Jihočeská univerzita v Českých Budějovicích

Přírodovědecká fakulta

Rozpoznávání predátora netrénovanými ptáky: obrana hnízda

Rigorózní práce

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České Budějovice 2020

Annotation

Nováková, N. 2020. Object categorization by wild-ranging birds in nest defence. RNDr. Thesis, in Englisch, -iii + 11 pp. University of South Bohemia, Faculty of Science, České Budějovice, Czech Republic.

Abstract

Despite object categorization being an important ability for the survival of wild animals, the principles behind this ability have been only scarcely studied using wild-ranging, untrained animals. Reiterating our previous study undertaken with wild-ranging titmice on winter feeders (Nováková et al. Behav Process 143:7–12, 2017), we aimed to test two hypotheses of object recognition proposed by animal psychology studies: the particulate feature theory and recognition by components in the methodological paradigm of nest defence. We tested whether the parents of the red-backed shrike (*Lanius collurio*) recognize the dummies of the common kestrel (*Falco tinnunculus*), which is a potential predator of large chicks or fledglings, as a threat in case when their body parts are scrambled. The kestrel dummy was presented with the head at the top, in the middle, and at the bottom of the body. We showed that the shrikes did not consider dummies of a kestrel with an inappropriately placed head as a threat to the nest and attacked it equally scarcely as the harmless control. These results support the theory of recognition by components, presuming that the mutual position of body parts is essential for appropriate recognition of the object. When the body parts were scrambled, most of shrikes were not able to identify the kestrel in such an object despite all local features (eye, beak, colouration, and claws) being present. Nevertheless, shrikes did not consider the scrambled dummies as completely harmless, because they fed their chicks in their presence significantly less often than in the presence of harmless control.

Finanční podpora

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Nela Nováková

Nováková Nela, Veselý Petr & Roman Fuchs

2020

Object categorization by wild-ranging birds in nest defence

ORIGINAL PAPER

Object categorization by wild-ranging birds in nest defence

Nela Nováková[1] · Petr Veselý[1] · Roman Fuchs[1]

Abstract

Despite object categorization being an important ability for the survival of wild animals, the principles behind this ability have been only scarcely studied using wild-ranging, untrained animals. Reiterating our previous study undertaken with wild-ranging titmice on winter feeders (Nováková et al. Behav Process 143:7–12, 2017), we aimed to test two hypotheses of object recognition proposed by animal psychology studies: the particulate feature theory and recognition by components in the methodological paradigm of nest defence. We tested whether the parents of the red-backed shrike (*Lanius collurio*) recognize the dummies of the common kestrel (*Falco tinnunculus*), which is a potential predator of large chicks or fledglings, as a threat in case when their body parts are scrambled. The kestrel dummy was presented with the head at the top, in the middle, and at the bottom of the body. We showed that the shrikes did not consider dummies of a kestrel with an inappropriately placed head as a threat to the nest and attacked it equally scarcely as the harmless control. These results support the theory of recognition by components, presuming that the mutual position of body parts is essential for appropriate recognition of the object. When the body parts were scrambled, most of shrikes were not able to identify the kestrel in such an object despite all local features (eye, beak, colouration, and claws) being present. Nevertheless, shrikes did not consider the scrambled dummies as completely harmless, because they fed their chicks in their presence significantly less often than in the presence of harmless control.

Keywords Recognition · Categorization · Global and local features · Nest defence · Red-backed shrike · Kestrel

Introduction

Two basic principles of object recognition have been proposed in animal and human psychology. Particulate feature theory (PFT hereafter) assumes that animals recognize objects using perception of a particular, salient feature(s) of the object (Cerella 1980). The theory named recognition by components (RBC hereafter) supposes that every object is composed of simple components, called geons, and that these components can form any object (Biederman 1987). Numerous experiments have shown that birds categorize objects based on PFT, because they are capable of successfully recognizing highly fragmented pictures (Matsukawa

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et al. 2004) or of categorizing fragmented and even scrambled pictures of birds and mammals (Cook et al. 2013) as long as the salient features are present. In both these processes, the presence of a particular feature is essential for recognition and categorization, though its position within the object can be changed and the categorization is still successful. On the other hand, there is also evidence that birds are able to categorize stimuli according to the spatial organization of their parts, which is consistent with RBC theory, where the spatial position of geons is thought to be important (Van Hamme et al. 1992; Wasserman et al. 1993; Kirkpatrick-Steger et al. 1996; Peissig et al. 2000; Watanabe 2010). It could be concluded that birds are able to use both local salient features as well as geons (and their spatial setup) (Biederman 1987) for object recognition and categorization (Aust and Huber 2003; Cook et al. 2013). The mutual spatial orientation of features is essential for recognition only in cases where the presented stimuli do not provide any specific local features (Wasserman et al. 1993). At the same time, the importance of the spatial orientation of features is higher in stimuli that are more realistic (photographs) and/

or more relevant for the tested subjects (e.g., own species) (Watanabe 2010).

However, all of the above-mentioned experiments had been performed under laboratory conditions using birds (mainly pigeons) trained using operant conditioning protocol. Based on the above-mentioned conclusions, we would expect that the recognition of a relevant object in natural conditions would tend to follow the principles of RBC with a high importance placed on the spatial organization of the object. Our knowledge of the use of the principles of object recognition in natural conditions is, however, very poor. This is mainly due to the limitations of the experiment, as it is necessary to force the experimental subject to respond to the presented stimulus. This usually requires presenting a stimulus of high relevance to the subject. Predators are one such stimuli, because a bird not responding to the threat of predation may substantially decrease its fitness (Caro 2005).

There is some evidence of how untrained birds in natural conditions recognize predators. Classical ethologists have suggested the importance of the presence of particular individual key features, which tends to support PFT (Krätzig 1940; Nice and Pelkwyk 1941; Edwards et al. 1950; Scaife 1976; Smith and Graves 1978; Gill et al. 1997; Deppe et al. 2003). However, recently, it has begun to be seen as a much more complex process. The presence of a salient feature is not universal enough for proper recognition, and the context of these features matters as well, even though the presence itself can be sufficient, when there is no other stimulus (Curio 1975; Davies and Welbergen 2008; Tvardíková and Fuchs 2011; Welbergen and Davies 2011; Trnka and Prokop 2012; Beránková et al. 2014, 2015; Veselý et al. 2016; Nácarová et al. 2018; Němec et al. unpublished).

Our previous research (Nováková et al. 2017) aimed to show how wild, untrained birds recognize a predator using the methods of cognitive psychology. We presented dummies of the European sparrowhawk (*Accipiter nisus*), an extremely dangerous predator, to the titmice visiting a winter feeder. The dummy was presented in three body arrangements by changing the position of the head for each (correct position, middle, and bottom of the body). Birds responded to the two scrambled dummies in the same way as to the "correct" sparrowhawk (refraining to visit the feeder during its presence). Based on these results, we concluded that birds recognized the sparrowhawk according to certain salient features (curved beak, yellow eyes, and striped belly) and the importantly changed spatial organization did not weaken this ability as long as the features were present. Such a process of recognition corresponds rather to the PFT than the theory of RBC, which we did not expect according to the results of studies using operational conditioning (see above). Nevertheless, we were not sure about the intention of the birds that did not visit the feeder. They may have feared the presented stimulus, or they may have just been confused by

it, and wary of predation threat. Therefore, we decided to transfer the same task into a different situation where predators must be appropriately recognized and the response is clearly comprehensible—nest defence.

The bird nest is a vulnerable and most valuable item for the parents. When a predator discovers the presence of the nest, the last chance the parents have of protecting it is by active defence (Caro 2005). The decision of whether to defend the nest against a predator may substantially affect parental fitness. The parent may get hurt or even killed (Strnad et al. 2012), but if it manages to chase the predator away from the nest, it may secure successful reproduction (Goławski and Mitrus 2008). On the other hand, responding to a non-threatening species represents a waste of energy and time, which may lower fitness, as well. Therefore, the presentation of a predator near to the nest is an optimal experiment setup, because birds are required to correctly recognize the difference between a predator and a harmless animal. Numerous studies further show that birds are also able to assess the difference between predators differing in the threat which they represent to the chicks and to the defending parents (Krebs and Davies 1993; Martin 1993; Tryjanowski and Goławski 2004; Caro 2005), even when they are very similar in size and coloration (e.g., European sparrowhawk and European kestrel—*Falco tinnunculus*, Strnad et al. 2012).

Nest defence may vary in its intensity, from alarm calling (e.g., Curio 1975) to physical attacks to the predator (Tryjanowski and Goławski 2004). Attacking the predator is the riskiest strategy, which suits our purpose as the birds really need to recognize the predator correctly. Therefore, we chose red-backed shrikes (*Lanius collurio*) as the subjects, because they vigorously defend their nests against predators and their reactions can provide a better insight into their motivation. Red-backed shrikes are known to be able to distinguish between species of corvids and raptors (Strnad et al. 2012; Němec and Fuchs 2014; Němec et al. 2015; Syrová et al. 2016; Strnadová et al. 2018), even when they are quite similar, in the degree of threat that they represent to the nest.

In the present study, we presented dummies of the common kestrel. This raptor species is a specialized hunter of small mammals, but can also take bird fledglings (Korpimäki 1985). Nonetheless, it is harmless to adult shrikes, which commonly and vigorously attack it when they have chicks in their nests (Strnad et al. 2012; Syrová et al. 2016; Strnadová et al. 2018). To be able to describe the process of recognition of this predator species, we followed the experimental setup of our previous study (Nováková et al. 2017) and presented dummies with the three alternative head positions (correctly, in the middle, and at the bottom of the body).

We tested two alternating hypotheses.

1. Shrikes recognize the predators adopting the PFT principles. Shrike parents attack the kestrel with changed

spatial orientation of body parts equally as often as the unchanged kestrel. They do not provide food to their chicks in the presence of the scrambled kestrel dummy (equally as in case of the unchanged kestrel).

2. Shrikes recognize the predators adopting the RBC principles. Shrike parents attack the kestrel with changed spatial orientation of body parts equally as often as the harmless control, and significantly less often than the unchanged kestrel. They also provide food to their chicks in the presence of the scrambled dummies (equally as in case of the pigeon dummy).

Materials and methods

Experimental site and species

The experiments were conducted during the breeding seasons of 2015 and 2016 (from 8.6.2015 to 18.6.2015 and from 16.6.2016 to 18.6.2016) near the town of Znojmo, South Moravia, Czech Republic (48.85N, 16.05E). The localities with the occurrence of red-backed shrike were open dry areas with scattered thorny bushes mainly *Rosa canina* and *Crataegus sp.* in which the shrikes most often build their nests. The localities were situated at the borders of the Podyjí National Park and in the Načeratický kopec Protected Area, where the shrikes occur in high abundance.

Within this area, we searched for the shrike nests and assessed the stage of incubation/age of nestlings. The experiments were conducted at nests with nestlings 7–11 days old, because the antipredatory behaviour of parents is strong at this stage (Strnadová et al. 2018) and the nestlings are not sensitive to disturbances and thus not willing to leave the nest as older nestlings do.

The red-backed shrike is a medium-sized passerine of the family Laniidae. It is a predator of insects and small vertebrates (Tryjanowski and Golawski 2004). It was chosen as a model species because of its aggressive behaviour during nest defence, which includes physical attacks (Tryjanowski and Goławski 2004; Strnad et al. 2012), and because red-backed shrikes have previously been shown to categorize various predator species (Strnad et al. 2012; Němec and Fuchs 2014; Syrová 2011).

Dummies

We used three types of dummies (Fig. 1). The first dummy was the adult female of the common kestrel divided horizontally into three parts (head + neck, breast, and belly + tail + legs). The common kestrel was chosen for its dangerousness to the hatchlings of shrikes but not to the adults themselves, so adult shrikes attack it aggressively (Strnad et al. 2012; Syrová 2011). These scrambled dummies were presented in three positions: one with the head in the correct position, one with the head in the middle of the dummy, and one with the head at the bottom of the body. These combinations (out of six possible) were chosen to focus on the importance of the position of the head, because it carries the most conspicuous features (beak and eyes). This dummy was fabricated from felt-like hairy cloth stuffed with cotton, with glass eyes, and beak and legs made from a hobby modelling material. The surface was painted with acrylic colours, so that the appearance of the surface was not fluffy, but more compact and more similar to the texture of feathers. Němec et al. (2015) have shown that shrikes defending their nest respond similarly to these textile dummies as to stuffed birds.

Besides this scrambled dummy, there was a threatening control presented by a complete stuffed common kestrel and a non-threatening control presented by a stuffed domestic pigeon (*Columba livia* f. *domestica*).
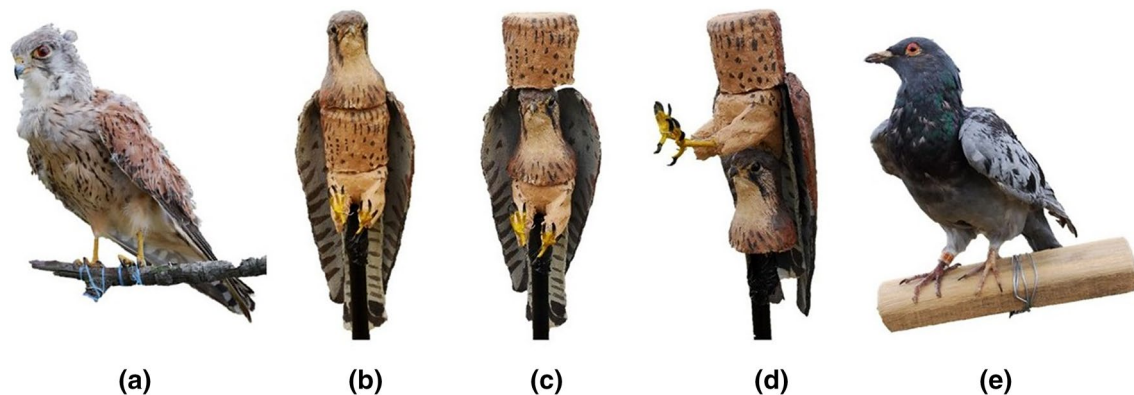
Fig. 1 Presented dummies: **a** stuffed common kestrel (*Falco tinnunculus*), **b** dismantled kestrel with the head on the top, **c** dismantled kestrel with the head in the middle, **d** dismantled kestrel with the head on the bottom, and **e** stuffed domestic pigeon (*Columba livia.* f. *domestica*)

Experiment

All five types of dummy (two controls and three arrangements of kestrel) were always presented during 1 day. Each dummy was brought to the shrub with a shrike nest and positioned facing the nest and on average 1.5 m from it. The dummies were placed on top of a 1.5-m-tall rod which had been fixed in the ground. The dummies were always carried to the nest covered by a cloth, so that shrikes could not make a connection between them and the experimenter. The camera was placed approximately 50 m away from the nest (depending on the terrain) and the behaviour of the adult shrikes was recorded during a 10-min-long blind trial. Then, the cloth was removed from the dummy. Every trial started at the moment of discovery of the dummy by the shrike parents. The shrike behaviour was recorded for 20-min beginning with the first spotting of the dummy by any parent. Dummy was removed immediately after end of recording. After each trial, a 1-h pause followed, to allow parents to calm down and supply food to their nestlings. Subsequently, another dummy was presented; no previous 10-min blind trial was recorded. The order of dummy presentation was random. See Supplementary material 1 for table and statistical comparison of the occurrence of particular dummies in particular order position. Trials started around 9:00 a.m. and lasted until 4:00 p.m., and were conducted only in calm weather (no strong wind or rainfalls).

Recorded activities

For each parent, we recorded three behavioural responses: (1) the number of direct attacks on the dummy with physical contact, which is the most intensive active defence and represents a significant threat to the defending bird, (2) the number of flight dives towards the dummy without physical contact (birds perform flyover while lowering their height as approaching the dummy), which represents the attempt of the parents to chase the predator away, but at the same time, it includes some level of wariness and maybe confusion, (3) feeding nestlings, which is an activity presuming that the focal parent perceives the dummy as non-threatening.

Data and statistical analysis

We conducted 12 series of trials in 2015 and 8 series of trials in 2016. Experimental sites did not overlap and distance between sites had been at least 800 m, which should secure different shrike pairs, because shrikes are well known for high-nest fidelity (Šimek 2001). The video recordings were captured and analysed by a single person (NN) who also commented on the behaviour of adults during the trial and transferred the observed behaviour into an ethogram. To check for the quality of rating the bird behaviour, another observer, unaware of our hypotheses, analysed part of our data to check for the inter-rater reliability, which showed high correlation in all recorded behaviours (attack with physical contact: $R^2 = 0.9753$, dives without physical contact: $R^2 = 0.8566$, feeding the chicks: $R^2 = 0.759$, altogether: $R^2 = 0.9551$).

To explain the variability in the response variables, we ran three generalized linear mixed models (GLMM). The pair ID was always included as a random factor, because male and female cannot be included as independent observations. As mentioned above, there were three response variables: number of direct attacks with physical contact, number of dives without physical contact, and the number of nestling-feeding events. In all three models, we included the predictors as follows: type of dummy (one of five), sex of tested shrike (male, female), order of dummy presentation (from first to fifth), and year of study (2015, 2016). We did not test the age of the nestling in the nest, as the variability of this predictor was too low (7–11 days).

All response variables were approximated by Poisson distribution. The effects of particular predictor variables were evaluated by likelihood ratio test for Poisson distribution (Chi-squared test). For a comparison of values of categorical predictors, we used a post hoc test for Poisson distribution (z test) with Tukey correction of repeated comparisons. All statistical analyses were performed in R for Windows software (version R 3.2.1).

Results

Attacks with physical contact

The number of attacks with physical contact performed by shrikes was significantly affected by the type of dummy presented (Table 1). The shrikes attacked the stuffed kestrel significantly more often than the dummy with the head on the top ($z = 14.869$, $p < 0.001$; Fig. 2), and the dummy with head in the middle ($z = 26.741$, $p < 0.001$; Fig. 2), and the dummy with head on the bottom ($z = 26.673$, $p < 0.001$; Fig. 2), and than the stuffed pigeon ($z = 26.778$, $p < 0.001$; Fig. 2). They also physically attacked the dummy with head on the top more often than the stuffed pigeon ($z = 18.065$, $p < 0.001$; Fig. 2) and they physically attacked the dummy with head in the middle more often than the dummy with the head on the bottom ($z = 17.507$, $p < 0.001$; Fig. 2). Responses to the dummies with the head in the middle and on the bottom did not significantly differ from the responses to the stuffed pigeon (middle = 1.145, $p = 0.7647$; bottom: $z = 1.405$, $p = 0.6004$; Fig. 2). The shrikes attacked the dummy with the head on top 51.6% as often as stuffed kestrel. The dummy with head in the middle was attacked 12.1% as often as stuffed kestrel. The dummy with head on the bottom was attacked 9.1% as

Table 1 Effects of tested predictors

Response variable	Predictor	DF	Chi	p
Number of physical attacks	**Dummy**	**4**	**2327.3**	**≪0.001**
	Sex	**1**	**255.96**	**≪0.001**
	Sequence	**4**	**138.8**	**≪0.001**
	Season	1	1.9388	0.1638
Number of dives without contact	**Dummy**	**4**	**607.95**	**≪0.001**
	Sex	**1**	**105.55**	**≪0.001**
	Sequence	**4**	**220.51**	**≪0.001**
	Season	1	0.0249	0.8745
Number of feeding nestlings	**Dummy**	**4**	**97.779**	**≪0.001**
	Sex	1	0.3631	0.5468
	Sequence	4	6.8934	0.1416
	Season	1	0.3669	0.5447

All models are generalized mixed-effect models with data residuals following Poisson distribution, including shrike pair ID as a random factor

DF degrees of freedom

Bold highlighted the predictors have significant influence

often as stuffed kestrel. Stuffed pigeon was attacked 10.7% as often as stuffed kestrel.

We further showed significant differences between the number of physical attacks performed by males and females (Table 1), males physically attacked dummies more frequently (Fig. 3). The sequence presentation of dummies had a significant effect (Table 1); the number of attacks declined

during the day (Fig. 4). Shrikes attacked dummies significantly less in last trial than in first ($z = 10.21$, $p < 0.001$), second ($z = 9.029$, $p < 0.001$), third ($z = 7.947$, $p < 0.001$), and fourth trials ($z = 8.517$, $p < 0.001$). The effect of season was not significant (Table 1).
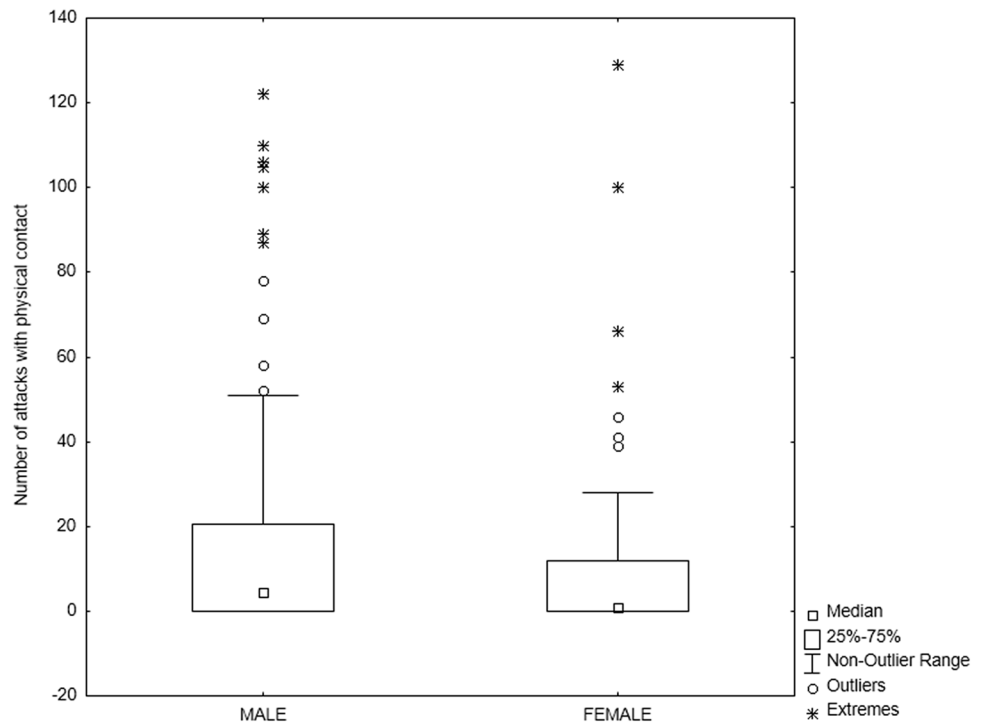
Dives without physical contact

The number of dives without physical contact performed by shrikes was significantly affected by the type of dummy presented (Table 1). The shrikes dived the stuffed kestrel significantly more often than the dummy with the head on top ($z = 4.564$, $p = 0.001$; Fig. 5), than the dummy with head in the middle ($z = 8.341$, $p < 0.001$; Fig. 5), than the dummy with head on the bottom ($z = 10.47$, $p < 0.001$; Fig. 5), and than the stuffed pigeon ($z = 14.469$, $p < 0.001$; Fig. 5). They also dived towards the dummy with head on the top more often than the dummy with head in the middle ($z = 12.388$, $p < 0.001$; Fig. 5), than the dummy with the head on the bottom ($z = 14.191$, $p < 0.001$; Fig. 5), and than the stuffed pigeon ($z = 17.099$, $p < 0.001$; Fig. 5). Shrikes also dived towards the dummy with the head in the middle ($z = 8.407$, $p < 0.001$; Fig. 5) and the dummy with the head on the bottom ($z = 6.350$, $p < 0.001$; Fig. 5) significantly more often than the stuffed pigeon. Responses to the dummies with the head in the middle and head on the bottom did not differ ($z = 2.441$, $p = 0.0974$; Fig. 5). The shrikes dived towards the dummy with the head on top 132.5% as often as stuffed kestrel. The shrikes dived
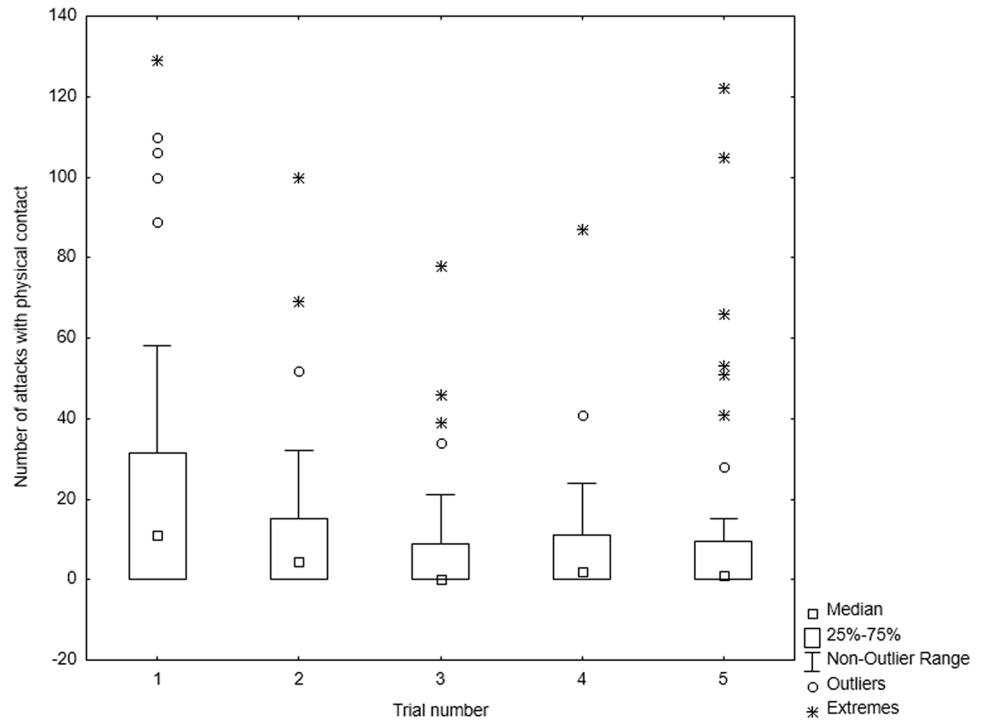

Fig. 2 Number of attacks with physical contact performed to particular dummies. Kestrel—stuffed kestrel, top—dismantled kestrel with the head on the top, middle—dismantled kestrel with the head in the middle, bottom—dismantled kestrel with the head on the bottom, and pigeon—stuffed pigeon
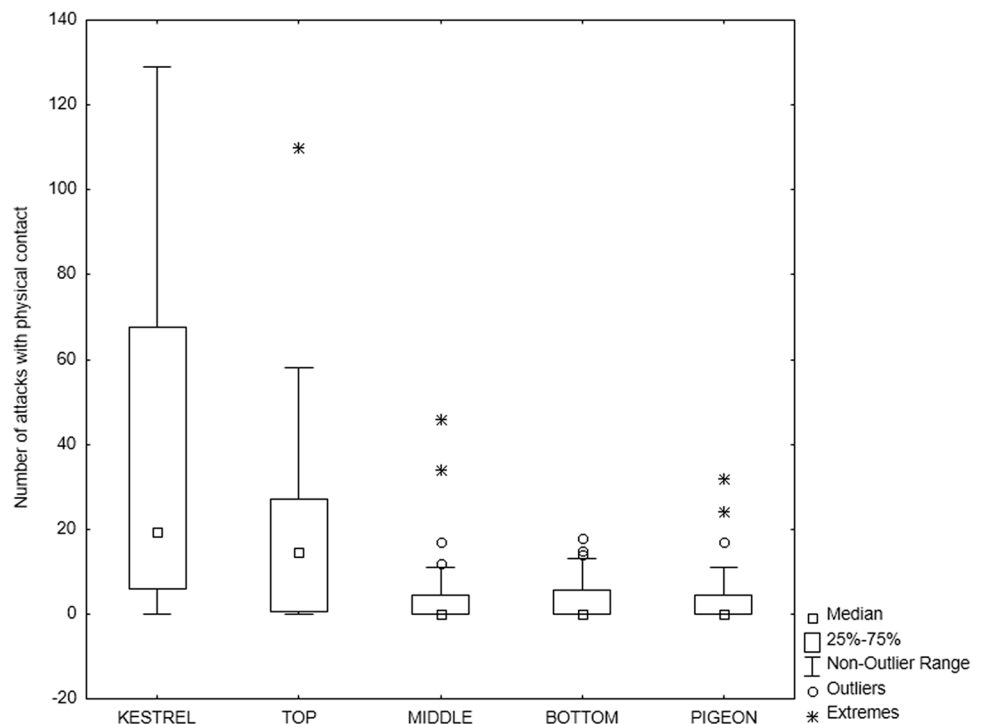
Fig. 3 Number of attacks with physical contact performed by both sexes


Fig. 4 Number of attacks with physical contact performed in the course of five trials during 1 day


towards the dummy with head in the middle 51.3% as often as stuffed kestrel. The shrikes dived towards the dummy with head on the bottom 40.4% as often as stuffed kestrel. The shrikes dived towards the stuffed pigeon 17.3% as often as stuffed kestrel.

We further showed a significant difference between the number of dives without physical contact performed by males and females (Table 1); males dive towards dummies significantly more frequently (Fig. 6). Sequence also had a significant effect (Table 1), with dive rate decreasing

Fig. 5 Number of dives without physical contact performed to particular dummies. Kestrel—stuffed kestrel, top—dismantled kestrel with the head on the top, middle—dismantled kestrel with the head in the middle, bottom—dismantled kestrel with the head on the bottom, and pigeon—stuffed pigeon
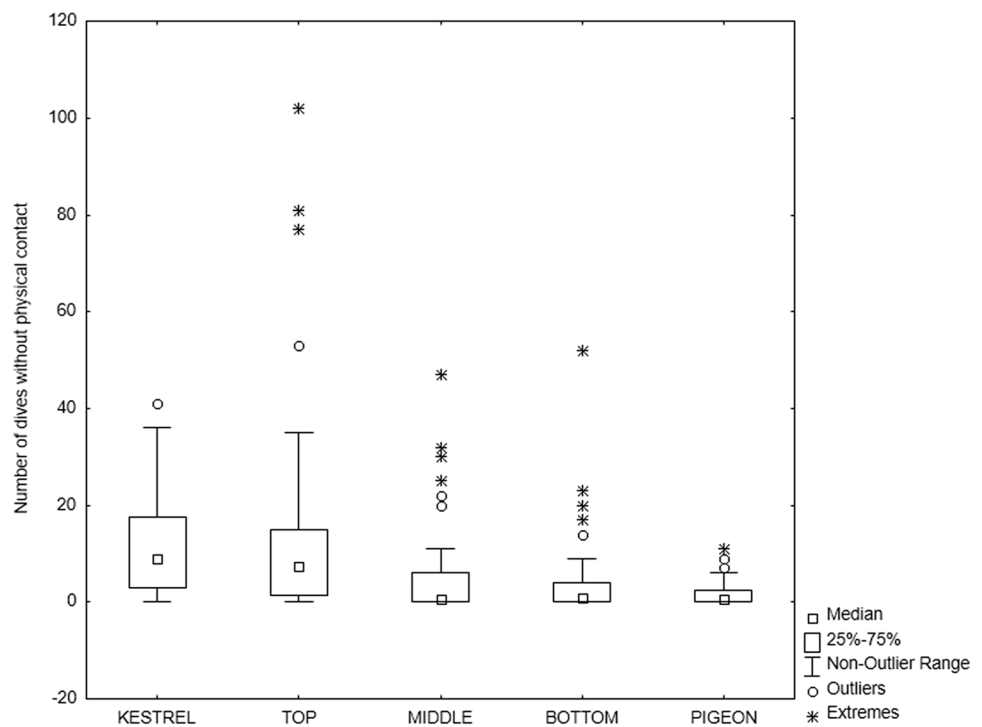

Fig. 6 Number of dives without physical contact performed by both sexes
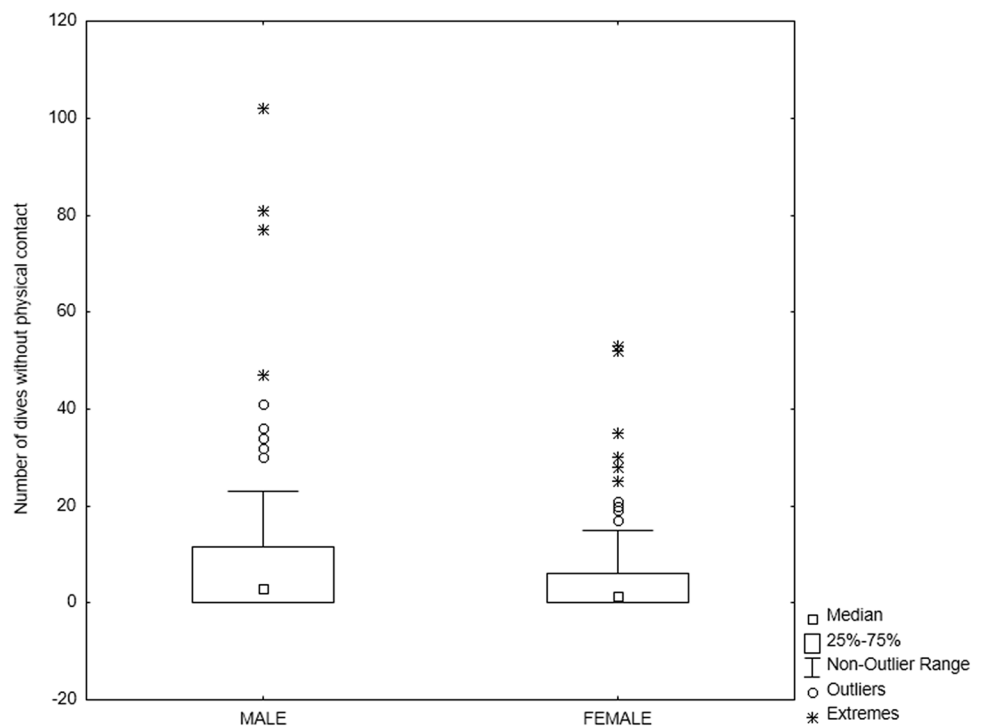
throughout the day (Fig. 7). Shrikes dived towards dummies significantly less in fifth trial than in first ($z = 12.072$, $p < 0.001$), second ($z = 10.199$, $p < 0.001$), third ($z = 4.821$, $p < 0.001$), and fourth trials ($z = 4.776$, $p < 0.001$). There had been also significantly less dives in the fourth trial than in first ($z = 6.397$, $p < 0.001$) and second trial ($z = 5.587$, $p < 0.001$). Also, there was significantly less dives in third trial than in first ($z = 6.765$, $p < 0.001$) and second trials ($z = 6.0484$, $p < 0.001$). The effect of season was not significant (Table 1).

**Fig. 7** Number of dives without physical contact performed in the course of five trials during 1 day
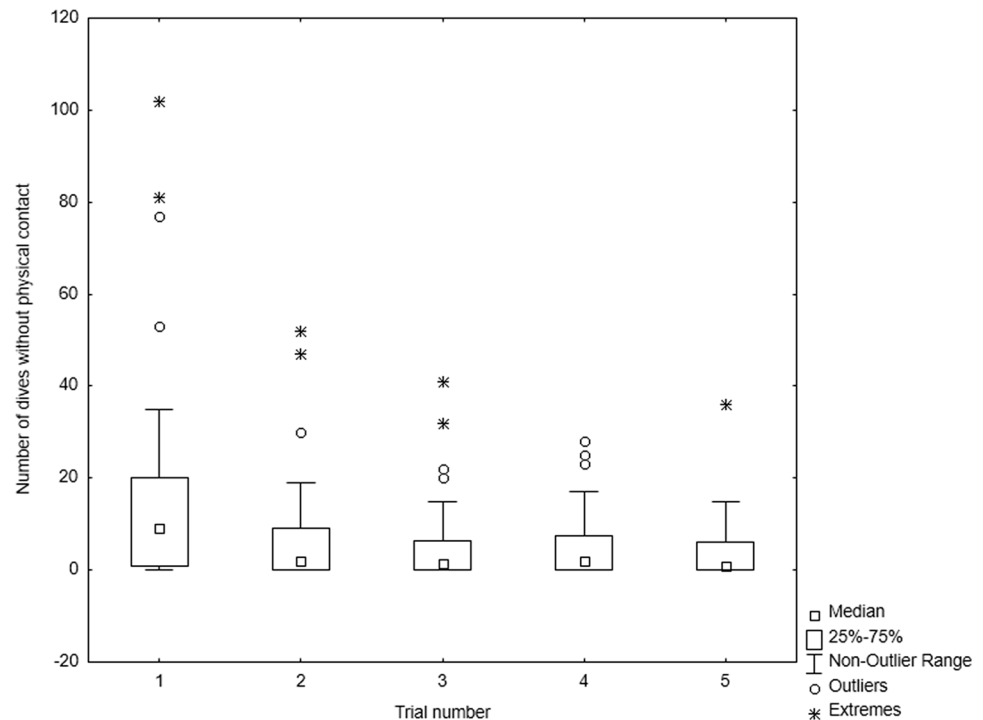
Feeding the offspring

The number of events when any parent provided food to the nestlings was significantly affected only by the type of presented dummy (Table 1). The number of feeding events during the presentation of the stuffed kestrel significantly differed from that of the dummy with the head in the middle ($z = 3.036$, $p = 0.0176$; Fig. 8), the dummy with head on the bottom ($z = 3.536$, $p = 0.00326$; Fig. 8), and from the stuffed pigeon ($z = 5.883$, $p < 0.001$; Fig. 8). The number of feeding events during the presentation of the dummy with head on the top significantly differed from that of the dummy with head in the middle ($z = 3.470$, $p = 0.00403$; Fig. 8), from the dummy with head on the bottom ($z = 3.860$, $p < 0.001$; Fig. 8), and from the stuffed pigeon ($z = 5.647$, $p < 0.001$; Fig. 8). The number of feeding events during presentation of the stuffed pigeon significantly differed from the number of feeding events during presentation of the dummy with the head in the middle ($z = 4.435$, $p < 0.001$; Fig. 8) and from the number of feeding events during presentation of the dummy with the head on the bottom ($z = 3.884$, $p < 0.001$; Fig. 8). There was no difference in the food provisioning between the dummy with the head on the top and the stuffed kestrel ($z = 0.174$, $p = 1.000$; Fig. 8) and between the dummy with head in the middle and the head on the bottom ($z = 1.242$, $p = 0.708$; Fig. 8). None of the other predictors significantly affected the occurrence of food provisioning (Table 1).

Discussion

Dummies with the head in the middle and head at the bottom are significantly less physically attacked than the dummy with head on the top and the stuffed kestrel. The results were similar for the dives without physical contact. This would suggest that shrikes perceive both dummies as harmless. Nevertheless, during the presence of these two types of dummies, adults feed their offspring significantly less than during the presence of the stuffed pigeon. It suggests that dummies with the head in the middle and head at the bottom of the body are not recognized as a kestrel, which would support the hypothesis suggesting the use of RBC principles. However, these dummies are, at the same time, not recognized as harmless objects. Shrikes do not feed their chicks in their presence and show vigilant behaviour. Alternative hypothesis could be that birds do not recognize the scrambled dummies as a relevant stimulus, and their behaviour is affected only by their neophobia to new and strange stimuli. Interpretation of our results could be also complicated by the view-dependent recognition as suggested by Logothetis et al. (1994) presuming that the proper recognition is affected by the view, the subject adopts. In our experiments, the proper recognition of the kestrel with head instead of its belly could be impossible simply due to the invisibility of the head (and the important cues) from behind. Nevertheless; during our experiments, the tested shrikes always had the opportunity

Fig. 8 Number of feeding events performed in the presence of particular dummies. Kestrel—stuffed kestrel, top—dismantled kestrel with the head on the top, middle—dismantled kestrel with the head in the middle, bottom—dismantled kestrel with the head on the bottom, and pigeon—stuffed pigeon
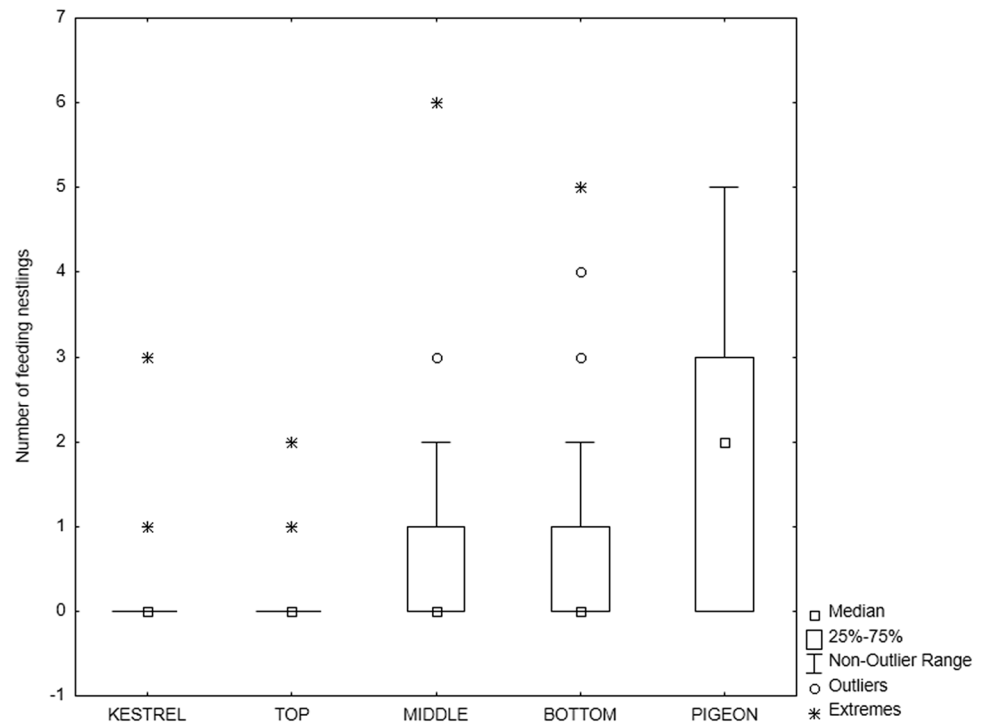
to view the presented dummies from multiple perches, and the birds always observe dummies from all sides. We can thus presume that they stored numerous views of the dummy.

The attack rate of shrikes towards the correctly composed dummy differed from the attack rate towards the stuffed kestrel. Anyway, the attack numbers were still significantly higher than towards the stuffed pigeon. These results do not correspond to those of our previous study (Němec et al. 2015), showing that textile dummies are perceived as equal in threat to stuffed birds. The explanation may reside in the fact that in the above-mentioned study (Němec et al. 2015), shrikes showed a certain degree of reinforcement by their very active defence behaviour during the previous trial, which caused some arousal in the parents that could bias the results of the succeeding trial. After such experiments, they also started attacking the slightly imperfect textile dummies. In our case, the order of dummy presentation was random (see Supplementary material 1); therefore, we expect this effect to be decreased by the fact that commonly attacked dummies (correct and stuffed kestrel) are presented in any possible order position. Additionally, there were relatively scarce experiments where the shrike parents attacked the presented dummy a lot (only the stuffed kestrel trials) and reinforcement was, therefore, of lower importance, and we were able to notice the differences between the textile and stuffed dummies. We may, thus, conclude that the textile dummies are

imperfect to a certain degree, but still elicit a recordable response and are, thus, useful for this type of research.

Anyway, we showed that the attack rate on both dummies with the head in an inappropriate position was significantly lower than towards the textile dummy with the head appropriately placed. We, thus, did not confirm the results of our previous study (Nováková et al. 2017), where we concluded that scrambled dummies are recognized on the base of the presence of local salient features despite their position (Cerella 1980). On the contrary, our results show that the spatial orientation of features on stimuli is especially important. These results support the principles of recognition based on the hypothesis of RBC (Biederman 1987). It corresponds with the assumptions of studies using operant conditioning that for the categorization of more realistic and relevant stimuli, the spatial orientation of parts of the stimulus is more crucial (Curio 1975; Van Hamme et al. 1992; Wasserman et al. 1993; Kirkpatrick-Steger et al. 1996; Peissig et al. 2000; Watanabe 2010). Therefore, in the natural conditions, when presenting 3D stimuli similar to living object and of high biological relevance at the same time, the use of principles of RBC is highly probable.

The explanation of the difference between the results of this study and our previous study may reside in the potential to assess correctly the motivation of the tested birds. In our previous study (Nováková et al. 2017), the birds not approaching the winter feeder during the presence of scrambled dummies may stay hidden in the shrubs because

of predator recognition, neophobia, or loss of motivation to forage. The observer cannot assess, which of these motivations were the case. Under the experimental paradigm of nest defence, it is clear that the motivation of parents is predator-related. This insufficiency in bird motivation assessment may mean that at least part of titmice visiting the feeder as well as part of shrikes defending their nests assess the scrambled dummies equally. Shrikes might consider the scrambled dummies as strange objects, which have to be guarded, but does not have to be attacked. However, most of tested shrikes do not feel relaxed, as they do not feed their chicks. The mental state could be the same in tits hidden in the shrub. It is just the measure which we use under these two methodological paradigms that brings different conclusion. Anyway, we cannot exclude the possibility, that part of titmice at the feeder recognized the sparrowhawk correctly only according the presence of specific features. At the same time, there were a few shrikes vigorously attacking the scrambled kestrels, suggesting that they also might use the principles of PFT in kestrel recognition.

We further demonstrated that males attack dummies more frequently than females. These findings correspond with many other studies observing the nest-defence behaviour of red-backed shrikes (Tryjanowski and Goławski 2004; Syrová 2011; Strnad et al. 2012). The reason for higher aggressiveness in males might be caused by a higher level of testosterone, especially during the breeding season (Wacker et al. 2009), or the greater body size and, thus, more significant activity of males during the antipredator behaviour (Tryjanowski and Goławski 2004). An alternative explanation is the higher investment of the male in the offspring. In red-backed shrikes, the male feeds the incubating female, and later feeds the hatched chicks (Rock and DiVita 1987, Lefranc 1997) together with the female. In our experiments, the chicks were between 7 and 11 days old, so we may conclude that the total investment of the male in the offspring is higher than of the female at this stage, and thus, the motivation of the male could be also higher (Patterson et al. 1980).

We showed a decrease of the number of attacks in the course of the day. In experiments conducted in the afternoon, the activity of shrikes was generally lower than in the morning. This effect has not been observed before in studies testing the nest defence of red-backed shrikes (Nemec and Fuchs 2014, Nemec et al. 2015). One possible explanation may reside in the exhaustion of tested shrike parents. During both experimental seasons, the afternoon temperatures were significantly higher than usual (up to 35 °C in the shade), which may have forced the birds to stay in the shade, reducing their activity. Another possible explanation would be that the parents habituate to the presence of kestrel (predator) during the course of the trials. Nevertheless, as the order of dummies was randomized, we would not see any differences between particular dummies in the numbers of attacks if there was any habituation.

Conclusions

Our results show that the presence of a specific feature alone may not be enough for proper recognition of a potential threat during the nest defence. Relevant, natural stimuli categorization represents a complex process, and thus, the importance of the context, in which the key features are present, is significant. However, it still remains unanswered if this principle of recognition is utilized generally in all situations of relevant stimuli in nature.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical note Experiments carried out in this research comply with the current laws of the Czech Republic. Authors are licenced for animal experimentation (Czech Animal Welfare Commission No. 489/01) and for conducting laboratory experiments with titmice (Ministry of Education, Youth and Sports, licence no. 8809/2011-30). Faculty of Science of the University of South Bohemia has accredited breeding of titmice (Ministry of Agriculture, licence no. 9103/2009-17210).

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