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"Risk related call learning and defence strategies against an avian brood parasite"

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Sandra Wiedermann, BSc

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Contents

1. Abstract

To minimise the costs of raising altricial offspring some species leave the nurture of their young to host species, which is known as brood parasitism. Interactions between these brood parasites and their hosts are a typical example for a reciprocal co-evolutionary arms race. In order to reduce the risk of parasitism, host species evolved species-specific defence strategies, the parasite develops counter adaptations, which again promote improvements of host defences. These adaptations affect the time from egg-laying to offspring development and result in alert aggression against the brood parasite as well as egg- or nestling rejection. To prevent parasitism, birds might also behave cryptic or even invent signature calls between parent and offspring.

Within this context this study compares early parasite detection behaviours by means of call recognition as well as behavioural plasticity through the breeding cycle in an experimental design.

For this purpose, host response was determined for a species naive to brood parasitism, the cave breeding blue tit (*Cyanistes caeruleus*), to investigate if a co-evolutionary context is necessary for this species to be sensible towards cuckoo calls or if risk related call learning occurs. The results suggest that blue tits are indeed able to learn adequate responses quickly as their behavioural patterns change significantly towards cuckoo calls.

Also, this study compared the response behaviour of a regular cuckoo host, the red-backed shrike (*Lanius collurio*) and its behavioural defences according to their breeding stage and the parasites distance from the nest. The results revealed changes in defence strategy towards a cuckoo dummy within the breeding stage (e.g. incubation, nestling stage or fledgling stage). The birds behaved most cryptic during incubation. Alarm calls and attacks were performed most obviously during the nestling stage, which fits the nesting-cue or offspring-value hypothesises.

Keywords: avian brood parasitism, host defence, call recognition, *Lanius collurio, Cyanistes caeruleus*

2. Introduction

For parents of altricial offspring raising young is an energy demanding task. Therefore, some species developed strategies to minimise their own costs and exploit others by relying on a host for the nurture of their young. This is commonly referred to as brood parasitism (Davies et al., 1989). Many species exploit foster parents of their own species, however, interspecific brood parasitism is a prevalent reproductive strategy within many taxa as well (Davies et al., 1989; Petrie and Møller, 1991). Some of the most famous examples of interspecific brood parasitism are found in hymenopterans, fish and birds, the avian system being the best studied one (Davies et al., 1989; Petrie and Møller, 1991; Stevens, 2013).

Because brood parasitism results in costly interactions between host and parasite, it often constitutes a serious impact on lifetime reproductive success (Wyllie, 1981). The hosts of *Cuculus* and *Chrysococcyx* species, for example, can lose their entire brood, hence selection should favour the development of efficient defence strategies (Davies et al., 1989; Langmore et al., 2003; Rothstein, 1990). In order to maintain successful reproduction hosts evolved species-specific defence strategies, the parasites in turn developed counter strategies to challenge the host (Rothstein, 1974, 1990; Takasu, 1998). These so-called host-parasite interactions are the result of a co-evolutionary arms race (Davies and Brooke, 1989a; Lovászi and Moskát, 2004) and provide an excellent model to study co-evolution (Rothstein, 1990).

Strategies to avoid parasitism occur during egg laying, incubation or even later through hatchling rejection (Soler, 2014) They appear strongest when the parasite is relatively large compared to the host and provisioning costs of raising the parasites are high. Also, costs may be more serious to species with a limited number of breeding attempts, e.g. species of the northern hemisphere, where the reproductive season is short (Brooker and Brooker, 1996; Langmore et al., 2005; Medina and Langmore, 2015).

In this context, some hosts evolved the ability to discriminate between their own and the brood parasite's eggs (Lotem, 1993; Moskát et al., 2008). In favour of egg recognition, some species reduce variation in egg coloration and colour patterns within a clutch but increase variation among clutches (Honza et al., 2004 a; Stokke et al., 1999).

To ensure their reproductive success, female common cuckoos (*Cuculus canorus*) developed a set of behavioural strategies as counter-adaptations. These involve rapid laying of small, mimetic eggs (Davies et al., 1989), thickened and solid eggshells (Antonov et al., 2010) and the removal of host eggs to maintain the original clutch size (Moksnes and Røskaft, 1989). Moreover, the cuckoo chick usually hatches first and evicts all other eggs or hatchlings to receive the absolute misdirected parental care of the host parent (Davies and Brooke, 1989a).

In other parasitic species like the brown-headed cowbird (*Molothrus ater*), the parasitic chick outcompetes the other nestlings in size and begging intensity which then leads to starvation of the true offspring (Kilner et al., 1999; Lichtenstein and Sealy, 1998; Payne, 1997). In order to avoid these costs some hosts evolved the ability to reject parasitic young, even if this is more delicate then egg rejection (Langmore et al., 2011). Unlike eggs, offspring appearance will dramatically change with time, and due to asynchronous hatching, the phenotype can vary within putative nestlings (Davies and Brooke, 1988). The risk, and consequently the costs, of rejecting the own offspring are high (Langmore et al., 2009). Still, some species like the superb fairy wren (*Malurus cyaneus*) specialised on nestling rejection, although the parasites even mimic the skin coloration (Langmore et al., 2011). To ensure parasite recognition the mother performs specific signature calls during incubation, which are learned by the embryo and later reflected in the begging calls of the young. The absence of this particular “password” indicates the presence of a brood parasite (Colombelli-Négrel et al., 2012).

Still, prior experience with parasites is often crucial to evoke an efficient host response. Less experienced or naive birds are less likely to respond to unknown calls or mistake the parasite for a small bird of prey (Davies and Welbergen, 2008a; Trnka and Prokop, 2012). Cuckoos, for example, share plumage and flight characteristics with European sparrow hawks (*Accipiter nisus*). This appearance could lead to a wrong impendence estimation in potential hosts and allows cuckoos to approach host nests (Davies and Welbergen, 2008a; Feeney et al., 2015; Welbergen and Davies, 2009).

Alternative options for hosts to avoid brood parasitism are to breed in inaccessible places like caves (Rutila et al., 2002), or to guard the nest aggressively by mobbing or attacking the

parasites, which should ensure reduced parasitism rates as predicted by the frontloaded parasite defence hypothesis (Strausberger, 2001; Yasukawa et al., 2016).

Incidentally, behavioural interactions like host aggression are more flexible than egg-rejecting behaviour (Røskaft et al., 2002; Yasukawa et al., 2016). Therefore, individuals should adjust their defence behaviour depending on the risk of receiving a parasitic egg. For example, reed warblers (*Acrocephalus scirpaceus*), attack parasites more often in areas with high parasite density and therefore high parasitism risk (Welbergen and Davies, 2009). However, studies on redwing blackbirds (*Agelaius phoeniceus*) suggest that aggression is not always beneficial. More aggressive hosts suffer more frequently from parasitism, since parasites use active and passive strategies to locate host nests, including systematic search and cryptic observations of nest-building (Robertson and Norman, 1976; Yasukawa et al., 2016). Host behaviour could therefore provide parasites with information of a potential nest which might stimulate parasites to increase the searching effort as a consequence (Norman and Robertson, 1975). Furthermore, aggressive interactions may cause injuries on both sides or attract predators (Welbergen and Davies, 2008).

Hence, defence behaviours should be adjustable, depending on current risk. Cryptic behaviour might be more suitable than offensive behaviour, at least during some breeding-stages. This idea is known as nesting-cue hypothesis and predicts that host should avoid to produce cues to prevent attention (Clotfelter, 1998). Further, the distance of the parasite to the nest and the breeding stage could influence the birds' decisions because of the changing possibility of receiving a parasitic egg (Clotfelter, 1998).

However, to optimise the response, early parasite detection and recognition is essential. Vocalisation patterns for example, represent an important cue, possibly indicating local parasite abundance over large spatial scales during the reproductive period (Feeney et al., 2012; Griffin et al., 2001; Kleindorfer et al., 2013). Still, the aspects of call recognition and early parasite recognition are so far widely unstudied, even so it is known that birds are able to associate heterospecific alarm calls with predators after only short training periods (Magrath et al., 2015). This behavioural plasticity could also be beneficial in parasite detection (Feeney et al., 2012), inducing a rapid development of anti-parasite behaviour and helping populations to cope with a dynamic environment (Garcia et al., 2014).

In order to gain a better understanding of call recognition and thus early parasite detection, as well as of behavioural plasticity throughout the breeding cycle, we conducted experiments featuring playbacks and a taxidermic specimen of the common cuckoo (*Cuculus canorus*). Their interspecific parasitic reproductive system is well studied, which makes them an ideal model for this study (Davies, 2000; Payne, 1997; Stevens, 2013).

However, to the best of our knowledge, most studies so far focus on egg rejection behaviour (Davies and Brooke, 1989a; Langmore et al., 2005; Moskát et al., 2008) whereby only few shed light on other facets of brood parasitism. For a better understanding of this co-evolutionary arms race, more studies in this direction are needed (Lovászi and Moskát, 2004). Therefore, the first aim of this study was to determine whether a co-evolutionary context is necessary for cuckoo recognition or if a parasite-naive species could learn to respond to cuckoo vocalisations. For this purpose, we exposed blue tits (*Cyanistes caeruleus*) to cuckoo playbacks, combined subsequently with a mounted taxidermic specimen, to see if risk related call learning induces behavioural adjustments. As a species naive to brood parasitism we predict blue tits to be less responsive towards initial cuckoo calls, with the possibility of quick learning progress. Further, we predict a selective advantage for hosts able to detect cuckoo songs as they attempt to attract a mate before egg laying.

The second aim was to investigate the behavioural plasticity of a regular host. Our focus was on cryptic defence behaviour specific to the breeding stage and distance to the nest of red-backed shrikes (*Lanius collurio*), a regular cuckoo host (Davies and Brooke, 1989a). Since risk of parasitism varies in time we suspect differences specific to the breeding stage. During egg laying and incubation we predict shrikes to behave cryptic (Banks and Martin, 2001), whereas parent behaviour should become more offensive with nestling age (Montgomerie and Weatherhead, 1988). We also predict adaptations concerning the distance of the dummy from the nest, assuming more cryptic behaviour in short-distance experiments.

Behavioural observations like this study represent a shorter and less invasive disturbance compared to egg swap experiments, but still provide information about a shared evolutionary history. For this reason, this method should be preferred for ethical reasons (Moksnes et al., 1991; Røskaft et al., 2002).

3. Methods

3.1. Study species and area

3.1.1. Blue tit (*Cyanistes caeruleus*) Linnaeus 1758

The blue tit is an ideal model species to investigate the importance of cuckoo call recognition in terms of early parasite detection, as well as the learning ability after visual presence of cuckoos. Since only few cases of natural parasitism are known, they represent a model species naive to cuckoos (Grim et al., 2014). Due to the low parasitism rate, they can be expected to have less or no experience with cuckoos and cuckoo parasitism and to have not evolved any recognition patterns. This fact is also reflected in the acceptance of foreign eggs in blue and great tits (Davies, 2000; Davies and Brooke, 1989a).

The experiments were conducted from April to May in a nest-box population in Pressbaum, near Vienna (48°18´N, 16°8´E), containing 200 nest boxes whereof 50 were occupied by blue tits. The nest boxes were located in a forest mostly composed of hornbeams and European beeches. Despite the sympatric cuckoo distribution, blue tits are less susceptible to cuckoo parasitism because their reproductive periods don't intersect (Davies, 2000).

3.1.2. Red-backed shrike (*Lanius collurio*) Linnaeus 1758

Red-backed shrikes represent an ideal model species to investigate the plasticity in anti-parasite behaviours throughout the breeding cycle. Multiple traits, like an invertebrate diet or open-cup nest in thorny pastures, characterise this species as an excellent and frequently used host for the common cuckoo (Davies, 2000; Welbergen and Davies, 2009). The shrike's usual habitat includes open areas containing solitary trees or bushes, providing suitable perches (Lefranc and Worfolk, 1997) which are also used by cuckoos to observe the hosts (Welbergen and Davies, 2009). Further, the breeding seasons of red-backed shrikes and cuckoos concur.

The experiments were conducted during the breeding season from May to July (Harris and Franklin, 2010) in an extensive study area in Lower Austria which reached from the Wagram (48°25'N 15°46'E) over the Tullnerfeld (48°13'N 15°57'E) (Figure 1). The distribution can be explained by territory claims and habitat quality, since the preferred habitat is vulnerable due to the intensification of extensive agriculture (Golawski and Golawska, 2008; Lefranc and Worfolk, 1997).

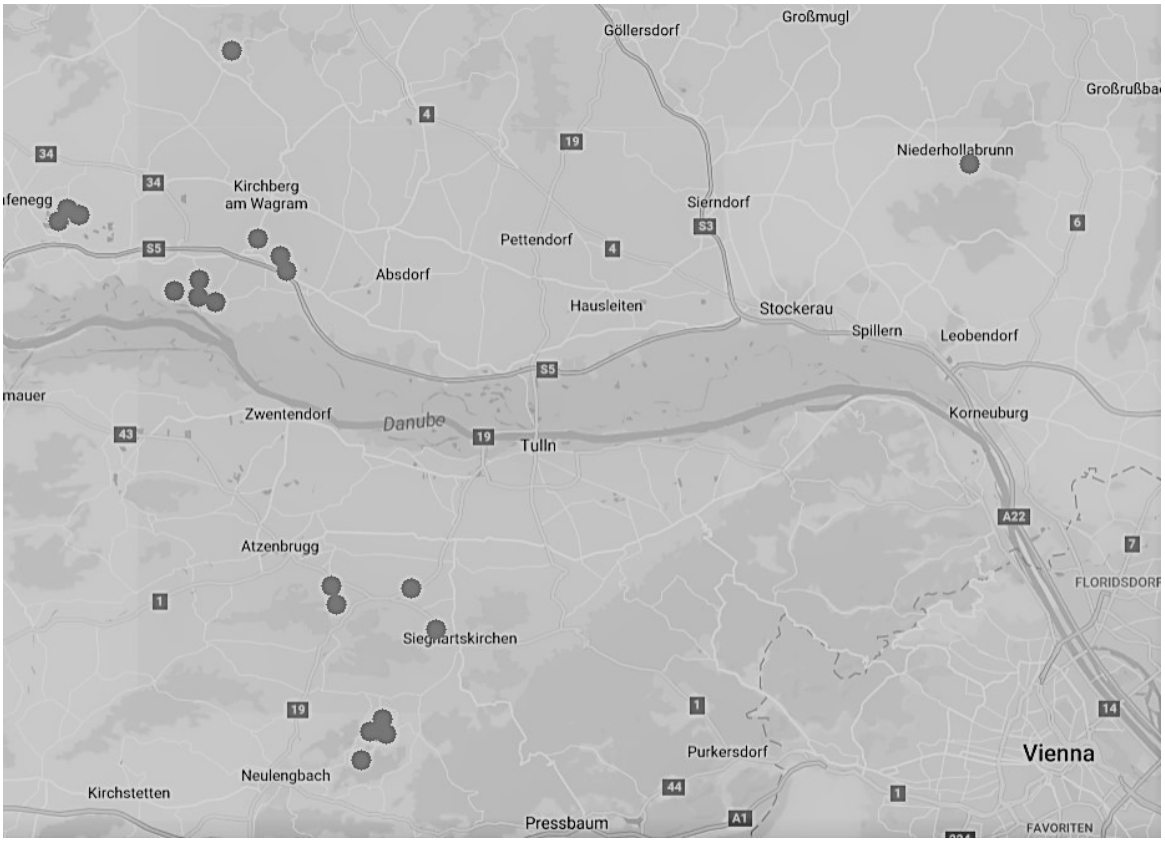

Figure 1. Red-backed shrikes nest sites distribution throughout lower Austria. The breeding pairs are marked with dots (Map data ©2018 Google).

3.2. Experimental design

For the playback experiments three different cuckoo calls were used, originating from cuckoos in south Germany and Austria. Playbacks were edited with version 2.1.2 of Audacity® (Pittsburgh, Pennsylvania: Audacity Team), to simulate a natural call frequency, which resulted in alternating 30 seconds of calls and 10 seconds of silence. The files where

played via Bluetooth as .wav files from an iPhone 6s (Cupertino, California: Apple Inc.) via Pure-Fi Mobile speakers (Lausanne, Swiss: Logitech).

The nests of both study species have been monitored regularly to track the breeding stages and locate the best time to conduct the experiments.

The specimen was placed on a tripod close to shrubs or, if possible, directly in shrubs facing towards the nest. The speaker was mounted directly underneath the specimen. Due to observations prior to the experiments (pre-trials), we confirmed that the birds reacted towards the dummy and not towards the disturbance in general.

Observations were performed via binoculars from 15 - 20 meters to minimise the impact. In order to ensure the wellbeing of the host pair, their behaviour was observed for further five minutes after the trials.

Since the ejection of parasitic eggs occurs mostly during incubation, no experiments were performed during the laying period (Moskát and Fuisz, 1999). Further, we intended to minimise the risks of nest desertion, due to the higher contributed investment (Mayfield, 1975).

3.2.1. Risk related call learning in a naive host species

This experiment investigated whether a parasite-naive species, namely blue tits, recognise the isolated calls of a brood parasite and/or whether they can learn them.

The experiments started on day 12±1 of incubation and consisted of three parts: For the initial trial (A), a speaker was set up close to the nest to play cuckoo playbacks. The experimental procedure was started after a three-minute pre-trial period where the behaviour was recorded without any stimuli. Then cuckoo calls were played for three minutes.

The learning trial (B) started after two hours. Now, in addition to the speaker, a cuckoo dummy was mounted one meter from the nest and presented for one minute. This procedure was repeated three times with at least one-hour intermittences. Again, the behaviour was recorded prior to the start of the call playback.

The third part of the experiment was conducted on the following day to minimise the risk of a customisation. For the habituation trial (C) the isolated calls were played to see if the blue tits may readjust their response in comparison to the initial playback trial (A) (Figure 2).

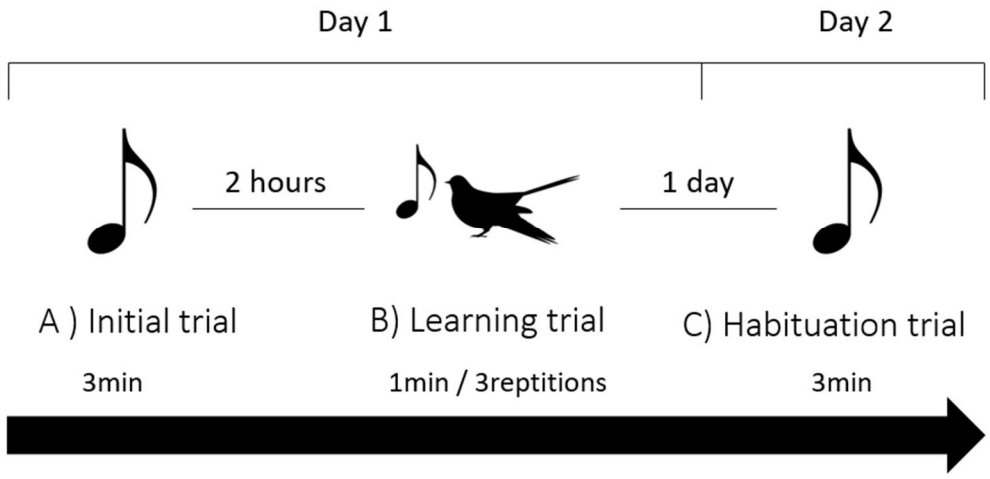

Figure 2: The experimental design to investigate the learning ability in a naive host species, the blue tit. During the initial trial (A) the birds were confronted with isolated cuckoo playbacks, whereas playbacks were combined with a dummy for the three learning trials (B). Conclusive, again isolated playbacks were offered for the habituation trial (C) to see if any behavioural adjustment occurred. The musical note represents playback trials, whereby the note combined with cuckoo silhouette represents learning trials featuring the dummy.

The following defence behaviours were recorded in 10s intervals: the number of approaches within 2m (approaches), the intervals spent vocalising (alarm calls), the nearest approach to speaker or dummy (minimal distance, in m) and the time until the birds started to react from the start of the call playback (latency, in s). These behaviours, as well as attacks, represent nest defence behaviour which might increase the success of the brood but also impose survival costs on adults (Montgomerie and Weatherhead, 1988). Mahr et al. (2014) also notes that minimal distance behaviour poses a higher risk for the parents than alarm calls.

This experiment was originally designed to compare a naive species with a regular cuckoo host. In addition to the blue tits we therefore also tested red-backed shrikes within this experimental design. However, the first two red-backed shrike pairs we tested abandoned

their nests after or during the experiment. Thus, we decided for ethical reasons to terminate the experiments with this species.

Both breeding pairs tested expressed cryptic behaviour, neither performing alarm calls nor attacks. Still, both nests were abandoned after the experiments. Therefore, we suggest that red-backed shrikes are already able to estimate the dangers of brood parasitism, at least in this population, and developed behaviour patterns to react. In this case they reacted with nest desertion, which represents no uncommon response towards a brood parasite (Hosoi and Rothstein, 2000).

3.2.2. Behavioural plasticity and host response in relation to breeding stage and parasite distance

This experiment was conducted to investigate the impact of the breeding stage as well as the distance of the parasite from the nest on defence strategies of red-backed shrikes.

Therefore, the experiment was conducted at three different breeding stages. At first, during late incubation (day 12±1 of incubation), second, when the nestlings were 6±1 days old and third, when fledglings were 15±1 days old.

The experiment started when at least one parent was within a range of 20m and not influenced by human disturbance. The cuckoo dummy was placed either in short-distance (5m) or long-distance (15m) from the nest. Each nest was tested with both distances on subsequent days, alternating the beginning sequence. The trial was completed after a third experiment consisting of cuckoo playbacks without a dummy to detect effects due to habituation (Figure 3).

To minimise disturbance by the cuckoo dummy to the host pair, it was removed after 10 minutes exposure at the latest. The behaviour was recorded in 10s intervals, noting characteristic defence variables which included the following behaviours: the intervals spent vocalising (alarm calls), the minimal distance to dummy or speaker, the time until the birds started to react from the start of the call playback (latency) as well as tail-whipping, approaches within 2m and attacks.

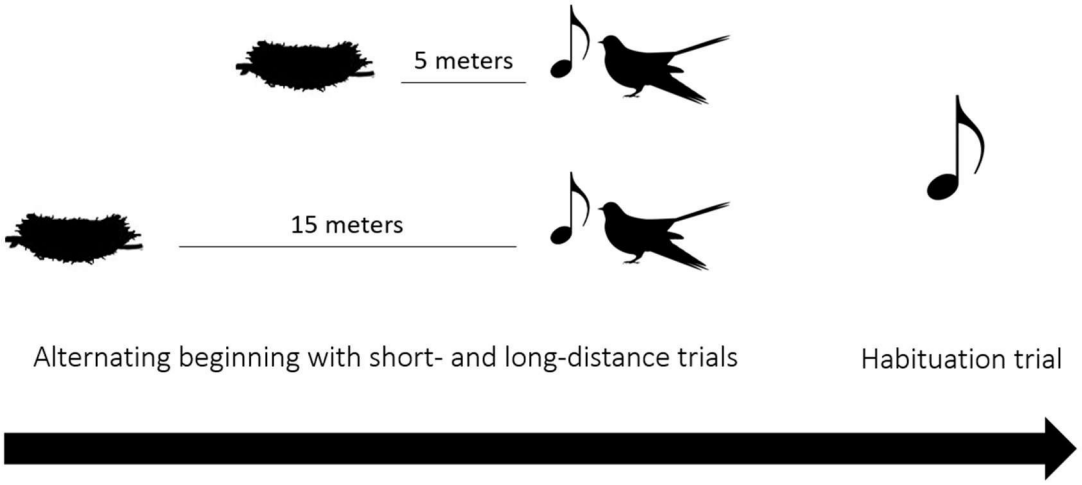

Figure 3: The experimental desgin to investigate the impact of the breeding stage as well as the distance of the parasite from the nest on defence strategies of red-backed shrikes. The short-distance (5m) and long-distance (15m) trials were performed with each breeding pair on subsequent days. A final habituation trial with isolated playbacks was performed to investigate probable behavioral adjustments. The experiment was performed during three different breeding stages (incubation, nestling stage and fledgling stage). The musical note represents playback trials, whereby the note combined with cuckoo silhouette represents learning trials featuring the dummy.

3.3. Statistical analysis

For statistical analyses IBM SPSS Statistics 21.0 (Armonk, NY: IBM Corp.) was used. Absolute values were used for graphs, which were constructed with Sigma Plot 4.0 (Erkrath, Germany: Systat Software GmbH). For visual representation, bar charts using means and standard errors were applied.

To test call recognition and a possible learning ability, we tested a total of 15 breeding pairs of blue tits. A one-way repeated measured analysis of variance (ANOVA) was conducted to evaluate the differences between the experiments of the following variables: minimal distance, latency and alarm calls. We used a post hoc analysis (Fisher's least significant difference test) for single comparisons in a multiple design.

In order to test the importance of breeding stage and parasite distance for host response 14 red-backed shrike pairs in three different breeding stages were tested. A Mixed-Design ANOVA (repeated measures with a between subject factor) with the nest stage as between subject factor was used to investigate the differences between the chosen traits (latency and minimal distance) depending on the experiments and nest stage.

Alarm calls mostly occurred during the nestling stage and not at all during incubation, we used presence/absence data and performed a Chi-squared test. We combined data from males and females to reflect the total response (Gill et al., 1997).

Two nests were tested in 2 stages. The data was still treated as independent, given the experiments were two weeks apart, and there are no indications that a learning effect occurred (Tryjanowski and Goławski, 2004).

3.4. Ethics statement

Discussed and approved by the institutional ethics and animal welfare committee in accordance with GSP guidelines and national legislation (licence number: ETK-11/12/2017).

4. Results

4.1. Risk related call learning in a naive host species

The results of the consecutive experiments initial trial (A), learning trial (B) and habituation trial (C) indicate significant effects between each of the tested behaviours: alarm calls, minimal distance and latency (Table 1).

The blue tits performed significantly more alarm calls during the learning trials (B) and the habituation trials (C), than during the corresponding pre-trials (no stimulus). Further, they reduced the minimal distance as well as the latency after the playbacks started.

Table 1. Results for the response of blue tits to cuckoo playbacks and dummy in the behaviours alarm calls, minimal distance and latency between the experiments initial trial (A), learning trial (B) and habituation trial (C). Results of a one-way repeated measured ANOVA comparing each trial with its associated pre-trial. The musical note represents playback trials, whereby the note combined with cuckoo silhouette represents learning trials featuring the dummy.

	Experiment	Mean ± SE	F	p	N
Alarm calls (s)		4.667 ± 12.184	0.147	0.707	15
		-3.333 ± 1.189	7.857	**0.013**	15
		-19.333 ± 29.391	6.491	**0.023**	15
Minimal Distance (m)		0.500 ± 1.846	0.073	0.790	15
		1.722 ± 0.586	7.659	**0.011**	15
		6.133 ± 2.376	6.662	**0.022**	15
Latency (s)		8.667 ± 23.378	0.137	0.716	15
		8.889 ± 2.715	14.979	**0.006**	15
		38.933 ± 14.475	7.235	**0.018**	15

A post hoc test revealed no significant difference between the pre-trial and trial of the initial trial (A). The results of the pre-trial and the habituation trial (C) however differ significantly in all tested variables.

During the initial trials (A), average alarm call performance was lower than during the pre-trials (Figure 4). The alarm call performance significantly increased during the learning trials (B) and even more during the concluding habituation trials (C).

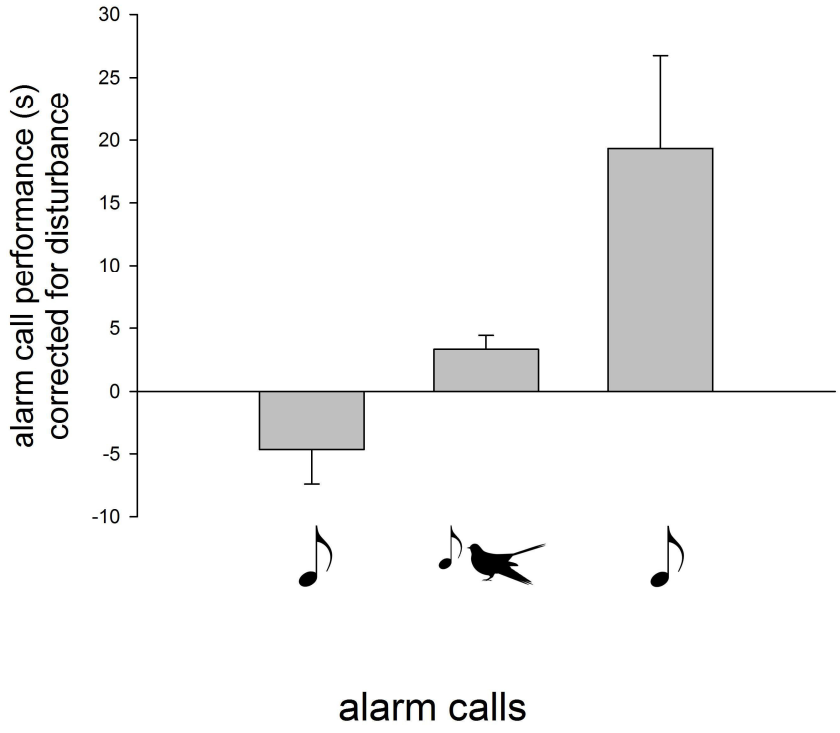

Figure 4. Average alarm call performance in seconds during cuckoo playback and dummy experiments. The x-axis represents the pre-trials and results are shown as mean ± SE. During the initial trial (A), confronted with cuckoo calls, the birds performed less alarm calls compared to the corresponding pre-trial, resulting in negative values. The reaction towards the calls during the habitation trials (C) differed significantly from the reactions of the corresponding pre-trial. The musical note represents playback trials, whereby the note combined with cuckoo silhouette represents learning trials featuring the dummy.

The average distance to the speaker was similar during both playback trials (A: 15.0±2.1m and C: 15.3±2.7m) but differentiate within their pre-trials. During the learning trials (B) the birds kept a greater distance (19±8.6m).

A one-way repeated measures ANOVA revealed no significant difference between the pre-

trial and trial of the initial trial (A) but suggests significant results between the learning trials (B) and the habituation trial (C) within the minimal distance (Figure 5). If the birds exceeded a distance of 25 meters we treated them as absent.

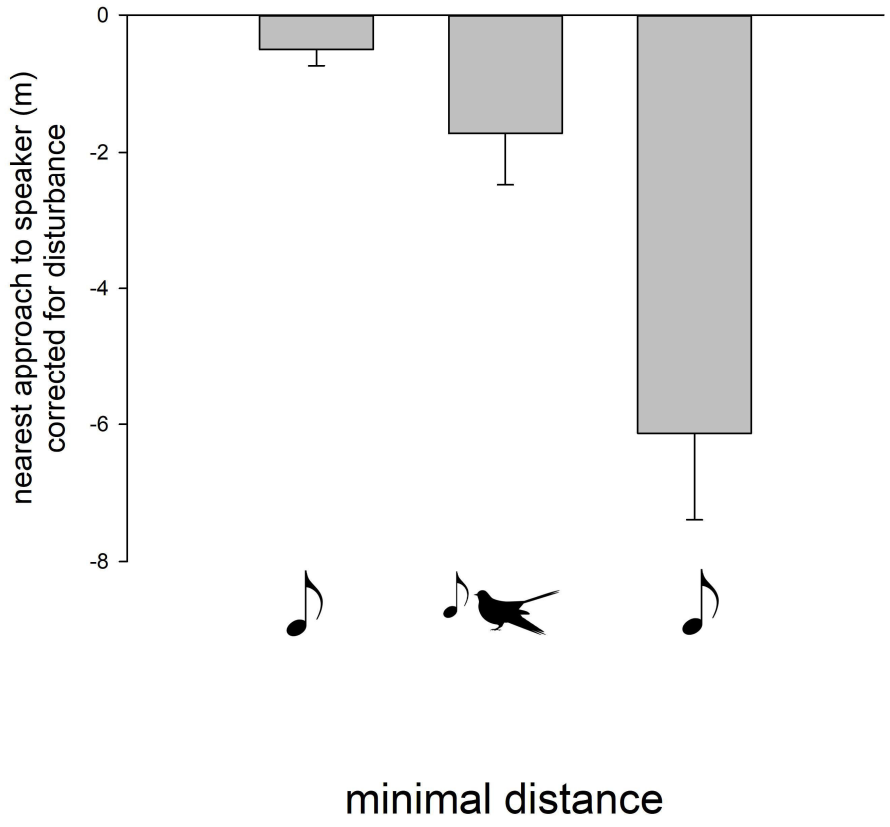

Figure 5. The nearest approach to cuckoo playbacks and dummy in meters. The x-axis represents the pre-trials and results are shown as mean ± SE. During both playback trials (A and C) the birds approached on average 15 meters. The distance differed significantly from the corresponding pre-trials during the learning trial (B) as well as during the habituation trial (C). The musical note represents playback trials, whereby the note combined with cuckoo silhouette represents learning trials featuring the dummy.

The variable "latency" revealed similar results. The initial trials (A) delivered comparable data, while the learning trials (B) as well as the concluding habituation trials (C) differ significantly from each other (Figure 6).

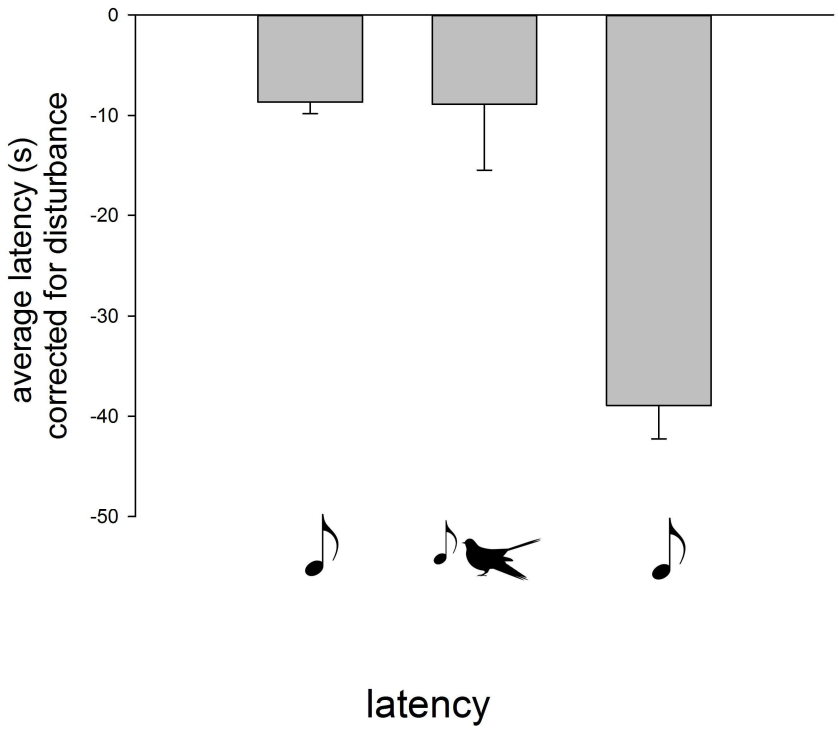

Figure 6. The average latency during the experiments in seconds. The x-axis represents the pre-trials and results are shown as mean ± SE. The latency differed significantly from the corresponding pre-trials during the learning trial (B) as well as during the habituation trial (C). The musical note represents playback trials whereby the note combined with cuckoo silhouette represents learning trials featuring the dummy.

4.2. Behavioural plasticity and host response in relation to breeding stage and parasite distance

Within the second experiment design red-backed shrike breeding pairs (n=14) were tested with regard to their reaction towards a cuckoo dummy according to their breeding stage and distance to the nest. Each nest was tested three times, in short- and long-distance experiments as well as the concluding habituation trial, which resulted in 42 experiments in total. Observations of breeding pairs to naturally occurring cuckoo calls revealed cryptic behaviour reaction.

Alarm calls never occurred during incubation and were performed mostly during the nestling stage. Still, they also occurred during the playback trial in the fledgling stage (Figure 7). Both sexes performed calls. During the short-distance trials, male vocalisations prevailed (80 vs.

6s), contrary to the long-distance trials, where the females performed more alarm calls (32 vs. 66s). A Chi-squared test revealed no differences in the experiments (short-distance, long-distance and habituation) but suggests significant differences in nest stages ($\chi^2 = 15.173$, df = 2, p = 0.001).

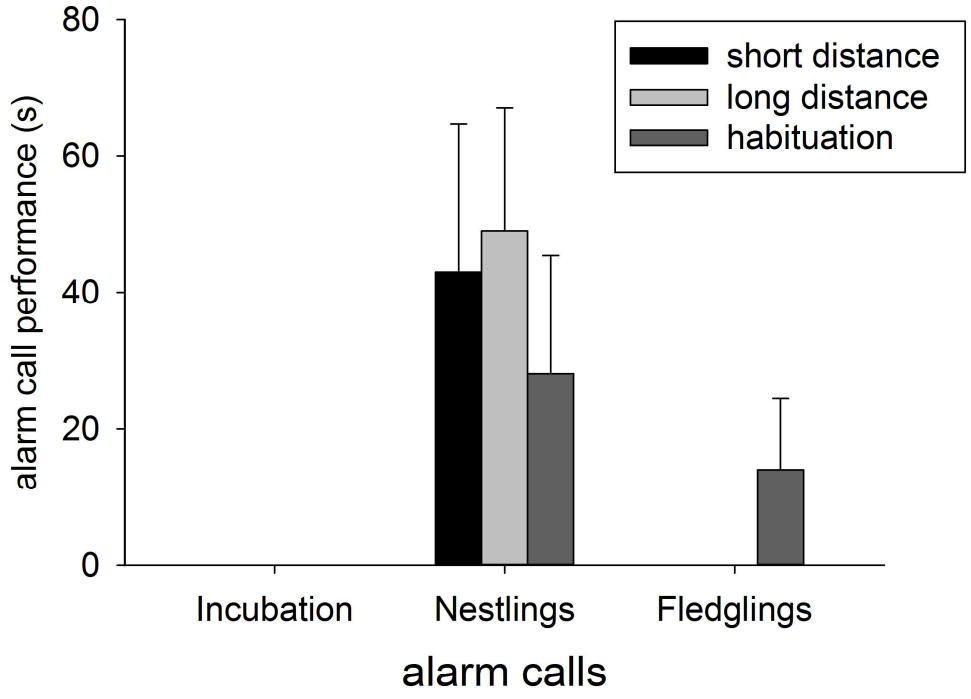

Figure 7. The alarm call performance in the different nest stages: incubation, nestling and fledgling stage. The cuckoo specimen was placed at different distances from the nest, resulting in short-distance (5m) and long-distance (15m) experiments. During the habituation trials the birds were confronted with playbacks only. No alarm calls were performed during incubation and the majority was exhibited during the nestling stage, which results in significant differences in a Chi-squared test. In the fledgling stage, alarm calls were only performed during the habituation trial.

In total, 6 attacks towards the dummy were observed during the nesting stage. 3 attacks occurred during the short-distance trial, the other 3 during the long-distance trial.

The latency to respond revealed, with one exception during incubation, quick behavioural responses. In the exceptional case, the reaction set in delayed compared to the other experiments (187.5±64.2s). A post hoc test revealed no significant differences within the

experiments (short-distance, long-distance and habituation). The latencies vary from 60±40.2 to 92±26.2s during the long-distance trial and from 28±14.7 and 112±47s during the habituation trials (Figure 8).

A mixed design ANOVA revealed significant differences between the experiments (short-distance, long-distance, habituation). Also, the interaction between the experiments and nest stage (experiment*nest stage: Wilk's Lambda 0.398, F (4, 20) = 2.928, p = 0.047) revealed significant results.

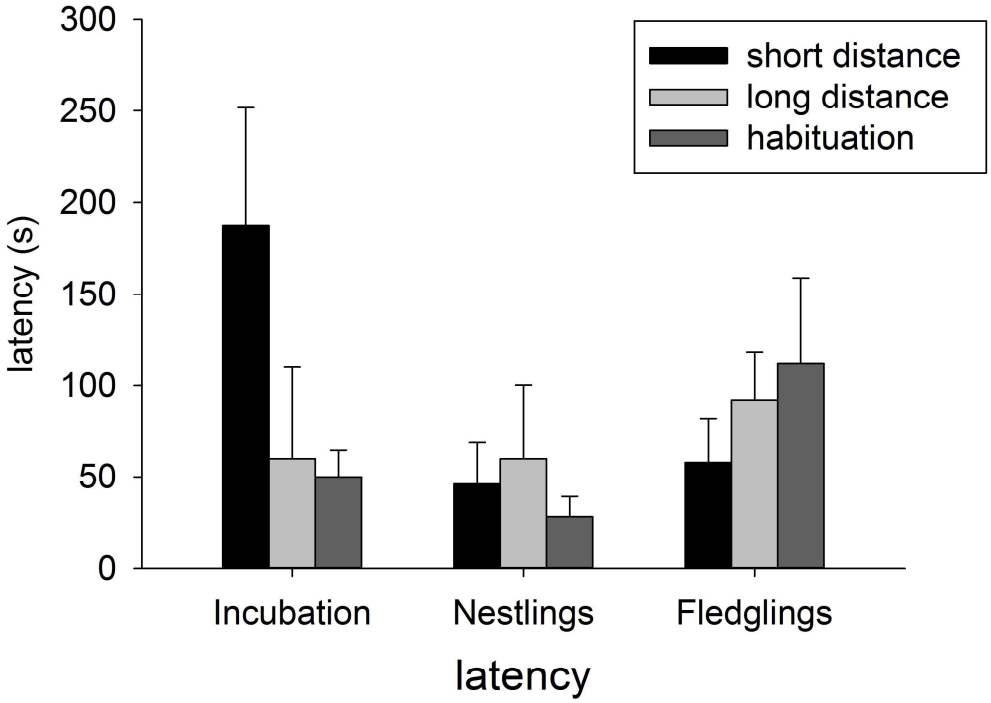

Figure 8. The latency during the different nest stages: incubation, nestling and fledgling stage. The cuckoo specimen was placed at different distances from the nest, resulting in short-distance (5m) and long-distance (15m) trials. During the habituation trials, the birds were confronted with playbacks only. The longest reaction-time occurred during the short-distance trial during incubation which differs significantly from the other experiments conducted during incubation. The interaction between the experiments and the nest stage also revealed significant results.

The minimum distance of the birds to the dummy was shortest during the short-distance trials (6.3±0.99m) and had a greater range within the long-distance trials (10.8±0.13m).

Tail-whipping was displayed by both, males and females and most distinctively performed during the long-distance trials in the nestling stage. Still, a mixed design ANOVA revealed no significant differences between the nest stages and experiments (Wilk's Lambda 0.991, F (2, 10) = 0.043, p = 0.948).

The reactions during the habituation trials were on average the least distinct, hence we can't assume that any kind of behaviour adjustment occurred.

5. Discussion

5.1. Risk related call learning in a naive host species

Our results revealed that blue tits increase reactivity towards the calls of the common cuckoo after they learned to associate the call with a model of the parasite. This is reflected by increased numbers of alarm calls as well as by a decreased time to react (latency) after the onset of playbacks and the closest approach (minimal distance).

Brood parasitism evolved within a co-evolutionary context (Davies and Brooke, 1989a), hence the blue tit represents a species naive to cuckoo parasitism. We therefore expected them to be less adapted to cuckoo parasitism and being less responsive than species which are frequently parasitised. However, our results indicate that they may be able to quickly learn a risk related signal.

In fact, blue tits reacted less towards cuckoo vocalisations (advertised by initial playback, see results) but response intensity increased in combination with a cuckoo dummy and was even higher to isolated cuckoo calls after being exposed together (combining visual and acoustic stimuli). Thus, blue tits performed the fewest alarm calls during the original presentation of cuckoo calls, call intensity increased during the learning trials featuring the dummy (B) and further increased in the subsequent call presentation (C). There is a significant difference in all behavioural traits recorded, also including the nearest approach to the speaker as well as the latency to respond.

These results indicate a learning effect caused by three short preceding dummy confrontations even though blue tits are usually not vulnerable towards brood parasitism. Their cavity nests are less accessible for cuckoos (Grim et al., 2014; Røskaft et al., 2002) and their breeding cycle starts in April, whereas cuckoos only start laying mid-May, which prohibits high rates of parasitism of blue tits and other related species (Davies, 2000). However, there are still few negligible cases recorded with blue tits being foster parents of the common cuckoo, which were most likely possible due to an enlarged entry to the breeding cavity (Grim et al., 2014). Even if blue tits would be a more accessible host, populations with no current parasitism should still express less adaptations (Davies and

Brooke, 1989b) and from longstanding monitoring in the study population no cases of cuckoo parasitism have been observed.

One possible explanation for the rapid association between call and danger could be the presence of the experimenters. As intruders to their territory they might associate the cuckoo calls with our disturbance. However, the repeated presence of humans or even potential predators with no negative connotation should decrease the birds excitement and results in loss of fear and decrease in defensive behaviour (Cooke, 1980; Knight and Temple, 1986). Further, we observed a significant increase in defensive behaviours after the pre-trials (no stimulus) in comparison to the habituation trials (C). Hence, we assume the impact of our disturbance decreased during the experiments and exclude significant effects of human disturbance on the behaviour of the target individuals.

The question arises, whether learning is of importance in parasite defence. Early parasite detection and adequate behavioural responses could for instance prevent the parasite from laying and therefore save the investment (Feeney et al., 2012; Sherman et al., 1997). Hence, learning could facilitate a quick adaptation to brood parasitism to optimise behavioural responses. In this context cuckoo vocalisations could offer an especially extensive cue of local parasite abundance and current parasitism risk (Feeney et al., 2012; Kleindorfer et al., 2013).

However, our results suggest that blue tits are quickly able to associate an acoustic signal with a negative audible indicator (Davies and Welbergen, 2008b). This behavioural plasticity is already known from predator recognition studies (Magrath et al., 2015). Rapid behavioural adjustments are essential adaptations to diversifying environments such as changes in community composition, urbanisation, climate change or invasive species (Garcia et al., 2014; Møller, 2009). Still, context dependent call learning in relation to an event of parasitism is unlikely because cuckoos usually behave secretive during nest searching as well as during laying (Honza et al., 2002).

The cryptic plumage of cuckoos further reduces the risk of detection by hosts and therefore improve the laying success of parasitic cuckoos (Krüger et al., 2007). However, due to their barred chest plumage naive birds might mistake cuckoos for birds of prey with the same pattern of lines like the European sparrow hawk (*Accipiter nisus*) (Welbergen and Davies,

2009). This could also be reflected in our results, since the blue tits stayed farther when the dummy was in display. Sparrow hawks represent no threat for eggs or nestlings but constitute a considerable danger for adults and fledged young. For these reasons, adults do not attack sparrow hawks and stay at safe distance compared to other predators like snakes (Mahr et al., 2014). Hence, it is still unclear if blue tits associated the taxidermic specimen as cuckoo or as predatory bird (Davies and Welbergen, 2008a). The shortened distance during the conclusive call presentation (habituation trial, C) could indicate a correct association. Still, even if our results suggest this interpretation more research is needed, e.g. with control specimens.

This rapid association between cuckoo call and a possible threat could be induced by the same characteristics which provide cuckoos access to host nests. Owing to their appearance naive birds could answer their presence with increased attention and therefore, prevent them from laying. Hence, our results suggest that hawk mimicry could also bear disadvantages for brood parasites.

5.2. Behavioural plasticity and host response in relation to breeding stage and parasite distance

In our second experiment we tested the nesting-cue hypothesis by investigating whether red-backed shrikes vary their responsiveness towards the dummy and the playback of a cuckoo regarding their breeding stage. Our results are in line with this idea since the individuals neither performed alarm calls nor attacks during incubation but expressed these behavioural patterns frequently during the nestling stage.

Red-backed shrikes are a highly parasitised species and evolved a variety of behavioural adaptations to decrease the risk of cuckoo parasitism and hence the loss of the brood. They evolved a high degree of egg rejection and are also known to mob the parasite aggressively (Lovászi and Moskát, 2004). Hence, they represent an excellent model to study pre-parasitic nest defence (Lovászi and Moskát, 2004; Moskát and Fuisz, 1999).

However, in order to minimise the risks of parasitism or predation birds remain in a constant conflict whether to be active and attack a brood parasite or to stay cryptic and not attract attention (Lima and Dill, 1990). Both strategies may be beneficial or bear costs since

aggression could help to dispel the parasite and prevent it from laying but it could also attract attention to the nest (Lima and Dill, 1990). We therefore predicted that our model species would change their strategy with altering risks, e.g. the breeding stage or the distance of the parasite from the nest.

In fact, our results revealed that red-backed shrikes confronted with a cuckoo dummy displayed no conspicuous behaviour and performed neither alarm calls nor attacks during incubation. These results are in line with the nesting-cue hypothesis, which conveys that defence behaviour could reveal the nesting site. For example, brown-headed cowbirds (*Molothrus ater*) use different cues to locate host nests and lay more eggs in nests where the hosts are active. Also, vocalisations close to the nest delivers important information for the parasite, e.g. in willow flycatchers (*Empidonax traillii*) nests with males singing close by get parasitised more often (Banks and Martin, 2001). Therefore, it might be advantageous to behave inconspicuously and to not react towards a brood parasite like the common cuckoo (Robertson and Norman, 1976).

Further, parasites and predators are dependent on cues for locating nests and probably only find them if they are already relatively close (Clotfelter, 1998; Montgomerie and Weatherhead, 1988). Only if the threat undercuts a certain threshold distance which enables it to see, hear or smell the nest, the parents reduce the probability of detection by confusing the predator with defensive behaviours or silencing the offspring (Montgomerie and Weatherhead, 1988). This behaviour is described by the chick-reaction hypothesis, which suggests that the alarm calls are directed towards the nestlings to inform them about possible threats and how to react e.g. hide in the nest or maybe even leave the nest (Kleindorfer et al., 1996). Still, the risk of an encounter is facilitated by the conspicuousness and cryptic behaviour could also be beneficial (Skutch, 1976).

During egg laying and incubation few cues reveal the nest site, hence parents perform less compensation behaviours. This is also reflected in our results regarding tail-whipping behaviour. This sign of arousal (Zack, 1986) was displayed most distinctive during the nestling stage, which could also be explained by the nesting-cue hypothesis. The performance exceeded during the long-distance trial, presuming it fell below the defence-threshold distance. On the other hand, the short-distance trial could have been too close, rather leading to secretive behaviour. However, the results didn't differ significantly,

therefore this behaviour might be less meaningful in this context. Still, more research with an increased sample size is needed for a convincing conclusion.

Incidentally, red-backed shrikes might mistake the cuckoo dummy for another species, even though there is strong evidence that hosts are often able to discriminate cuckoos from sparrow hawks or jays (Duckworth, 1991; Moksnes and Røskaft, 1989). The hawk like appearance of cuckoos could be reflected in the brood-value hypothesis, which addresses that increasing offspring value should lead to increased parental defences (Onnebrink and Curio, 1991). Brood-value arises through already invested care, reduced time to re-nest and the increased likelihood of the offspring to reach reproductive age (Montgomerie and Weatherhead, 1988; Tryjanowski and Goławski, 2004). Hence, parents increase their effort with nestling age by compensating the arising movements and sounds (Harvey and Greenwood, 1978). Still, cuckoos represent no survival threat to either adult or already hatched birds (Wyllie, 1975), and we cannot ensure a correct recognition of the dummy.

The latency to respond was the only behaviour significantly changing between different nest stages, resulting in a longer timespan during incubation. The latency was also the only behaviour with significant differences considering the distance of the dummy from the nest. The first response set in latest during the short-distance trial while incubation. This time can be regarded as most vulnerable period for a breeding pair. Any behaviour could have contained cues, leading the parasites attention to the nest. As long as the risks of parasitism are high, only few suspicious sounds are produced. Hence cryptic behaviour seems beneficial for the hosts at this breeding stage (Robertson and Norman, 1976).

Except for the latency, we found no significant differences between the tested distances. Interestingly, Clotfelter (1998) found a stronger response towards a cowbird dummy below a 5-meter distance, whereas our results rather suggest increased responses with increasing distance. These differences could be explained by the different risks of the brood parasites since cowbird parasitism does not necessarily lead to a complete loss of the brood (Davies, 2000). Further, the tested breeding stages could influence these results, since Clotfelter performed all his experiment during the laying period.

We found no evidence that any kind of behaviour adjustment occurred after the experiments featuring the dummy. On average, the reactions during the concluding

playback-only experiment were least distinct. However, we suggest that the birds are already able to estimate the dangers of brood parasitism correctly (Lovászi and Moskát, 2004) and already know the association between cuckoo calls and the brood parasite itself. This is also reflected by the results of the terminated experiments with different experimental design. Both tested red-backed shrikes deserted their nest after the dummy was attached close to the nest. Some species evolved this behaviour in response to nest visits of cowbirds (Rothstein, 1975), hence this could also be applicable for cuckoo hosts.

Moreover, because we only used one taxidermic specimen, which represented the rufous/brownish female morph, the dummy might represent a possible error source. There are no studies on red-backed shrikes reacting differently to the two morphs, but the great reed warbler (*Acrocephalus arundinaceus)* treated the rufous coloured morph the same way as the grey one (Honza et al., 2006). We also understand that our sample size is rather small and more studies in this direction are needed. For increased validity we suggest to perform similar experiments with more control groups, even if previous studies revealed that cuckoo hosts behave differently towards cuckoo specimens compared to other specimens (Duckworth, 1991; Moksnes and Røskaft, 1989).

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7. Figures

Figure 1

Distribution map, Map data ©2015 Google, 18.01.2018

https://www.google.at/maps/@48.3711673,16.0867448,11z

Table 1, Figure 2 - 6

Cuckoo silhouette, 05.02.2018

https://image.shutterstock.com/image-vector/collection-bird-silhouettes-set-birds-260nw-616208333.jpg

Musical note, 05.02.2018

https://pixabay.com/de/note-musik-notenschl%C3%BCssel-melodie-1314939/

8. Zusammenfassung

Um die Kosten von anspruchsvollem Nachwuchs zu minimieren, nutzen einige Arten die Ressourcen anderer. Eine Möglichkeit um sich einen Vorteil zu sichern, ist die komplette Jungenaufzucht an Wirtstiere zu übergeben. Dies ist als Brutparasitismus bekannt. Interaktionen zwischen diesen Brutparasiten und deren Wirten verursachen einen reziproken Co-evolutionären Prozess, welcher als Wettrüsten bezeichnet wird. Durch eine gemeinsame evolutive Geschichte haben die Wirtspezies spezifische Strategien entwickelt um die Auswirkungen von Brutparasitismus zu reduzieren. Der Parasit beantwortet diese mit Anpassungen seinerseits. Diese Adaptionen betreffen meist die Zeitperiode zwischen der Eiablage und der Entwicklung der Jungtiere und können als verwerfen von Eiern oder Nestlingen oder als Aggressionen gegenüber dem Brutparasiten ausgebildet sein. Auch kryptisches Verhalten oder Signaturrufe zwischen Eltern und Jungtieren können die Chancen parasitiert zu werden verringern.

In diesem Kontext untersucht diese Studie die Früherkennung von Brutparasiten anhand von Rufen sowie die Verhaltensplastizität innerhalb des Brutzyklus in einem experimentellen Versuchsdesign.

Das Verhalten von einer normalerweise nicht von Brutparasitismus betroffenen Art, der höhlenbrütenden Blaumeise (*Cyanistes caeruleus*), wurde analysiert um zu erforschen ob ein co-evolutionärer Kontext notwendig ist um Kuckucksrufe zu erkennen, oder ob risikobezogenes Lernen möglich ist. Die Ergebnisse zeigen, dass Blaumeisen dazu in der Lage sind Rufe schnell mit Gefahr zu assoziieren, da sich ihr Verhalten gegenüber Kuckucksrufen signifikant verändert.

Weiters, wurde im Rahmen dieser Studie das Verhalten eines geeigneten Wirtes, dem Neuntöter (*Lanius collurio*), hinsichtlich seiner Reaktionen in verschiedenen Brutstadien untersucht. Die Ergebnisse zeigen, dass Neuntöter ihre Verteidigungsstrategie gegenüber dem Kuckuck dem Brutstadium anpassen (z.B. während Inkubation, Nestlingsphase oder flüggen Jungtieren). Die Vögel verhielten sich während der Inkubation eher kryptisch. Während der Nestlingsphase zeigten die Vögel die meisten Alarmrufe und Attacken, was mit den „nesting-cue“ oder „offspring-value“ Hypothesen übereinstimmt.