Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

One trait is not enough: visual discrimination between cuckoos and hawks by red-backed shrikes

Michaela Syrová

syrovm00@prf.jcu.cz

University of South Bohemia

Jaroslav Bače

University of South Bohemia

Ladislava Zelenková

University of South Bohemia

Johanka Bláhová

University of South Bohemia

Jan Čapek

University of South Bohemia

Roman Fuchs

University of South Bohemia

Petr Veselý

University of South Bohemia

Research Article

Keywords: key features, brood parasite recognition, cuckoo-hawk mimicry, multiple visual cues

Posted Date: November 26th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11718278/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations: No competing interests reported.

Abstract

Accurate discrimination between brood parasites and predators is essential because these enemies require different defensive strategies. Although birds are known to use visual cues for enemy recognition, it remains unclear whether single diagnostic traits are sufficient for categorization. We experimentally tested the importance of bill shape in discrimination between the common cuckoo () and the Eurasian sparrowhawk () by red-backed shrikes (). Breeding shrikes were presented with life-sized models of a cuckoo, a sparrowhawk, a non-threatening control, and two hybrid models in which cuckoo and sparrowhawk bills were experimentally exchanged. We quantified attack behaviour and alarm calling as complementary defensive responses. Changing bill shape modified both behavioural responses but did not cause the manipulated models to elicit the responses typical of the species whose bill they carried. A hawk-like bill reduced attacks on the cuckoo model, whereas a cuckoo-like bill reduced alarm calling in response to the sparrowhawk model. Nevertheless, both manipulated models elicited responses intermediate between those directed at the original cuckoo and sparrowhawk. These findings demonstrate that bill morphology contributes to enemy recognition but is insufficient on its own to determine enemy identity. Instead, they suggest that red-backed shrikes distinguish brood parasites from predators using combinations of visual traits rather than a single diagnostic feature.

Introduction

Correct assessment of threat is essential for reproductive success in birds because different enemies impose different fitness costs and require different defensive strategies (Curio 1976; Caro 2005). Nest predators reduce reproductive success directly through egg or nestling predation, whereas predators of adult birds threaten parental survival and future breeding opportunities. Brood parasites represent another distinct category of threat, as successful parasitism may impose substantial energetic and reproductive costs on hosts (Davies 2000). Because inappropriate responses can themselves be costly, selection should favour the ability to discriminate accurately among different types of enemies and to adjust antipredator behaviour accordingly (Newton 1986; Martin 1995).

Birds have developed a broad spectrum of defensive behaviours against predators and brood parasites, ranging from passive avoidance and alarm calling to intense mobbing attacks (McLean et al. 1986; Caro 2005). The intensity of defence usually reflects the level and type of danger posed by a particular intruder. For example, many passerines respond aggressively to nest predators such as corvids but react more cautiously to predators of adult birds such as sparrowhawks, for which direct attacks may be extremely dangerous (Tryjanowski and Goławski 2004; Strnad et al. 2012). Efficient defence therefore depends on the ability to recognize biologically relevant cues and categorize potential threats correctly.

Visual recognition of predators and parasites is often based on key morphological traits. Birds possess highly developed visual and cognitive abilities enabling rapid categorization of objects according to characteristic features (Lorenz 1937; Zentall et al. 1986). Previous studies suggest that recognition may depend on specific visual signals such as eye colour, body patterning, or silhouette (Scaife 1976; Trnka et

al. 2012; Beránková et al. 2014). The bill shape can also affect the appropriate recognition substantially. Gill et al. (1997) showed that warblers (*Setophaga petechia*) respond less to a brood parasite (*Molothrus ater*) with prolonged bill. However, successful discrimination between similar-looking species likely requires integration of multiple cues rather than reliance on a single feature (Davies and Welbergen 2008).

An especially interesting system for studying visual discrimination is the resemblance between the common cuckoo (*Cuculus canorus*) and the Eurasian sparrowhawk (*Accipiter nisus*). The grey morph of the cuckoo closely resembles the adult sparrowhawk in plumage coloration with barred underparts, yellow eyes, flight style, and silhouette, a phenomenon known as cuckoo-hawk mimicry (Davies and Welbergen 2008; Welbergen and Davies 2011). This resemblance is thought to reduce host aggression during parasitic egg laying by exploiting host fear of hawks. Nevertheless, several host species can distinguish cuckoos from sparrowhawks and respond more aggressively to cuckoos than to hawks (Campobello and Sealy 2010; Trnka and Prokop 2012). The visual cues underlying such discrimination remain incompletely understood. However, it seems plausible that the prolonged bill in cuckoo can be used as a cue for its recognition by potential hosts.

The red-backed shrike (*Lanius collurio*) represents a particularly suitable model species for investigating this question. Red-backed shrikes aggressively defend their nests and show distinct responses toward different classes of intruders, including physical attacks, alarm calls, and mobbing behaviour (Gotzman 1967; Němec and Fuchs 2014). Although cuckoo parasitism in this species has become rare or nearly absent in recent decades (Lovászi and Moskát 2004; Adamík et al. 2009), shrikes still recognize and strongly attack cuckoos while responding more cautiously to sparrowhawks, usually only giving alarm calls (Krausová et al. 2022). The mechanism underlying this discrimination, however, remains unclear.

In this study, we experimentally tested whether bill shape contributes to discrimination between cuckoos and sparrowhawks by red-backed shrikes. We presented models of cuckoos and sparrowhawks with experimentally manipulated bill shapes to breeding shrikes. Specifically, we tested the hypotheses that (1) shrikes respond similarly (attacking more) to cuckoo models and sparrowhawk models fitted with a straight cuckoo-like bill, and (2) shrikes respond similarly (giving more alarm calls) to sparrowhawk models and cuckoo models fitted with a hooked hawk-like bill.

Material and Methods

Study Area

All experiments were carried out during the 2024 nesting period of the red-backed shrike, from 6 June to 7 July, in the Podyjí National Park (48.81°N, 16.00°E) and in Načeratický kopec Natural Monument (48.8323° N, 16.0977° E), close to the town Znojmo in the Czech Republic. The dominant habitat in this area consists of pastures with common hawthorn (Crataegus sp.), wild rose (Rosa sp.), and blackthorn

(Prunus sp.). The red backed shrike frequently nests in these shrubs (Söderström 2008), and favourable nesting conditions in the Podyjí National Park support a large local population.

Studied Species

The red-backed shrike is a small migratory passerine of the Lanius family widely distributed across Europe and western Asia. It inhabits open landscapes with scattered shrubs and trees, such as meadows, pastures, and forest-steppe habitats, where it nests in dense bushes or low trees. The red-backed shrike prays mainly on large insect from the orders Orthoptera, Coleoptera and Hymenoptera (Cramp and Perrins 1994; Olsson 1995) and it is also capable of hunting various vertebrates, such as small rodents, songbirds, lizards, frogs, and it is known to even catch small fish (Hernandez 1995; Lefranc and Worfolk 1997). The species is known for its conspicuous territorial and antipredator behaviour, including alarm calling and active mobbing of potential threats near the nest, as well as for its remarkable ability to discriminate among different types of predators and brood parasites and to adjust its defensive behaviour according to the level and nature of the perceived threat (Strnad et al. 2012; Němec et al. 2015; Syrová et al. 2016; Veselý et al. 2022; Fišer et al. 2025).

Nest Stage Assessment and Experimental Timing

After finding the nest of red-backed shrike, the nesting stage was determined. Incubation stage was assessed using the water flotation method based on egg buoyancy, ranging from eggs resting on the bottom to eggs floating at the water surface (Westerskov 1950). Nestling age was assessed directly at the nest based on eye opening and plumage development (Diehl and Myrcha 1973).

Experiments were conducted at 19 nests containing 3-8-day-old chicks. At this stage, parents have already made a substantial reproductive investment, the likelihood of nest abandonment is reduced, and the probability of strong defensive responses are more likely (Montgomerie and Weatherhead 1988; Strnadová et al. 2018). This ensured that behavioural reactions would reliably reflect parental threat assessment rather than variation in reproductive commitment.

Experimental Stimuli and Morphological Manipulation

To test the role of a single morphological trait in enemy recognition, we presented each breeding pair with artificial bird dummies in randomized order. The models represented: (1) a Eurasian sparrowhawk, (2) a common cuckoo, (3) a cuckoo body with a sparrowhawk bill, (4) a sparrowhawk body with a cuckoo bill, and (5) a European turtle dove (*Streptopelia turtur*) as a familiar non-threatening control similar in body size.

This design allowed us to experimentally isolate the contribution of bill morphology while keeping overall body shape, posture, and plumage pattern constant within each species configuration. By exchanging

bills between the cuckoo and sparrowhawk models, we manipulated a single putative recognition cue while preserving the remaining visual features of the model. This approach enabled us to test whether shrikes rely on a specific diagnostic trait (bill shape) or instead integrate multiple visual cues when discriminating between predators and brood parasites.

All dummies (see Fig. 1) were life-sized and in perched posture with folded wings to approximate a natural threat scenario. They were constructed from a wire frame covered with felt textile and filled with cotton wool. Eyes were made of glass and legs from modelling compound (Modurit). The models were painted with acrylic paints. Comparable dummy methodology has been successfully used in previous studies (Němec et al. 2015; Krausová et al. 2022).

Experimental procedures

Each trial began with a 15-minute pre-exposure observation of a nest to verify that the presence of the observer did not provoke any antipredator reaction in the parent pair. If no defensive response occurred, the dummy was presented on a pole 0.5 meter from the nest and oriented towards it. This standardized positioning ensured equal visual exposure across treatments.

The presentation of each dummy lasted 15 minutes from the moment the dummy was detected by at least one parent. If no parent appeared within 30 minutes, the trial was terminated and the recorded behaviours scored zero values (2 cases out of 95). All dummies were presented on each nest with a minimum one-hour interval between dummies. All five dummies were presented to each pair within a single day to minimize between-day variation in parental motivation or environmental conditions.

Behavioural Recording and Response Measures

Behavioural responses were recorded on a Panasonic HDC-SD80 camera from a distance approximately 50 meters from the nest to avoid disturbance. Audio recordings were obtained using an Olympus WS-852 voice recorder placed beneath the dummy. In total, 19 breeding pairs were tested.

All behavioural and acoustic data were analysed using BORIS software (Friard and Gamba 2016). We quantified attack behaviour, defined as a directed flight towards the dummy, usually performed in the presence of a threat to the nest (Strnad et al. 2012). Attacks were classified as either contact attacks (physical contact with the model) or non-contact attacks (directed flights towards the model accompanied by a marked decrease in flight height, without physical contact). Ordinary flights over or past the model were not classified as attacks. For the main statistical analyses, both attack types were combined into a single response variable representing the total number of attacks per trial.

We also recorded the alarm calls, which represent a weaker form of antipredator behaviour, usually performed in the presence of a stimulus threatening the adult birds, which hesitate to attack it (Harris and Franklin 2000; Krausová et al. 2022). These measures allowed us to assess both physical aggression and vocal signalling as components of parental threat discrimination. Attack counts were

analysed separately for males and females. Because it was usually not possible to reliably attribute vocalizations to a specific parent, alarm calls were pooled at the pair level and analysed as the total number of calls produced during each presentation.

We analysed behavioural responses of 19 breeding pairs of red-backed shrikes toward five experimental models (95 trials in total).

Statistical Analyses

All statistical analyses were conducted with R (R software, version 4.3.3; www.r-project.org). Prior to analysis, count data were log-transformed to improve normality and stabilize variance. We used Linear Mixed-Effects Models (LMMs; *lmer* function; package *lme4*) to test the effects of experimental and ecological predictors on behavioural responses. For alarm calling, the fixed effects included: dummy type (cuckoo, sparrowhawk, dove, hawk with cuckoo bill, cuckoo with hawk bill), chick age (continuous predictor, 3–8 days), day in the breeding season (continuous predictor, 1–30), order of dummy presentation (categorical predictor, 1–5), number of chicks in the brood (1–6). For attack behaviour, the same predictors were included, with the addition of parent sex as a fixed effect.

Nest identity was included as a random intercept to account for repeated measures within breeding pairs.

Model significance was assessed using F-tests. When the main effect of dummy type was significant, pairwise comparisons between treatment levels were performed using Tukey's HSD post hoc tests with adjustment for multiple comparisons (*glht* function, *multicomp* package).

Results

Attacks on models

The number of attacks was significantly affected by model type (Fig. 2; LMM: $F_{4,154\cdot93} = 8.250$, $p < 0.001$) and by the sex of the responding shrike ($F_{1,154\cdot16} = 23.495$, $p < 0.001$). Brood size ($F_{1,24\cdot57} = 0.097$, $p = 0.758$), nestling age ($F_{1,19\cdot54} = 0.298$, $p = 0.591$), season date ($F_{1,18\cdot40} = 0.252$, $p = 0.621$), and presentation order ($F_{1,153\cdot14} = 0.049$, $p = 0.826$) had no significant effects on attack frequency.

Post hoc Tukey HSD tests showed that attack rates toward the common cuckoo and Eurasian sparrowhawk differed marginally ($z = 2.611$, $p = 0.068$). The cuckoo model elicited significantly more attacks than the control dove ($z = 5.441$, $p < 0.001$), and the sparrowhawk also differed significantly from the control dove ($z = 2.905$, $p < 0.05$). Responses toward the cuckoo fitted with a sparrowhawk-like bill did not differ from responses toward the original cuckoo ($z = 1.648$, $p = 0.467$), the sparrowhawk with a cuckoo-like bill ($z = -1.839$, $p = 0.351$), or the original sparrowhawk ($z = -0.964$, $p = 0.871$), but it differed significantly from the turtle dove control ($z = 3.841$, $p = 0.001$). The sparrowhawk fitted with a cuckoo-like

bill did not differ from the turtle dove ($z = 1.997$, $p = 0.267$) or the original sparrowhawk ($z = -0.890$, $p = 0.901$) but differed significantly from the cuckoo ($z = 3.460$, $p < 0.01$).

Males attacked the presented models significantly more often than females.

Alarm calling

Alarm-calling intensity was significantly affected by model type (Fig. 3; LMM: $F_{4,72.87} = 5.594$, $p < 0.001$), brood size ($F_{1,19.26} = 10.707$, $p = 0.004$), nestling age ($F_{1,16.11} = 6.609$, $p = 0.020$), and season date ($F_{1,15.80} = 4.784$, $p = 0.044$). Presentation order had no significant effect ($F_{1,70.27} = 0.076$, $p = 0.783$).

Post hoc comparisons revealed that shrikes alarm-called significantly more in the presence of the sparrowhawk than during presentations of the turtle dove ($z = 3.251$, $p = 0.010$), the cuckoo ($z = -4.560$, $p < 0.001$), and the cuckoo with a sparrowhawk-like bill ($z = 2.878$, $p = 0.032$). Alarm responses toward the cuckoo did not differ significantly from those toward the sparrowhawk fitted with a cuckoo-like bill ($z = -2.246$, $p = 0.163$).

Alarm-calling intensity increased with brood size, nestling age, and progression of the breeding season.

Discussion

Red-backed shrikes responded to the presented models using two distinct antipredator behaviours: direct attacks and alarm calling. As in previous studies, both the intensity and type of response depended strongly on the identity of the presented intruder (Strnad et al. 2012; Němec and Fuchs 2014; Krausová et al. 2022). Shrikes were able to distinguish among the common cuckoo, Eurasian sparrowhawk, and control turtle dove, confirming that the experimental design providing a reliable framework for testing the role of bill morphology in enemy recognition.

The strongest attack responses were directed toward the cuckoo model, whereas alarm calling was most intense in the presence of the sparrowhawk. This behaviour likely reflects different defensive strategies toward brood parasites and predators of adult birds. Cuckoos can be effectively countered through active mobbing and direct attacks near the nest (Welbergen and Davies 2008; Trnka and Prokop 2012). In contrast, sparrowhawks represent a potentially lethal threat to adult shrikes, making close physical attacks substantially riskier. Shrikes therefore appeared to maintain a greater safety distance and relied more heavily on alarm calling when confronted with sparrowhawks. Similar behavioural differences between responses to cuckoos and hawks have previously been described in shrikes as well as in other passerine hosts (Ma et al. 2018; Krausová et al. 2022).

The most striking result of our study is that bill manipulation did not produce a complete categorical switch between cuckoo and sparrowhawk phenotypes. Instead, the hybrid models elicited intermediate and partially contradictory responses. A sparrowhawk fitted with a cuckoo-like straight bill effectively lost its characteristic “hawk identity”: shrikes no longer responded with the intense alarm calling typical

for sparrowhawks, but at the same time they did not attack this model as aggressively as they attacked cuckoos. The model therefore elicited ambiguous behaviours – not corresponding to either a true sparrowhawk or a true cuckoo. On the other hand, adding a hooked sparrowhawk-like bill to the cuckoo increased the perceived danger of the cuckoo phenotype. Shrikes continued to attack this model intensely, similarly to the original cuckoo, but the hooked bill appeared to shift the model partially toward the predator category (though not creating a sparrowhawk).

These findings suggest that bill shape plays an important role in threat assessment but is not sufficient on its own for reliable cuckoo or sparrowhawk recognition. The hawk-like bill made the cuckoo model appear more dangerous, whereas the cuckoo-like bill reduced defensive responses toward the sparrowhawk model. However, neither manipulation caused a complete change in responses from one category to the other, suggesting that shrikes do not rely on bill shape as a single key feature. Similar patterns have been reported in previous studies of avian predator recognition. Beránková et al. (2014) showed that changing a single predator trait could modify birds' responses but was usually not enough to cause complete predator misclassification unless several visual traits were changed at the same time. Similarly, Němec et al. (2021) found that removing important raptor features, such as the hawk-like bill and talons, strongly reduced shrikes' aggressive responses toward a kestrel model. Fišer et al. (2025) further demonstrated that conflicting or artificially modified predator traits can produce ambiguous recognition responses. Together, these studies suggest that birds combine several visual cues during enemy recognition rather than relying on a single characteristic feature.

Our results support the hypothesis that shrikes integrate multiple visual cues when assessing danger. Previous studies have suggested that predator recognition in birds depends on combinations of visual traits, including eye colour, body posture, plumage patterning, body shape, and movement (Davies and Welbergen 2008; Beránková et al. 2014). Because the overall body shape and posture of our models remained unchanged after bill manipulation, these cues may have overridden or constrained the influence of bill morphology. In particular, sparrowhawks and cuckoos differ in their typical body configuration: sparrowhawks generally adopt a more upright perching posture, whereas cuckoos tend to perch more horizontally, often with the tail raised. Such differences could provide additional information for predator discrimination, although their relative importance cannot be determined from our experiment. This interpretation is consistent with Beránková et al. (2014), who demonstrated that replacing the body of a sparrowhawk with that of a pigeon greatly reduced fear responses in great tits (*Parus major*) despite the presence of hawk-like head traits.

The asymmetry between attacks and alarm calls further suggests that these two behaviours encode different aspects of risk assessment. Direct attacks appear to be associated primarily with defence against brood parasites, whereas alarm calling reflects caution toward predators dangerous to adult birds. The hybrid models disrupted these behavioural categories. Shrikes attacked the cuckoo with a hawk-like bill but did not strongly alarm-call, while the sparrowhawk with a cuckoo-like bill elicited neither strong alarm calling nor intense attacks. This pattern is consistent with the interpretation that shrikes perceived the hybrids as conflicting or biologically unusual stimuli.

Males attacked the models significantly more frequently than females, consistent with previous studies on red-backed shrikes (Strnad et al. 2012). This difference may reflect sex-specific investment in nest defence or higher male aggressiveness associated with testosterone levels (Wacker et al. 2010). Alarm-calling intensity increased with brood size, nestling age, and season progression, supporting the offspring-value hypothesis (Montgomerie and Weatherhead 1988). As the reproductive value of the brood increases and opportunities for replacement nesting decline later in the season, parents may invest more heavily in offspring defence.

Overall, our results demonstrate that red-backed shrikes discriminate between cuckoos and sparrowhawks using integrated combinations of visual cues rather than relying on a single key trait. Bill morphology contributes to this process, but alone it is insufficient to determine enemy identity. Instead, altered bill shape produces ambiguous intermediate phenotypes, suggesting that shrikes evaluate predators and brood parasites through multidimensional categorization processes within the cuckoo-hawk mimicry system.

Declarations

Author contributions

MS – conceptualization, methodology, investigation, formal analysis, original draft writing, review; JBa – original draft writing, data curation, investigation, formal analysis; LZ – investigation, data curation, review, funding acquisition; JBl – investigation, data curation, review; JČ – investigation, data curation, review; RF – conceptualization, review; PV – conceptualization, methodology, supervision

Conflict of Interest

Authors declare no conflict of interests.

Declaration of AI use

During the preparation of this manuscript, the authors used ChatGPT (OpenAI) to improve the language and readability of the text. The authors reviewed and edited the output and take full responsibility for the content of the manuscript.

Data Availability

The data and R code used in this study are available as Online Resource (Online Resource 1 – data).

Acknowledgements

We thank Jošt Havlice for invaluable assistance in the field and Matyáš Havelka for photographs of the experimental dummies. We are grateful to the administration of Podyjí National Park for permission to conduct the experiments within the park. We also thank the reviewers and editor for their constructive comments and helpful suggestions, which improved the manuscript.

Funding

The study was supported by the University of South Bohemia (GAJU 134/2025/P).

Statement of Animal Ethics

All procedures complied with current legislation of the Czech Republic governing research on wild animals. The study was conducted under permits issued by the Administration of Podyjí National Park and in accordance with national nature conservation regulations (MZP/2020/630/113). The experimental project underwent full ethical review by the Ethics Committee of the Faculty of Science, University of South Bohemia, before being approved by the Ministry of Agriculture of the Czech Republic (MZE-63257/2024-13143) and the Ministry of the Environment of the Czech Republic (MZP/2020/630/113). All procedures complied with Czech legislation and institutional guidelines for animal welfare.

Provisioning rates were not systematically quantified, but no experimental nests were abandoned as a consequence of the experimental manipulation, and no injuries or mortality occurred. The study followed the ASAB/ABS Guidelines for the ethical treatment of nonhuman animals in behavioural research and teaching.

References

1. Adamík P, Hušek J, Cepák J (2009) Rapid decline of Common Cuckoo Cuculus canorus parasitism in Red-backed Shrikes Lanius collurio. Ardea 97(1):17–22. https://doi.org/10.5253/078.097.0103
2. Beránková J, Veselý P, Fuchs R (2014) The role of key features in predator recognition by untrained birds. Anim Cogn 17:963–971. https://doi.org/10.1007/s10071-014-0728-1
3. Campobello D, Sealy SG (2010) Enemy recognition of reed warblers (Acrocephalus scirpaceus): threats and reproductive value act independently in nest defence modulation. Ethology 116:498–508. https://doi.org/10.1111/j.1439-0310.2010.01764.x
4. Caro TM (2005) Antipredator defenses in birds and mammals. University of Chicago Press, Chicago, IL
5. Cramp S, Perrins CM, Brooks DJ (1994) Handbook of the birds of Europe the Middle East and North Africa: The birds of the Western Palearctic. Volume VII flycatchers to shrikes. Oxford University Press, Oxford, UK
6. Curio E (1976) The Ethology of predation. Springer, Berlin, Germany
7. Davies NB (2000) Cuckoos, cowbirds and other cheats. T & AD Poyser, UK
8. Davies NB, Welbergen JA (2008) Cuckoo-hawk mimicry? An experimental test. Proc R Soc B 275:1817–1822. https://doi.org/10.1098/rspb.2008.0331
9. Diehl B, Myrcha A (1973) Bioenergetics of Nestling Red-backed Shrikes (Lanius Collurio). Condor 75:259–264. https://doi.org/10.2307/1366165

10. Fišer O, Strnadová I, Veselý P et al (2025) Strange features are no better than no features: predator recognition by untrained birds. Anim Cogn 28:5. https://doi.org/10.1007/s10071-024-01924-z
11. Friard O, Gamba M (2016) BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol Evol 7:1325–1330. https://doi.org/10.1111/2041-210X.12584
12. Gill SA, Neudorf DL, Sealy SG (1997) Host responses to cowbirds near the nest: cues for recognition. Anim Behav 53:1287–1293. https://doi.org/10.1006/anbe.1996.0362
13. Gotzman J (1967) Remarks on ethology of the red-backed shrike, Lanius collurio L. - nest defence and nest desertion. Acta Ornithol 10:83–96
14. Harris T, Franklin T (2000) Shrikes & Bush-Shrikes. A & C Black, London, UK
15. Hernandez A (1995) Temporal-spatial Patterns of Food Caching in Two Sympatric Shrike Species. Condor 97:1002–1010. https://doi.org/10.2307/1369539
16. Krausová L, Veselý P, Syrová M, Antonová K, Fišer O, Chlumská V, Pátková M, Pužej Š, Fuchs R (2022) Red-backed shrike (Lanius collurio) versus common cuckoo (Cuculus canorus): An example of ineffective cuckoo–hawk mimicry. Ecol Evol 12(12):e9664. https://doi.org/10.1002/ece3.9664
17. Lefranc N, Worfolk T (1997) Shrikes: A Guide to the Shrikes of the World. Pica, Sussex, UK
18. Lorenz K (1937) The Companion in the Bird's World. Auk 54:245–273
19. Lovászi P, Moskát C (2004) Break-down of arms race between the Red-backed Shrike Lanius collurio and Common Cuckoo Cuculus canorus. Behaviour 141:245–262. https://doi.org/10.1163/156853904322890843
20. Ma L, Qang C, Liang W (2018) Hawk mimicry does not reduce attacks of cuckoos by highly aggressive hosts. Avian Res 9:35. https://doi.org/10.1186/s40657-018-0127-4
21. Martin K (1995) Patterns and Mechanisms for Age-dependent Reproduction and Survival in Birds. Integr Comp Biol 35:340–348. https://doi.org/10.1093/icb/35.4.340
22. McLean IG, Smith JNM, Stewart KKG (1986) Mobbing behaviour, nest exposure and breeding success in the American Robin. Behaviour 96:171–186. https://doi.org/10.1163/156853986X00270
23. Montgomerie RD, Weatherhead PJ (1988) Risks and Rewards of Nest Defence by Parent Birds. Q Rev Biol 63:167–187
24. Němec M, Fuchs R (2014) Nest defense of the red-backed shrike Lanius collurio against five corvid species. Acta Ethol 17:149–154. https://doi.org/10.1007/s10211-013-0175-z
25. Němec M, Syrová M, Dokoupilová L, Veselý P, Šmilauer P, Landová E, Lišková S, Fuchs R (2015) Surface texture and priming play important roles in predator recognition by the red-backed shrike in field experiments. Anim Cogn 18(1):259–268. https://doi.org/10.1007/s10071-014-0796-2
26. Němec M, Kučerová T, Veselý P, Fuchs R (2021) A kestrel without hooked beak and talons is not a kestrel for the red–backed shrike (Lanius collurio). Anim Cogn 24:957–968. https://doi.org/10.1007/s10071-020-01450-8
27. Newton I, Poyser AD (1986) Calton, Waterhouses, UK

28. Olsson V (1995) The Red-backed Shrike Lanius collurio in southeastern Sweden: Habitat and territory. Ornis Svec 5:31–41. https://doi.org/10.34080/os.v5.23012
29. Scaife M (1976) The response to eye-like shapes by birds II. The importance of staring, pairedness and shape. Anim Behav 24:200–206
30. Söderström B, Pärt T, Rydén J (1998) Different nest predator faunas and nest predation risk on ground and shrub nests at forest ecotones: An experiment and a review. Oecologia 117:108–118. https://doi.org/10.1007/s004420050638
31. Strnad M, Němec M, Veselý P, Fuchs R (2012) Red-backed Shrikes (Lanius collurio) adjust the mobbing intensity, but not mobbing frequency, by assessing the potential threat to themselves from different predators. Ornis Fenn 89:206–215. https://doi.org/10.51812/of.133807
32. Strnadová I, Němec M, Strnad M, Veselý P, Fuchs R (2018) The nest defence by the red-backed shrike Lanius collurio – support for the vulnerability hypothesis. J Avian Biol 49:jav–01726. https://doi.org/10.1111/jav.01726
33. Syrová M, Němec M, Veselý P, Landová E, Fuchs R (2016) Facing a clever predator demands clever responses - Red-backed shrikes (Lanius collurio) vs. eurasian magpies (Pica pica). PLoS ONE 11(7):e0159432. https://doi.org/10.1371/journal.pone.0159432
34. Trnka A, Prokop P (2012) The effectiveness of hawk mimicry in protecting cuckoos from aggressive hosts. Anim Behav 83:263–268. https://doi.org/10.1016/j.anbehav.2011.10.036
35. Trnka A, Prokop P, Grim T (2012) Uncovering Dangerous Cheats: How Do Avian Hosts Recognize Adult Brood Parasites? PLoS ONE 7:e37445. https://doi.org/10.1371/journal.pone.0037445
36. Tryjanowski P, Golawski A (2004) Sex differences in nest defence by the red-backed shrike Lanius collurio: Effects of offspring age, brood size, and stage of breeding season. J Ethol 22:13–16. https://doi.org/10.1007/s10164-003-0096-9
37. Veselý P, Syrová M, Voháňková M, Havlíček J, Nácarová J, Fuchs R (2022) Cowards or clever guys: an alternative nest defence strategy employed by shrikes against magpies. Anim Cogn 25(2):307–317. https://doi.org/10.1007/s10071-021-01552-x
38. Wacker DW, Wingfield JC, Davis J, Meddle SL (2010) Seasonal changes in aromatase and androgen receptor, but not estrogen receptor mrna expression in the brain of the free-living male song sparrow, melospiza melodia morphna. J Comp Neurol 518:3819–3835. https://doi.org/10.1002/cne.22426
39. Welbergen JA, Davies NB (2008) Reed warblers discriminate cuckoos from sparrowhawks with graded alarm signals that attract mates and neighbours. Anim Behav 76:811–822. https://doi.org/10.1016/j.anbehav.2008.03.020
40. Welbergen JA, Davies NB (2011) A parasite in wolf's clothing: Hawk mimicry reduces mobbing of cuckoos by hosts. Behav Ecol 22:574–579. https://doi.org/10.1093/beheco/arr008
41. Westerskov K (1950) Methods for Determining the Age of Game Bird Eggs. J Wildl Manage 14:56–67. https://doi.org/10.2307/3795978

42. Zentall TR, Jackson-Smith P, Jagielo JA, Nallan GB (1986) Categorical shape and color coding by pigeons. J Exp Psychol Anim Behav Process 12:153–159

Figures

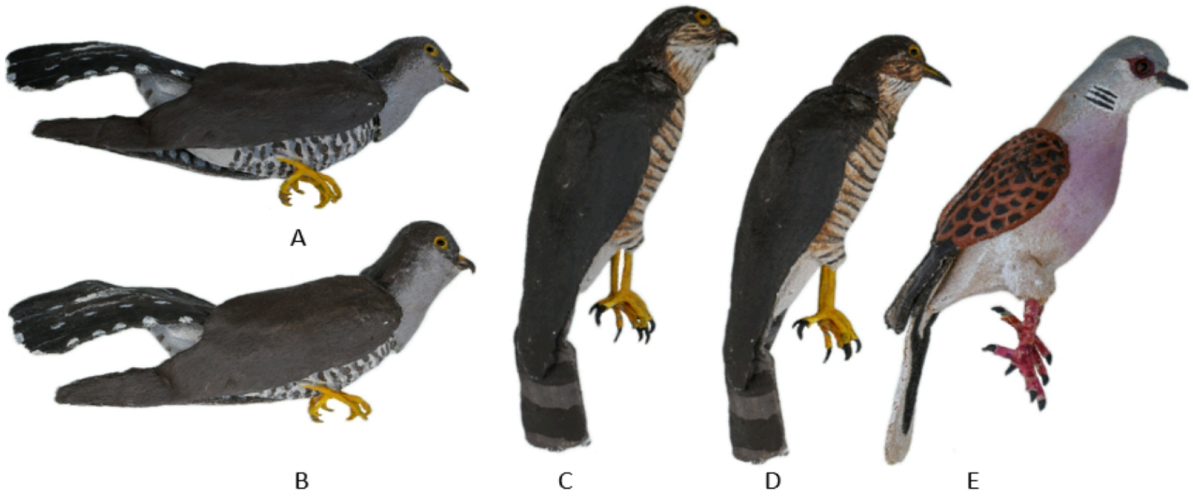


Figure 1

Models of individual species and stimuli used in the experiments. A – common cuckoo (*Cuculus canorus*), B – cuckoo with a hawk-like bill, C – Eurasian sparrowhawk (*Accipiter nisus*), D – sparrowhawk with a cuckoo-like bill, E – European turtle dove (*Streptopelia turtur*).

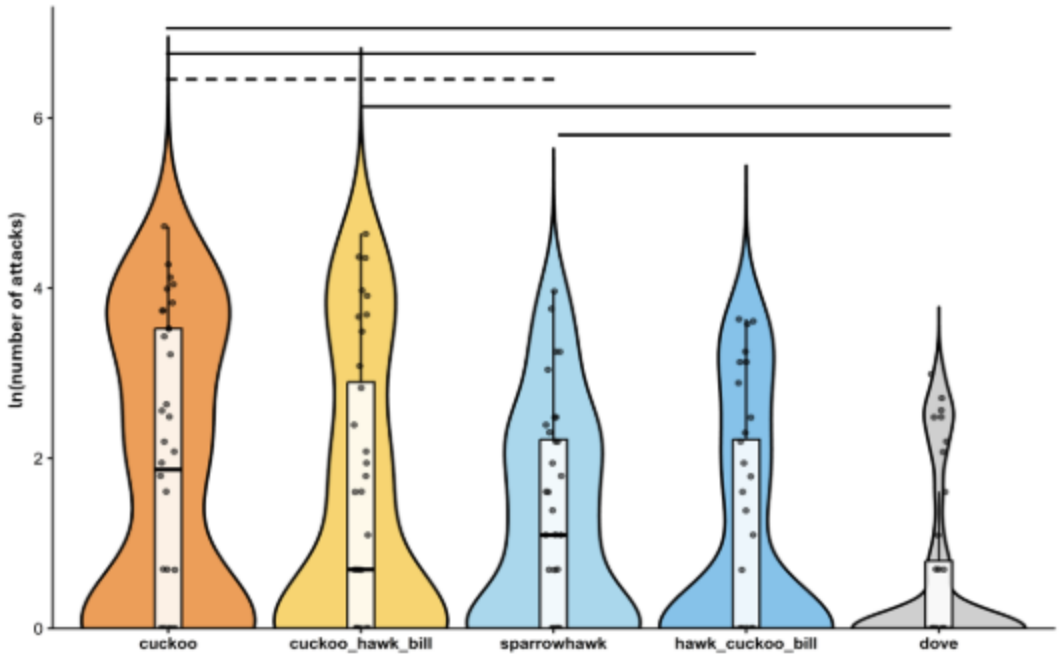


Figure 2

Number of attacks (with and without physical contact) performed by shrikes against the individual dummies (log-transformed). Solid black lines indicate pairs of dummies that elicited significantly different responses, whereas the dashed line indicates a difference approaching statistical significance.

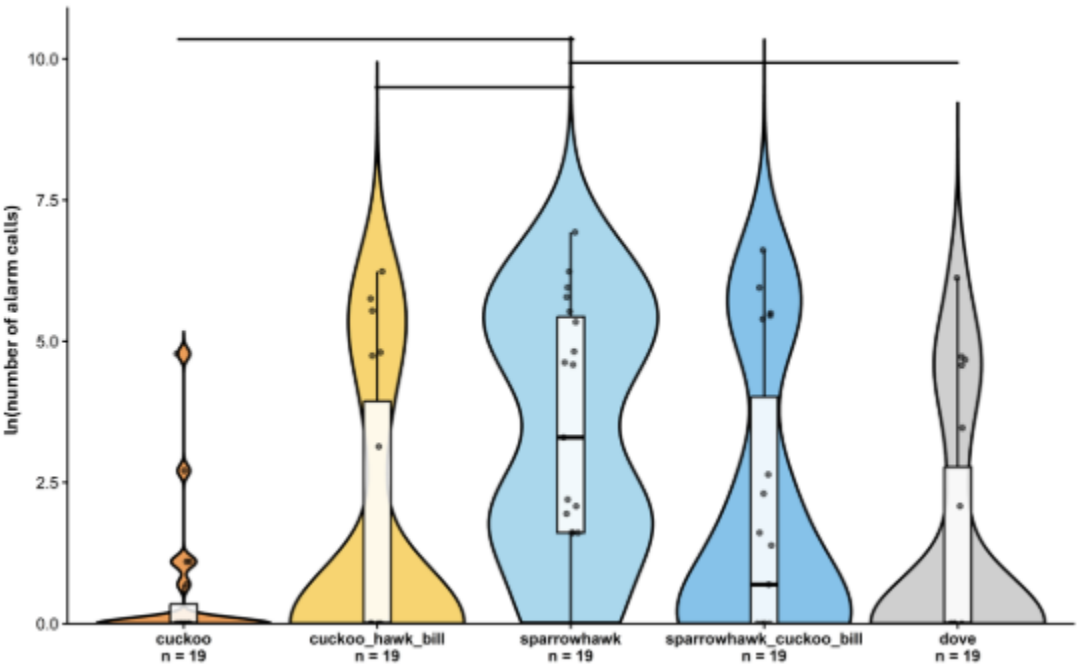


Figure 3

Number of alarm calls produced by shrikes in response to the individual dummies (log-transformed). Solid black lines indicate pairs of dummies that elicited significantly different responses.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- OnlineResource1data.xlsx
- Onlinefloatimage1.png