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Reaction of the red-backed shrike (*Lanius collurio*) to the presence of the common cuckoo (*Cuculus canorus*)

Bachelor thesis

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Annotation

In this work, I tested the reaction of the red-backed shrike (*Lanius collurio*) against a nest parasite, the common cuckoo (*Common cuckoo*) (grey and rusty forms), predator, Eurasian sparrowhawk (*Accipiter nisus*) and harmless intruder, turtle dove (*Streptopelia turtur*). I proved that shrikes can differ between presented stimuli and adequately respond to them. Moreover, I proved that the cuckoo-hawk mimicry is not successful against shrikes.

Prohlašuji, že jsem autorem této kvalifikační práce a že jsem ji vypracovala pouze s použitím pramenů a literatury uvedených v seznamu použitých zdrojů.

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Ladislava Krausová

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Literature review

1 Brood parasitism

Brood parasitism is a way to transfer the care for the young to someone else, and besides some fish, insects, and frog (Spottiswoode et al. 2012), it is well studied in birds. This method is logistically simple for birds as the nest parasite lays eggs in the host's nest. The host incubates these eggs, and the hatched nestlings are also usually fed by them (Payne 1977).

One of the advantages of this reproductive strategy for parasite is the reduced cost of parental care, which is very demanding. At the same time, it reduces host reproductive success, which may result in evolving a strong selection pressure by hosts defending them against the parasite (Cichoń 1996).

According to Hamilton & Orians (1965), nest parasitism has evolved five times in birds independently. Rothstein (1990) and Spottiswoode et al. (2012) suggested that it has evolved seven times. Cuckoos (Cuculidae) can be treated as one of the best-known groups of nest parasites, with almost 50 species of the family adopting this reproductive strategy. Parasitism evolved independently in three groups of cuckoos. Besides, this strategy is also used by whydahs (*Viduidae* including *Anomalospiza*), cowbirds (*Molothrus*), honeyguides (*Indicatoridae*) and one species of duck (*Heteronetta atricapilla*), use this strategy too (Moskát 2005).

1.1 Types of brood parasitism

Brood parasitism can be divided into intra- and interspecific, i.e., according to the preference of the parasite (Lyon & Eadie 1991, Fiorini et al. 2019).

- Intraspecific – parental care of eggs and nestlings by another individual of the same species (e.g., *Hirundo rustica*) (Petrželková et al. 2015, Mann 2017).
- Interspecific - parental care of eggs and nestlings by adults of another species (e.g., *Cyanistes caeruleus*, *Parus major*) (Müller et al. 1990, Barrientos et al. 2015).

The brood parasitism can be further divided into two main types, obligate and facultative (Lyon & Eadie 1991, Fiorini et al. 2019). We recognize about 100 species of obligate brood parasites and 35 species facultative brood parasites in birds.

- Obligate – species or individuals completely resign to their parental care and lay all their eggs into the host nests, leaving the entire parental care to the host due to not building their nests (e.g., *Cuculus canorus*) (Fiorini et al. 2019).
- Facultative – species or individuals occasionally lay eggs in hosts' nests, but at the same time, they care for their clutches (Lyon & Eadie 1991). This type of parasitism prevails in precocial birds (e.g., Anserimorfes, Galliformes) (Barrientos et al. 2015, Mann 2017).

2 Common cuckoo (*Cuculus canorus*)

The common cuckoo is one of the most well-known and long-studied obligate brood parasites. This species is widespread throughout Europe and northern Asia, with wintering areas lie in Sub-Saharan Africa (Morelli et al. 2017, Svensson 2018). It occurs in almost all habitats (all types of forests, cultural landscapes, but also mountainous terrain and marshlands), but the presence of a suitable host is important. Its food includes large invertebrates, mainly locusts, beetles, and larvae of butterflies with a high preference for large hairy caterpillars (Wyllie 1981, Cramp 1985, Svensson 2018). Each cuckoo female is adapted to parasitising only one or a few host species (with similarly looking eggs). Accordingly, the cuckoo is divided into several clans or *gentes* producing particular egg types. Throughout Europe, cuckoo parasitizes more than 100 species of birds, usually small insectivorous passerines (Wynne-Edwards 1933, Stokke et al. 2005). Despite the fact that egg collections in European museums very often show poor mimicry with host´s eggs, the adaptation to host preference can work with many host species (Honza et al. 2002).

2.1 Taxonomy

Common cuckoo is classified in order Cuckoos (*Cuculiformes*). This order forms a monophyletic group together with turacos (*Musophagidae*) and bustards (*Otitidae*) named Otidimorphae. Together with doves (*Columbiformes*), sandgrouse (*Pterocliformes*) and mesites (*Mesitornithiformes*) they form a monophyletic group named Columbaves (Jarvis et al. 2014, Prum et al. 2015).

As far as parasitism is concerned, this has developed independently three times in cuckoos. In Old World *Cuculinae*, in New World *Neomorphinae*, and Old World crested cuckoo (genus *Clamator*) (Rothstein 1990, Krüger & Davies 2002, Krüger et al. 2007, Davies 2011). Sixty-five species in family *Cuculidae* are obligate brood parasites, and only two species are facultative brood parasites in the genus *Coccyzus* (Mann 2017).

2.2 Physical appearance

The common cuckoo is a medium-size species with colour sex dimorphism. The shape of the wings is rather pointed, and the tail is rounded.

Male – Head, chest and upper body are grey to blue-grey. The underparts are white with transverse dark stripes. The tail is blackish brown with white tipped and spots. Bill is greyish with a yellow base. Feet and eye-rings are yellow with light brown to the orange iris (Payne et al. 2005, Svensson 2018).

Female – We recognize two colour forms of females. Grey form looks very similarly to the male, usually with brown-beige to rufous shade on neck, breast and belly with thinner stripes on the abdomen. The rufous form has rusty to rufous upperparts and chest, with a dark brown barred pattern. Dark brown and rufous wings and usually also darkly striped (Payne et al. 2005, Svensson 2018).

Juveniles are grey-brown with white nape spot and white tips of feathers on upperparts and brown iris (Payne et al. 2005).

2.3 Adult cuckoo mimicry

Several species of cuckoos tend to resemble to co-occurring raptor species (Gluckman & Mundy 2013) . The striking resemblance of the grey form of the common cuckoo and the Eurasian sparrowhawk (*Accipiter nisus*) is probably the most often studied system. This form of mimicry is generally called Batesian mimicry, where a harmless individual mimics the appearance of a threatening predator to increase its fitness (Davies & Welbergen 2008, Feeney et al. 2012). Actually, cuckoo cannot be treated as fully harmless species. Thus this type of mimicry is often called Kirby mimicry.

According to Krüger et al. (2007), cuckoo-hawk mimicry evolved after the evolution of brood parasitism, suggesting that this mimicry is useful to avoid attacks from host parents while laying the parasitic egg. This was supported by results of the study by Davies & Welbergen (2008), showing that titmice avoid visiting winter feeders equally when a dummy sparrowhawk and dummy cuckoo are present. On the contrary, studies on warblers, which are common cuckoo hosts (contrary to titmice) show different responses to cuckoos and sparrowhawks (Welbergen & Davies 2008, Trnka & Prokop 2012). An alternative explanation of the cuckoo appearance resides in defence against predators attacking the cuckoo (Davies & Welbergen 2008).

The rufous form of common cuckoo is supposed to resemble the common kestrel (*Falco tinnunculus*) (Trnka & Prokop 2012). Nevertheless, Trnka et al. (2015) showed that sparrows respond very differently to kestrel and rufous cuckoo dummies.

2.4 Behaviour

2.4.1 Host selection

Parasites tend to develop abilities to find a suitably locate the host nest without being detected by the host (Honza et al. 2002). Cuckoos observe their potential host from an elevated position (e.g., perching on a tree branch) to get a good view. Therefore, it is better for a potential host to choose habitats and nesting sites away from the nearest trees. Solitary birds also often nest in dense vegetation (scrub, thickets or reeds), which makes finding their nest by cuckoos more time-consuming (Øien et al. 1996, Payne et al. 2005).

Some host species are more suitable than others. Cuckoos prefer insectivorous songbirds with open nests and short nesting period. Such species can provide a higher rate of food and parental care for cuckoo nestlings (Soler et al. 1999, Payne et al. 2005). However, insectivorous species such thrushes (*Turdus* spp.) may also be unsuitable for cuckoos. They have a deep nesting bowl and large eggs, which puts cuckoo chicks at a disadvantage when ejecting nestmates.

As mentioned above, cuckoos specialize usually in one host species. They aim to mimic their eggs. The question remains, how do they identify the particular host species? Vogel et al. (2002) proposed five hypotheses for finding the corresponding host-type egg.

1. Inheritance – genetically determined host preference.
2. Host imprinting - learning the characteristics of foster parents by cuckoo chicks before or immediately after hatching.
3. Natal philopatry - return to or near the place of birth (Weatherhead & Forbes 1994).
4. Nest site choice - randomly searching for nests in a group of hosts laying similarly coloured eggs at the same nesting site (Moksnes & Roskaft 1995). This hypothesis does not explain the paradox of how cuckoos search for the group of hosts (Teuschl et al. 1998).
5. Habitat imprinting - laying eggs in a similar environment where the young cuckoos grew up and learned its characteristics by imprinting process (Vogel et al. 2002).

2.4.2 Egg laying

Laying the parasitic egg is supposed to be as cryptic as possible. In some cuckoo species, including the common cuckoo, the males facilitate the act of oviposition by drawing attention of host parents to themselves and providing the unguarded nest for the female (Payne et al. 2005).

Cuckoos synchronise their laying period with the host´s one because earlier, there is a very high probability of parasitic egg rejection. On the other hand, laying eggs into an already finished clutch can be disadvantageous for the cuckoo because the host chicks are likely to hatch earlier than the cuckoo chick. As the cuckoo chick throws out the host eggs after hatching, it is more difficult to throw the chick than the egg. That's why the cuckoo prefers to lay its eggs during the host´s egg-laying period (Davies 2000). Cuckoos regularly lay their eggs in the afternoon, when the host is usually absent from the nest, representing a lower risk for the cuckoo to be caught red-handed (Moksnes & Roskaft 1995).

The cuckoo usually reduces the host's brood by eating or removing one or more host eggs before its own egg laying (Moksnes et al. 1991, Krüger 2007). There are more theories explaining this behaviour:

1. ‘Parasite competition hypothesis’ - a cuckoo removes eggs from a host nest to get rid of a parasitic egg of another cuckoo female (Honza et al 2007).
2. ‘Mimicry improvement hypothesis’ - improving the mimicry of one's own egg by removing one host egg, thus keeping the clutch size equal and increasing the chance of acceptance (Šulc et al. 2016).

Reducing the clutch also increases the probability of cuckoo egg hatching, while decreasing the host's reproductive success (Lotem et al. 1992, Barabás et al. 2004). The cuckoo lays one mimetic egg in particular host nest at two-day interval. Its clutch can contain up to 20 eggs per one breeding season. The incubation period of cuckoo eggs is 12 days, which contrast to 13-14 days common in most of host species. Egg laying is very fast (e.g., about 10 seconds). Speed may reduce the chance of another parasite or predator noticing the nest or the chance of a host attack (Moksnes et al. 1991, Davies 2000, Barabás et al. 2004, Hargitai et al. 2010, Šulc et al. 2016).

2.5 Cuckoo´s egg

Eggs of the parasitic cuckoos are generally smaller than those of non-parasitic cuckoos (Krüger & Davies 2004). Smaller eggs enable the cuckoo female to produce more eggs per season (Payne et al. 2005). Cuckoos have evolved eggs similar in size to their host to prevent their identification and rejection. Similar size can also enhance heat transfer during incubation (Payne 1974, Hargitai et al. 2010). To reduce detection by the host, cuckoos have also evolved colour mimicry (matching the host egg in colour and pattern) (Stoddard & Stevens 2011). Besides the smaller size and colour mimicry, the cuckoo egg has a thicker shell, which evolved as a defence against puncturing and rejecting it or total damage (Hargitai et al. 2010, Spottiswoode 2010, Stoddard & Stevens 2011). In addition to the high strength of the eggshell, the cuckoo egg also has a high density of porosity, which allows better gas exchange and thus faster embryo development.

2.6 Cuckoo´s chicks

Although the eggshell in cuckoo is thick, there must be some compromises for the young to hatch. Honza et al. (2001) dealt with this problem in their study comparing the hatching of common cuckoo and great reed warbler young. They found that cuckoo chicks need more time (e.g., start earlier), more effort by pecking and special egg-opening tactics despite the same pecking speed.

In addition to the ability to hatch, nutrition is also important for the young. The greater amount of nutrients and antioxidants that female cuckoos provide to eggs increases the size, growth rate and competitive ability of the chick (Hargitai et al. 2010).

After hatching, the cuckoo nestling throws out all host eggs and hatchlings placed in the nest. The probability of survival of host eggs or chicks in the presence of a cuckoo egg is, therefore, almost zero (Moksnes et al. 1991).

To secure food from foster parents after hatching, cuckoo chicks take advantage of excessive begging calls (Hargitai et al. 2010, Spottiswoode & Stevens 2011). Feeding the chicks continues for another 2-3 weeks after fledging (Payne et al. 2005).

3 Arms race

The cuckoo has adapted very well to parasitism. Nevertheless, the host species had to come up with some counter-adaptations to resist the parasitism. This parasite and its host phenomenon is generally called an arms race (Cichoń 1996). The arms race describes the principle of evolving adaptation (predators/parasites) and counter-adaptation (prey/host) to change the selection pressure. Dawkins & Krebs (1979) describe the arms race between a brood parasite and its host as an example of the asymmetric interspecific arms race.

3.1 Counter-adaptation

One of the more basic forms of defence against parasitism can be inhibitory or deceptive strategies such as nesting in unfavourable places for the parasite, deceptive nest structure or synchronised group nesting (Feeney et al. 2014). Another way of defence is to actively attack the parasite i.e., mobbing. The counter-adaptation to the mobbing could be the cuckoo-hawk mimicry, which probably induces fear in the host, thus limiting mobbing against the cuckoo. In some cases, individuals may use a very loud alarm call in the presence of the parasite, which may attract some interspecies or conspecifics to join in mobbing against the parasite (Kilner & Langmore 2011). However, the more studied counter-adaptations of hosts are the revealing of the egg mimicry.

One of these counter-adaptations to egg mimicry is the development of a more complex surface pattern, leading to poorer egg imitation ability. Host species may develop either high interclutch and/or lower intraclutch egg variability. This hypothesis was tested by Øien et al. (1995) on 75 European passerine species divided into two groups (suitable and unsuitable as the cuckoo hosts). Individual clutches were photographed separately on a neutral grey plate, and the variability of colouration was measured. The conclusion of this work was the confirmation of the importance of the interclutch variability on the success of brood parasitism, but the effect of intraclutch variability was lower. However, intraclutch variability is generally lower in Europe than in North America, suggesting that in Europe, the host-parasite system has reached a more advanced level (Øien et al. 1995, Stokke et al. 2005). Also, general behaviours such as burying eggs (continuing to build the nest), throwing eggs out of the nest (as nest cleaning) or abandoning the nest seem to be very effective in this respect. However, these behaviours cannot be considered as purely anti-parasitic adaptations (Moskát 2005).

One possible response to parasitism may also be discrimination and rejection of the parasitic young, but this phenomenon is rarely known. We can presume that these methods are rarer than counter-adaptations to eggs. Chicks' discrimination may simply be the result of the young making too high demands on a host that is physiologically unable to cope with care. Other ways of rejecting the parasitic young can be nest desertion, providing less food or less quality food, pecking the parasitic chick or evicting the young from the nest (Schuetz 2005, Stokke et al. 2005, Grim 2006, Feeney et al. 2014).

4 Antipredator defence

Most species have evolved numerous ways how to protect themselves from predators. Predator avoidance has two meanings – 1) prey behaviour changing in purpose to avoid a predator detection (mainly change of the foraging behaviour), 2) prey behaviour changing in purpose to escape the predator after being detected (Caro 2005). Curio (1993), on the other hand, mentioned primary and secondary defence. Primary defence serves to protect against predator attack (mimicry, crypsis, aposematism), while secondary defence (mobbing, attacking, bluffing) serves to discourage predators from attacking, but with enough time in advance to deploy them. In order to use these methods, the prey must first recognise and locate the predator, which is very costly in terms of time, risk, and energy.

4.1 Red-backed shrike defence

Red-backed shrike (*Lanius collurio*) is one of the species that defends its nest very aggressively against predators using an active defence, so-called mobbing (Curio 1978, Tryjanowski & Goławski 2004). Mobbing is one way to drive a predator or nest parasite away from the nest (McLean et al. 1986). An individual can use either active mobbing - flight over the vicinity of the predator, which may culminate in attacks without or with physical contact with predator or passive mobbing i.e. mobbing calls - warning and/or attracting other individuals to defend against predators (Strnadová et al. 2018, Dutour et al. 2019).

Shrikes place their nests in thorny shrubs, which could be a good protection against predators, but Farkas et al. (1997) did not confirm this theory in their study. Nevertheless, the height of the nest location provides an antipredator protection in shrikes (Tryjanowski et al. 2000).

As shown by Strnad et al. (2012), the shrike can recognise predators such as Eurasian jay (*Garrulus glandarius*), common kestrel, Eurasian magpie (*Pica pica*) or Eurasian sparrowhawk and react to them adequately, according to their level of threat. The nest defence increases at the nestling stage as the parent investment increases compared to the incubation period.

During nest defence, shrike uses typical alarm calls, such as 'gek gek gek' – on the alert or 'tskek tskek' similar to 'chack' close to danger. When attacking the mentioned jay, they make 'zèè' sounds similar to 'dschrää' (Ash 1970, Lefranc & Worfolk 1997, Harris & Franklin 2000).

4.2 Shrike-cuckoo relationship

Until recently, the red-backed shrike was a common host of the common cuckoo. However, an experimental study by Lovászi & Moskát (2004) found that there have been no cases of cuckoo parasitism in Hungary for the last three to four decades. Adamík et al. (2009) compared ringing data in the Czech Republic and Slovakia and also found a rapid decline between 1964 and 2006, with an average parasitisation rate of 2.19% at the beginning of the study and only 0.37% at the end. This suggests that shrikes won the arms race with the cuckoo, probably due to their high ability to recognise and reject cuckoo eggs. This is confirmed by a Lovászi & Moskát (2004), who studied the ability of shrikes to distinguish between parasitic and its own eggs and found that it rejected parasitic eggs in 93.3%.

5 Aims

1. To test the reaction of the red-backed shrike to the presence of adult common cuckoo at the nest.
2. To compare the reaction to a nest parasite – the common cuckoo, with the reaction to a predator – the Eurasian sparrowhawk, and to a harmless intruder – the turtle dove.
3. To test the reaction in two phase of nesting – laying and incubation.

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Manuscript

Title: Abandonment of red-backed shrike as a potential host: an ineffective cuckoo-hawk mimicry?

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Abstract

Red-backed shrikes (*Lanius collurio*) used to be one of the most common host of the common cuckoo (*Cuculus canorus*). Nevertheless, during the last 30 years, rising evidence from central Europe exists that cuckoo chick in shrike nests are scarcer and, on some locations, they disappeared completely. There are multiple hypotheses suggested explaining this abandonment. Here, we test the hypothesis that shrikes vigorously attack adult cuckoos, potentially resulting in ineffective parasitism. Adult common cuckoos resemble in appearance Eurasian sparrowhawk (*Accipiter nisus*), a common predator of small passerines. One hypothesis supposes that this mimicry aims to avoid being attacked by small passerines when searching for their nests. Our results show that shrikes defending their nests attacked cuckoos (two colour forms, grey and rufous) very vigorously and more often than sparrowhawk. In the presence of sparrowhawk dummy, parent shrikes only produced alarm calls, which were used scarcely in the presence of cuckoos. This suggests that cuckoo-hawk mimicry is ineffective in the case of shrikes and that they attack them much often than any other intruder. Therefore, this activity could possibly result in the abandonment of shrike as a potential host for cuckoos.

Keywords

Nest defence, brood parasitism, red-backed shrike, cuckoo-hawk mimicry

Declarations

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Author contributions:

LK collected most of the data, participated on the data analyses and wrote most of the manuscript. PV participated in the design of experiments and manuscript preparation. MS participated in the design of experiments, data collection, data analyses and manuscript preparation. KA and OF participated in data collection and manuscript preparation. VC, MP, ŠP participated in the data collection. RF participated in the design of experiments.

Ethics approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Permission for studies on wild red-backed shrikes was granted by the Ministry of the Environment of the Czech Republic (13842/2011-30), the license permitting experimentation with animals no. CZ01629 was offered by the Ministry of the Agriculture of the Czech Republic. This research adhered to the ASAB/ABS guidelines for the use of animals in research. The authors declare that the experiments comply with the current laws of the Czech Republic (and European union).

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Introduction

Brood parasitism is one of the reproductive strategies when animals lay their eggs in the nests of other species (hosts). We can distinguish two types of parasitism, intraspecific when parasites and host belong to the same species and interspecific when the egg is laid in a nest of the different species (Yamauchi 1995). Another possible differentiation of brood parasitism is to obligate, and facultative, where parental care is transferred entirely to the host (obligate) or the own parental care is preserved (facultative) (Mann 2017). The brood parasites are known in about 1% of all bird species, and cuckoos (Cuculidae) represent almost half of the bird brood parasites. (Hamilton & Orians 1965, Payne 1977, Spottiswoode et al. 2012).

In Europe, the common cuckoo (*Cuculus canorus*) is the most common and most studied brood parasite. The parasitic strategy of the cuckoo is very complex, with arms races developed with multiple host species. As the adult cuckoo appears in the host nest vicinity, the host parents usually increase its vocalisation, which should chase the cuckoo away, but instead, it usually draws the cuckoo attention to the host nest. The parasitic event itself is very fast and cryptic and planned in the period before incubation and after the first host egg have been laid (Payne et al. 2005). The newly hatched cuckoo chick kills all the host eggs and chicks. Therefore, the host developed counter-adaptation to prevent parasitism (Davies & Brooke 1989, Lovászi & Moskát 2004). The most common include the ability to recognise the parasitic egg, but hosts may also rely on nest and eggs crypsis or actively defend it (Montgomerie & Weatherhead 1988, Goławski & Mitrus 2008, Polak 2013).

The red-backed shrike (*Lanius collurio*) is one of the species, who defend its nest very aggressively, including physical attacks and flyovers (Tryjanowski & Goławski 2004, Němec & Fuchs 2014, Strnadová et al. 2018). In addition to aggressive attacks, shrike also uses specific alarm calls, more common sounds like ‘chack’, usually accompanied by tail wagging. However, shrike also uses other warning voices against predators, such as elongated voice like ’zèè’, similar to ‘dschrää’ or ‘tchraa’ or when attacking predator, it also uses a beak snap or very fast ‘trrtr-trr’ (Ash 1970, Harris & Franklin 2000).

Shrike used to be one of the most common cuckoo host in the past, but since the 1960s, the parasitism occurrence has decreased (Takasu 2003, Lovászi & Moskát 2004). There are multiple theories explaining this phenomenon. Lovászi & Moskát (2004) suggest the high ability of shrikes to recognise parasitic eggs in populations in Hungary. Adamík et al. (2009) suggest a low breeding density of shrikes result in abandoning this species by cuckoos in Czechia. Another assumptions is that the high level of shrike aggression towards adult cuckoos may have discouraged them.

The common cuckoo adopts a colouration and body size and shape very similar to the Eurasian sparrowhawk (*Accipiter nisus*), a very common predator of small passerines. Davies & Welbergen (2008) showed that titmice (*Parus major*, *Cyanistes caeruleus*) respond equally to dummies of these two species and cannot recognise them. Reed warblers (*Acrocephalus scirpaceus*), as well as great reed warblers (*A. arundinaceus*) were able to distinguish between them and respond differently (Welbergen & Davies 2008, Trnka & Prokop 2012)

In this study, we tested the response of the red-backed shrike to the presence of the adult common cuckoo in the immediate vicinity of its nest and compared this response with the reaction to the sparrowhawk and the harmless turtle dove (*Streptoptelia turtur*). We hypothesised that the shrikes are able to differentiate between the nest parasite, the predator of adults and the harmless control and respond to them adequately.

Moreover, we tested the reaction of the shrike in two phases of nesting – the egg-laying phase, when the likelihood of nest parasitism is higher, and during the incubation phase, when the clutch is completed and the threat of parasitism is lower. Therefore we expect that nest owners will react more intensively to parasites during the egg laying phase (Gill & Sealy 1996).

Materials and methods

Study area

The study took place in Doupovské hory, near the town Karlovy Vary on the southern border of the military area; 50°10´N,13°9´E. The experiment was conducted in the two phases of the breeding season (egg-laying and incubation period) from May to July during the years 2018, 2020, and 2021. The main habitat is old meadows or pastures with many shrubs but without settlements. The study area reaches quite high densities of nesting pairs (up to 18 pairs per km^2; Němec, personal observation).

Study species

As a model species, we chose the red-backed shrike. It is a mostly insectivorous passerine bird, but despite of its medium size, it is also able to hunt small vertebrates (Cramp 1994, Lefranc & Worfolk 1997). The red-backed shrike is a migratory species, which migrates to the tropical Africa in the winter. It arrives during May at the breeding sites and leaves in August (Morelli 2012). Shrike chooses a semi-open habitat with scattered shrubs. It prefers shrubs with spikes and thrones, especially species like the wild rose (*Rosa canina*), blackberry (*Rubus spp.*), blackthorn (*Prunus spinosa*) or hawthorn (*Crataegus spp.*) (Olsson 1995).

The red-backed shrike is strictly territorial in the breeding season, as well as outside it. Open nest is built by both sexes, especially by males, who also chose the nest site. The first clutch contains 3-7 eggs. It can also have a replacement clutch in a new nest. The incubation lasts 14-16 days on average. After hatching, the young stay in the nest on average for 14-16 days. After 25 days the young are able to hunt some insects and in approx. 42 days it become independent (Lefranc & Worfolk 1997, Lovászi & Moskát 2004).

Shrikes can be very aggressive against intruders, distinguish between them and possibly attack them (Goławski & Mitrus 2008, Strnad et al. 2012, Strnadová et al. 2018). In our experiment, intruders were represented by two forms (rufous and grey) of the common cuckoo, by the Eurasian sparrowhawk, and a harmless baseline control, the turtle dove. The females of common cuckoo have two colour forms – grey and rufous. The grey form is supposed to mimic the Eurasian sparrowhawk, while the rufous mimics common kestrel *(Falco tinnunculus*) (Davies & Welbergen 2008, Trnka & Prokop 2012). The Eurasian sparrowhawk is one of the predators of adult birds, including the red-backed shrikes (Götmark 1996, Trnka & Prokop 2012), while kestrels usually hunt on fledglings. As a harmless control, we chose the turtle dove, which regularly occurs in our study area, is comparable in size to the cuckoo and the sparrowhawk (Payne et al. 2005, Davies & Welbergen 2008) and represents no threat to shrike adults as well as nest.

Experimental design

Dummies of intruders were presented as perching in an upright position on a 1.5 m high pole and 1 m far from the nest. All dummies had their wings folded and facing the nest. In this study, we used artificial dummies made of plush which are successively used in antipredator experiments (Němec et al. 2015; see Supplement Fig. S1). Dummies were covered by cloths to prevent an early reaction before installation. For each nest, were recorded GPS coordinates, number of eggs, and we determined the phase of the nesting. Because the trials were conducted only at nests containing eggs, we presented only one dummy at each nest to reduce the disturbance time at the nest and possible nest abandoning.

Before the start of the trial, we observed the visit rate of the nest by adults for 10 minutes. After this period, we started the trial, when one of the dummies was placed near to the nest. The trial lasted for 10 minutes, and the beginning of the trial was the moment when at least one of the parents noticed the dummy. If at least one of the parents did not notice the dummy, the trial was terminated and included in the data set as a zero reaction. The reaction of the shrike was recorded on a camera Panasonic HDC-SD80 associated with detailed description of the behaviour by a human observer. The camera was c. 50 m far from the nest to prevent the reaction to experimenter. The acoustic record was taken by voice recorder Olympus WS-852, which was hidden under the presented dummy to ensure that all alarm calls are recorded.

Statistical analyses

For statistical analyses, we used two behaviours: the number of attacks (both with and without physical contact) and the number of warning (‘chack’ calls) to each dummy during the trials. Both data types were transformed by logarithmic transformation to meet the demands of normal distribution (log (no of swoops + 1) and log (no of alarms + 1)). To evaluate the effect of the predictor variables, we used the linear mixed effect model (LMM), command lmer in R 4.1.1 package lme4.

Firstly, we tested the difference in the number of swoops. Categorical predictors were sex of the parent (male or female), the phase of the nesting season (laying or incubation), and the number of eggs (1-6).

Secondly, we tested differences in number of alarm calls used by shrikes in each trial. As we were not able to determine the sex of the warning parent, the number of alarm calls performed by shrikes in a trial were counted together and entered the analyses as a number for the whole pair. Categorical predictors were the phase of the nesting season (laying and incubation) and the number of eggs (1-6).

Results

We examined 118 nests in total, of which 57 nests were in the egg laying phase and 61 nests were in the incubation phase of nesting. The dummy type and sex of shrike parent significantly affected the number of attacks, while the phase of nesting and number of eggs did not (LMM, Table 1). Shrikes were more aggressive against the grey and rufous form of the common cuckoo than against Eurasian sparrowhawk and turtle dove (Fig. 1, Table 2). Both cuckoo forms were attacked equally often, and sparrowhawk was attacked very scarcely, equally often as the baseline the turtle dove dummy (Table 2). Males were more aggressive towards the presented dummies than females (Fig. 2).

Table 1 – Effect of predictors on the number of attacks to presented dummies (LMM, n = 118). Significant effect in bold.

	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Dummy	**3**	**21.445**	**7.148**	**9.180**	**<0.001**
Sex	**1**	**12.374**	**12.374**	**15.889**	**<0.001**
Phase of nesting	1	0.002	0.002	0.002	0.963
Number of eggs	7	6.581	0.940	1.207	0.300
Residuals	221	172.099	0.779		

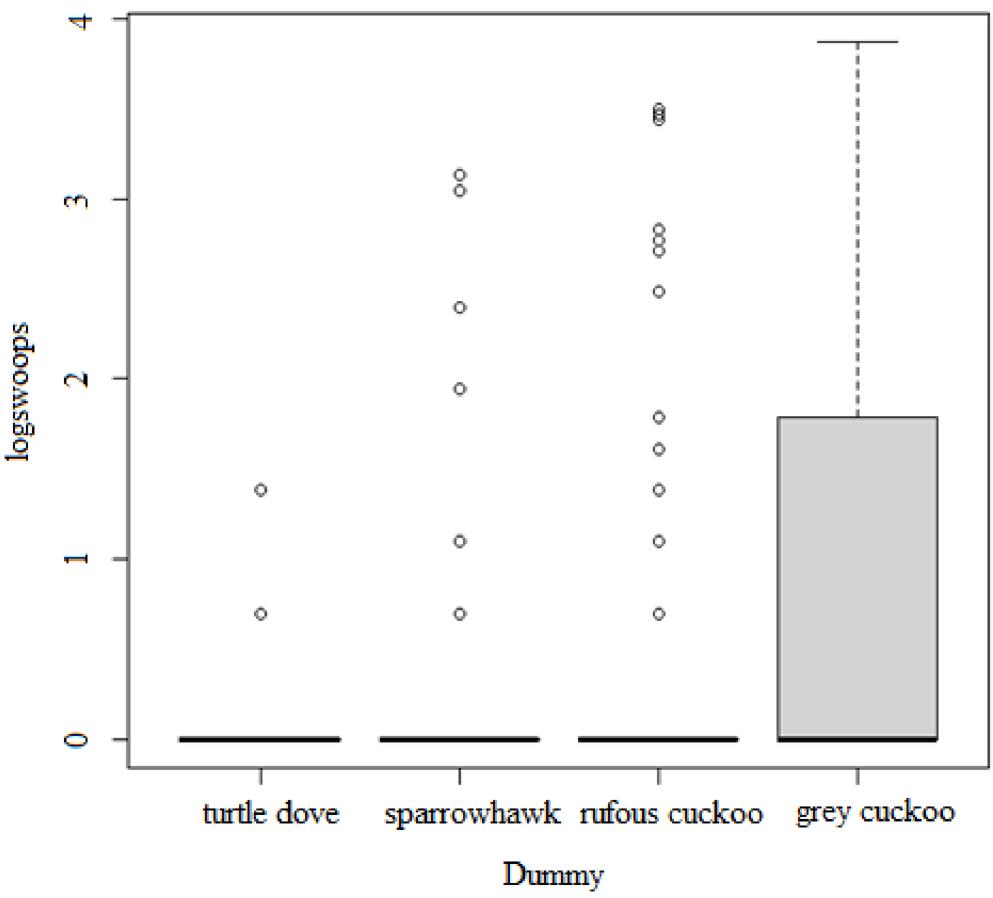

Fig. 1 – Number of attacks (log-transformed) performed by red-backed shrikes towards particular dummies. The bold line refers to the median, box shows 50-75% of data, whiskers show 10-90% of data, and dots are outliers.

Table 2 – The difference between each dummy in the number of attacks performed by shrike parents (Tukey HSD post hoc test). A significant difference in bold, difference bordering significance in italics.

	Estimate	Std. Error	t value	Pr (>|t|)
sparrowhawk – turtle dove	0.063	0.167	0.374	0.982
rufous cuckoo – turtle dove	**0.464**	**0.164**	**2.825**	**<0.050**
grey cuckoo – turtle dove	**0.739**	**0.167**	**4.422**	**<0.001**
rufous cuckoo – sparrowhawk	*0.401*	*0.171*	*2.351*	*0.090*
grey cuckoo – sparrowhawk	**0.676**	**0.167**	**4.040**	**<0.001**
grey cuckoo – rufous cuckoo	0.274	0.171	1.601	0.380

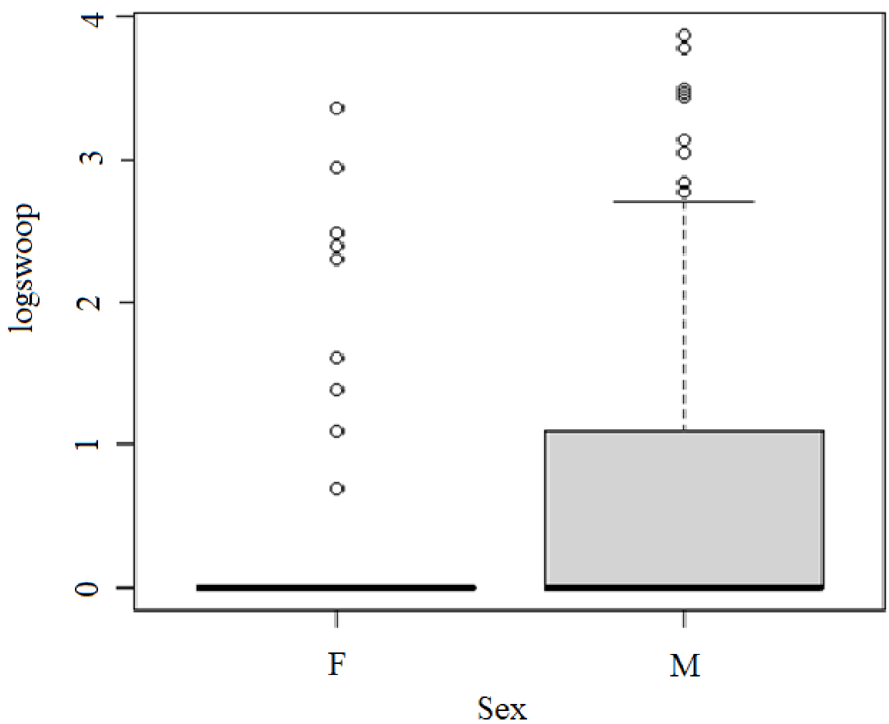

Fig. 2 – Number of attacks (log-transformed) performed by females (F) and males (M) red-backed shrikes against presented dummies. The bold line refers to the median, box shows 25-75% of data, whiskers show 10-90% of data, and dots are outliers.

The number of alarm calls was significantly affected by the type of presented dummy, the effect of the nesting phase and number of eggs in the nest was not significant (Table 3). In the presence of the sparrowhawk, the shrikes use the ‘chack’ call significantly more often than in the presence of both forms of the cuckoo and the baseline turtle dove, which do not differ from each other (Fig. 3, Table 4).

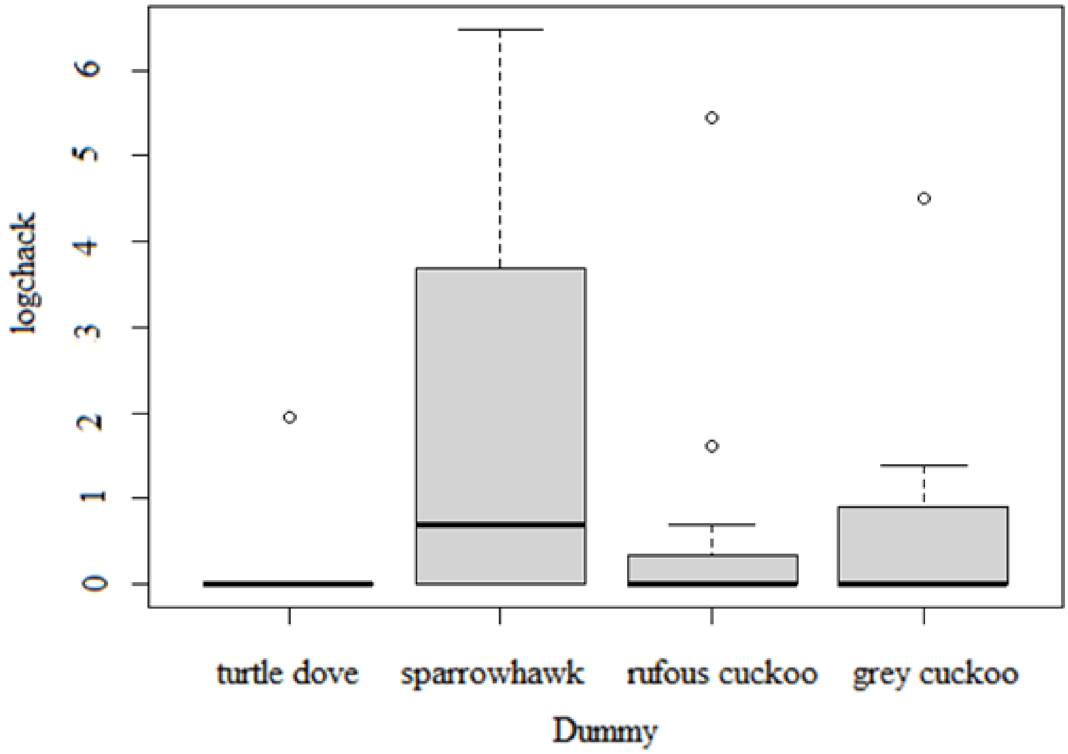

Fig. 3 – Number of ‘chack’ calls (log-transformed) performed by shrikes in the presence of presented dummies. The bold line refers to the median, box shows 25-75% of data, whiskers show 10-90% of data, and dots are outliers.

Table 3 – Effect of predictors on the number of 'chack'calls performed (LMM, n = 118). Significant effect in bold.

	Df	Sum Sq	Mean Sq	F value	Pr (>F)
Dummy	**3**	**21.765**	**7.255**	**3.154**	**<0.050**
Phase of nesting	1	0.100	0.100	0.043	0.836
Number of eggs	1	3.413	3.413	1.484	0.229
Residuals	46	105.818	2.300		

Table 4 - The difference between dummies in the number of 'chack' calls (Tukey HSD post hoc test). A significant difference in bold, difference bordering significance in italics.

	Estimate	Std. Error	t value	Pr (>|t|)
sparrowhawk – turtle dove	**1.845**	**0.609**	**3.031**	**<0.020**
rufous cuckoo – turtle dove	0.328	0.552	0.933	0.933
grey cuckoo – turtle dove	0.358	0.550	0.915	0.914
rufous cuckoo – sparrowhawk	**-1.517**	**0.568**	**-2.672**	**<0.050**
grey cuckoo – sparrowhawk	*-1.487*	*0.564*	*-2.636*	*0.052*
grey cuckoo – rufous cuckoo	0.030	0.505	0.059	1.000

Discussion

We found a significant difference between the reaction of the red-backed shrike to the presence of the common cuckoo (brood parasite) and the reaction to the Eurasian sparrowhawk (predator). In the presence of the cuckoo, shrikes react very aggressively using attacks, whereas shrikes are rather inconspicuous and use mainly alarm calls in the presence of the sparrowhawk. These results confirm that shrikes are able to distinguish between the cuckoos and sparrowhawk and that the cuckoo-hawk mimicry is not effective in the case of red-backed shrikes (Davies 2015).

Our results are in accordance with the study of Trnka & Prokop (2012), who tested the effect of cuckoo-hawk mimicry as a protection of cuckoo against the aggressive host, great reed warbler (*Acrocephalus arundinaceus*). In this study, three dummies were presented near to the warbler nest - common cuckoo, Eurasian sparrowhawk, and the harmless control - the turtle dove. Reed warbles were able to discriminate between presented dummies and reacted differently to them. Warblers did attack both cuckoo and sparrowhawk, but the reaction to the cuckoo was significantly more aggressive and frequent. Authors conclude that the cuckoo-hawk mimicry was thereby disputed. Similarly, Welbergen & Davies (2008) showed that reed warblers (*Acrocephalus scirpaceus*) also showed a higher level of antipredation behaviour in the presence of cuckoo than in the presence of sparrowhawk, which suggest low efficacy of cuckoo-hawk mimicry on this species. On the contrary, Davies & Welbergen (2008) observed the attendance of great tits (*Parus major*) and blue tits (*Cyanistes caeruelus*) at the feeder in the presence of four dummies – the common cuckoo, Eurasian sparrowhawk and harmless controls - collared dove (*Streptopelia decaocto*) or teal (*Anas crecca*). The authors did not proof the difference in attendance to feeders in the presence of the cuckoo and sparrowhawk (attendance was zero in both cases), which suggest that tits are not able to differentiate between cuckoo and sparrowhawk. There should be noted that tits are not common hosts of cuckoo as they commonly breed in tree hollows inaccessible for cuckoos (Yu et al. 2017). The evolutionary pressure to recognise between cuckoo and sparrowhawk may thus not be as strong as in the case of warblers or shrikes, common cuckoo hosts.

The reaction to the rufous form of the cuckoo almost did not differ from the reaction to the grey form. The rufous cuckoos occur regularly in Hungary and adjacent parts of Slovakia, Austria and Czechia (Honza et al. 2006, Trnka & Grim 2013, Koleček et al. 2019). They do not occur at our studied locality. Therefore, we found the ability of shrikes to recognize it as a cuckoo quite surprising. On the other hand, some studies (e.g. Honza et al. 2006, Strnad et al. 2012, Trnka & Grim 2013) suggest that a rufous form of cuckoo may imitate common kestrel, the predator often attacked by shrikes. On the other hand. Trnka et al. (2015) showed that sparrows (*Passer domesticus* and *P. montanus*) are able to differentiate rufous cuckoos from kestrels, suggesting that this mimicry do not work. Our results suggest that the mimicry may work on shrikes; nevertheless, in our previous study (Strnadová et al. 2018) we showed that shrikes attack the common kestrel presented near nests containing eggs only seldom. The reaction of shrikes in Strnadová et al. (2018) was significantly lower than the reaction to rufous cuckoo in this presented study. Although the kestrel and the rufous cuckoo was not presented to shrikes in one study, we suggest that shrikes are able to distinguish between them and treat the rufous cuckoo as a cuckoo.

Higher male aggression towards intruders in our results is consistent with a number of previous studies on passerines (e.g., Brunton 1990, Pavel & Bureš 2001, Klvaňová et al. 2011 or Kryštofková et al. 2011, even in shrikes e.g., Němec et al. 2015). This effect can be explained, for example, by higher testosterone levels or perception of risk in males (Polak 2013). On the other hand, females are supposed to defend their nests due to higher certainty of parenthood (Montgomerie & Weatherhead 1988). Moreover, in agreement with the brood value hypothesis, female aggressiveness should be higher in the laying phase of nesting because their investments in brood are higher than males' (Curio 1987, Redondo & Carranza 1989). However, e.g. Strnadová et al. (2018) showed that there were no significant differences in reaction between males and females in the stage of incubation.

The reaction of shrikes to the presented dummies was not affected by the phase of nesting. This result is surprising because the cuckoo prefers to parasite its hosts in the egg-laying phase rather than incubating phase to increase the likelihood of acceptance of the egg (Davies 2000). Based on this theory, host species should react to cuckoo presence more in the phase of eggs laying. On the other hand, as the cuckoo can depredate the whole clutch and force the host to rebreed, it is dangerous during whole nesting season (Davies 2011), even in the phase of nestlings (Šulc et al. 2020). Moreover, it was documented that most of the host species react very aggressive against cuckoo adults during the whole nesting season (Jelínek et al. 2021).

In addition, the response of shrikes was not affected by clutch size, although the higher amount of eggs represent higher investments into the brood and therefore the nest defence should be stronger in larger clutches (Wiklund & Anderssen 1994, Redondo 1989). However, there are also studies showing no effect of clutch size (Curio et al. 1984, Lazarus & Inglis 1986). In our data, the small clutch size means not only low parental investment but also incomplete clutches, which could also weaken the effect of the clutch size.

We showed that shrikes used the 'chack' alarm calls (Ash 1970, Lefranc & Worfolk 1997, Harris & Franklin 2000) with significantly higher intensity in the presence of sparrowhawk dummy than in case of both forms of the cuckoo and the dove. This suggests that shrike fear the sparrowhawk and avoid attacking it directly, only guarding it and giving alarm calls. On the contrary, reed warbler responded to cuckoo presence with graded alarm calls, while in the presence of the sparrowhawk it stays at a longer distance from the nest (Welbergen & Davies 2008).

Conclusions

Our results show that shrikes are not mistaken by the cuckoo-hawk mimicry, are able to differentiate these two species and attack cuckoos vigorously. This high level of aggression may be a reason why the common cuckoo abandoned the shrike as a potential host, as the adults were not able to successfully parasitise the shrike nests. At our study locations, the shrike population has not been parasitised by cuckoos at least for 20 years, but the shrikes obviously treat the adult cuckoos as a threat to their nests and spend a lot of energy chasing them away. Obviously, it is too short time period for a decline in aggression towards cuckoos, but we may expect that it will decrease after some time. It is very likely that there are more reasons why cuckoos abandoned shrikes as potential hosts. Another reason can be the ability of the shrike to recognizse the difference between parasitic and its own egg, which was suggested in Hungary populations, but it needs further experiments.

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Supplement 1

A B C D

Fig. S1: Plush dummies presented in the experiments. A – common cuckoo (*Cuculus canorus*) (grey form), B – common cuckoo (*Cuculus canorus*) (rusty form), C – Eurasian sparrowhawk (*Accipiter nisus*), D – turtle dove (*Streptopelia turtur*). Photo by Kamila Horáková.