chick decreased the average host fitness (no. of fledged redstart chicks) approximately twice: non-parasitized redstart nests fledged on average 5.7 redstart chicks, whereas parasitized nests with mixed broods fledged on average 2.4 redstart chicks (Samaš et al. 2016). Adjusting these values to original clutch size leads to quantitatively almost identical conclusion (i.e. a ratio between the fitness of the two types of broods): non-parasitized redstart nests fledged on average (mean ± SE) 0.84 ± 0.03 chick per egg laid (*n* = 87 broods), whereas parasitized nests with mixed broods fledged on average 0.38 ± 0.05 chick per egg laid (*n* = 14 broods). Overall host fitness across all parasitized broods where the cuckoo has hatched (i.e. mixed and solitary cuckoos) was 0.10 ± 0.03 chick per egg laid (*n* = 75 broods). Thus, an average non-parasitized brood has 8.4 times higher fitness than an average parasitized brood.

Comparing these values to available data from reed warblers leads to an unexpected result. Non-parasitized nests fledged on average 0.48 chick per egg laid, whereas parasitized nests fledged on average only 0.05 chick per egg laid (Øien et al. 1998). Thus, an average non-parasitized nest has 9.6 times higher fitness that an average parasitized brood. Therefore, the impact of parasitism per host nest is very similar between the only regular cuckoo cavity-nesting host known and a typical open-nesting host. However, at population level the selection exerted by cuckoos should be higher in redstarts than reed warblers: an average parasitism rate across regularly parasitized host populations is much higher in redstarts (29%, *n* = 8 populations; Samaš et al. 2016) than in reed warblers (12%, *n* = 7 populations; Stokke et al. 2008; non-parasitized populations excluded; see also Grim 2017).

Concluding Remarks and Future Directions

Peculiar biology and ecology of the redstart-cuckoo system provides specific suggestions for future research in this unique brood parasite–host pair. The mechanistic simplicity of redstart-cuckoo mimicry (plain eggs, typically no spots) makes it a more tractable system to study mimicry than most other gentes which show a highly complex egg markings. Future studies should also

(continued)

test if redstarts use spots (Fig. 16.1b), together with witnessing the laying cuckoo female (as already documented), as a cue to desert parasitized nests. Cohabitation of unsuccessful "evictors" with their surviving "victims" creates a stage for fosterer-offspring communication that is not paralleled in any other common cuckoo gens and which might be comparable to what happens in non-evictor cuckoo species. Fledglings from such mixed broods create a unique (in the common cuckoo) opportunity to study mechanisms of brood division which results in host male and female communicating with and feeding conspecific vs. heterospecific chick(s).

Different type of questions relates to redstart nest type. If nest design (nest cup size, shape and position within the nest box) is an adaptation against parasitism, does nest design prevent the cuckoo female from successful laying (egg stage), or does it constrain the success of cuckoo chick's eviction attempts (chick stage), or both? Future studies should quantify whether some aspects of nest design could play a role in eliminating parasite success at the two breeding stages, or whether the different stages could inflict opposite selection pressures on nest design.

Still other questions relate to studying all developmental stages of parasite–host relationships, namely, to the so far least studied post-fledging period. The focus should be on chick (both cuckoo and host) development of flying abilities, parental/fosterer provisioning, defence of young and even growth outside the nest cavity—it is possible to catch and measure majority of chicks during the first week after they leave host nests because they firstly do not fly at all and later only poorly.

Apart from these mostly redstart-cuckoos-specific topics, there are also various questions that reflect general interests of evolutionary and behavioural biologists in communication, coevolution, competition and parental investment. Cavity nesting, in both redstarts and other hosts breeding in cavities or dome nests, provides a different setting from typical passerine open nests and allows to realize experimental tests that are unfeasible in open nests. For example, both eviction success and growth performance of redstart-cuckoos show large variation. Is this variation caused by seasonally varying weather, host pair quality, nest cup design and composition, eviction of eggs vs. chicks or the proportion of time when the cuckoo chick pushed the host progeny against a nest-box wall? The nest sharing raises another question: are cuckoo chicks from the redstart gens more competitive than cuckoo chicks from other gentes where cuckoos almost never share a nest with host nestlings? This might be tested by cross-fostering, for example, reed warbler-cuckoo chicks into redstart nests, and examining their performance in mixed broods. Similarly, are host redstart chicks more competitive than typical passerine chicks because of their evolutionary experience with a large alien "sibling"?

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