School of Doctoral Studies in Biological Sciences
University of South Bohemia in České Budějovice
Faculty of Science

Research on cognitive abilities in untrained birds

Ph.D. Thesis

Mgr. Jana Nácarová

Supervisor: doc. RNDr. Roman Fuchs, CSc.
Jihočeská univerzita v Českých Budějovicích, Přírodovědecká fakulta

České Budějovice 2017

This thesis should be cited as:

Nácarová, J. 2017: Research on cognitive abilities in untrained birds. Ph.D. Thesis Series, No. 20, University of South Bohemia, Faculty of Science, School of Doctoral Studies in Biological Sciences, České Budějovice, Czech Republic, 109 pp.

Annotation

This study investigates the cues used for predator recognition by wild-living untrained birds – great tits (*Parus major*). The experimental approach is used to test the reaction to the variously modified dummies of sparrowhawk (*Accipiter nisus*) and pigeon (*Columba livia* f. *domestica*) under laboratory conditions. The role of key features (yellow eye, hooked beak and talons), colour and size is tested. The results imply that the presence of raptor-specific features is mostly necessary but not sufficient to recognize predator in the presented dummies. Following research revealed that the part of the variability in response of great tits can be taken on the account of personality.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

České Budějovice, 1.12. 2017

....

Jana Nácarová

This thesis originated at the Faculty of Science, University of South Bohemia, in the study programme Zoology.

Přírodovědecká
fakulta
Faculty
of Science

Financial support

This thesis was supported by Grant Agency of the University of South Bohemia (GA JU 159/2013/P; GA JU 04-151/2016/P).

Acknowledgements

In the first place, I thank my supervisor, Roman Fuchs, who came up with the whole idea of crazy raptor dummies and refused to abandon it. In return, he had to spent hours with me and the manuscripts persuading the reviewers and editors about the importance of our research.

The next thanks belong to Petr Veselý for his obsession with bird ringing that ensured me the unlimited source of experimental subjects. In general, I am grateful to all the people in the neighbouring room for “my spot” on the drawers and occasional chat. And if I mention chatting, I cannot forget Honza Havlíček for peaceful coexistence in “předštetčí”, gossips and news in ornithology.

I am also grateful to my family for their support and Zuzka for being perfect sister (mostly). And last but not least, I thank to my David for his support, help and occasional destructive comments on the meaning of my work.

List of papers and author's contribution

The thesis is based on the following papers (listed chronologically):

I. **Beránková J**, Veselý P, Sýkorová J, Fuchs R (2014) The role of key features in predator recognition by untrained birds. Animal Cognition 17:963–971. doi: 10.1007/s10071-014-0728-1
(IF = 2.2)

Jana Nácarová collected the majority of behavioural data, evaluated and statistically analyzed the data, and wrote the manuscript with the help of co-authors.

II. **Beránková J**, Veselý P, Fuchs R (2015) The role of body size in predator recognition by untrained birds. Behavioural Processes 120:128–134. doi: 10.1016/j.beproc.2015.09.015
(IF = 2.7)

Jana Nácarová collected the majority of behavioural data, evaluated and statistically analyzed the data, and wrote the manuscript with the help of co-authors.

III. **Nácarová J**, Veselý P, Fuchs R (in prep.) Effect of behavioural syndrome on a bird's ability to categorize a predator.

Jana Nácarová collected, evaluated and statistically analyzed the behavioural data, and wrote the manuscript with the help of co-authors.

Contents

Introduction

How to study cognitive abilities

The cognitive abilities of animals are studied mainly within the scientific field labelled "cognitive ethology" defined as the study of the mental experiences of animals as they behave in their natural environment in the course of their normal lives (Griffin 1978). It developed as a fusion of cognitive science and classical ethology to study conscious processes in animals (Allen and Bekoff 1997). Donald Griffin's original idea was aimed at wants, plans, beliefs, and intentions as causes of behaviour (Griffin 1978), since they were not recognized in classical ethology (Tinbergen 1963).

However, nowadays the main field of cognitive ethology has moved instead to rather in-depth studies of particular processes in one or a few species such as associative learning in rats, visual category learning in pigeons, and social cognition in baboons (Shettleworth 2010). In addition to pigeons, favourite bird model species are parrots and various corvids that appear to be cognitively superior to other birds (Emery 2006). Cognitive studies are largely focused on the learning of, to some extent, artificial stimuli which allows experimenters to study the mental processes of the model species under controlled conditions.

On the other hand, animals' reactions to natural stimuli and situations are studied within the field of behavioural ecology. It is a more zoological discipline than cognitive ethology and studies the evolutionary basis of animal behaviour caused by ecological pressures (Krebs and Davies 2009). Behavioural ecology relies largely on observational studies of wild-living animals under natural conditions (Huntingford 1984). Recently, the experimental approach has been involved as well but mostly includes untrained reactions to artificially set up situations (e.g. predator, mate or food source presence).

The experimental approach allows behavioural ethologists to study animal behaviour that occurs relatively scarcely or that is difficult to observe (Dawkins 2007). Artificial evocation of a reaction provides possibilities for precise timing and more standardized data collection. In field studies, the presence of unknown and/or uncontrollable variables is a persistent problem. It is possible to eliminate these variables under controlled conditions in a laboratory. Nevertheless, it is necessary to keep in mind that wild animals kept in captivity for longer periods of time tend to exhibit physiological and behavioural profiles that do not match those of their wild counterparts (e.g. Butler et al. 2006; Dickens and Bentley 2014).

If we compare the scientific approach of cognitive ethology and behavioural biology, we can see that behavioural ecology deals with the question: how does an animal react to stimuli and what is it good for. On the other hand, the aim of cognitive ethology is to find the releasers of a reaction and the underlying processes.

The main aim of my studies is the fusion of cognitive ethology and behavioural ecology. This can lead to interesting results because we can obtain the complete story concerning the natural reaction of wild-living untrained animals. We can test not only if the animals recognize the stimulus but also how they recognize it.

Object recognition in untrained birds

The cognitive abilities of untrained animals can be studied only through their reactions to natural stimuli. The presentation of an artificial unfamiliar object can be used to study neophobia or spontaneous object exploration but it does not allow for the study of the underlying mechanisms of recognition (Blaser and Heyser 2015). On the other hand, presentation of a biologically relevant stimulus should start an appropriate reaction even in an untrained animal. The relevant stimulus can be a potential mate (Jennions and Petrie 1997), conspecific or heterospecific competitor (Grether et al. 2009), nest parasite (Grim 2005) or predator (Cooper and Blumstein 2015). The latter two options are tested very often, because they pose a strong motivation for reaction. It is possible to ignore a potential mate and risk “only” the loss of a mating opportunity. However, ignoring a nest parasite can cause the loss of a whole clutch and ignoring a predator can have even more fatal consequences (Caro 2005).

As already mentioned, the observational approach provides only very limited possibilities for research on recognition. Most of the existing pieces of knowledge come from various experiments that increase the efficiency of research by staging a meeting of prey and an intentionally selected predator. To focus on the recognition process requires an experimental approach including manipulation of the appearance of the presented stimuli – predators or nest parasites (Edwards et al. 1950; Curio 1975; Scaife 1976; Smith and Graves 1978; Gill et al. 1997; Davies and Welbergen 2008; Trnka et al. 2012; Beránková et al. 2014, 2015).

Manipulation of a predators' appearance has mainly been used for recognition, by various bird species, of raptors and nest parasites. The main reason is that recognition of mammal species can be complicated by factors other than clearly visual cues. It has been proved that predator odour (Amo et al. 2008, 2015) can play a role in mammalian predators. In birds, additional features such as movement, calls or presence of dead prey can increase fear of the presented dummy, but they are not necessary to evoke a sufficient reaction (Carlson et al. 2017).

Features used for recognition

The idea that only a part of the stimulus could be important for proper recognition was already proposed by one of the founders of classical ethology, Konrad Lorenz. He hypothesized that any specific animal behaviour can be triggered by a specific cue, this he called "Auslöser" (Lorenz 1937a, b). Later, the term "sign stimulus" was defined by Tinbergen (Tinbergen 1948) for a signal that triggers a specific reaction in another animal. In the context of studies aimed at cognitive processes, the term "key feature" (Marr and Nishihara 1978) or "salient feature" (Schleidt et al. 2011) is used for cues whose presence is necessary for proper object recognition.

The role of key features as releasers of antipredator behaviour was for the first time demonstrated using the silhouettes of raptors. The studied species were chicks of western capercaillie, *Tetrao urogallus* (Goethe 1940), wild turkey, *Meleagris gallopavo* (Lorenz 1939), and domestic chicken, *Gallus gallus* f. *domestica* (Lorenz 1939). The results imply that it was the relative length of the silhouette's neck that played an essential role in releasing anti-predator behaviour. When the silhouette was moved in such a direction that it created the impression of a short neck in the front and a long tail at the back (predator), it gave rise to flight behaviour in the tested poultry. When the same dummy was moved in the opposite direction, therefore appearing like a bird with a long neck and a short tail (goose), no antipredator behaviour emerged.

Eye

Despite several doubts about the results of the aforementioned experiments (Schleidt et al. 2011), they were highly important, because they provide the basis for the study of predator recognition. Consequently, various potential key features were studied. The eye is one of the most frequently studied features. It is highly interesting because it is quite a small and simple feature, compared to the whole body, but many species of owls and raptors have very conspicuous eyes, contrasting with the head colouration. Additionally, distinctly coloured bare skin often occurs around the eye, underlining its conspicuousness even more.

The first experiments testing the importance of predators' eyes were done on the song sparrow (*Melospiza melodia*). Nice and Ter Pelkwyk (1941) used variously modified cardboard models of the barred owl (*Strix varia*). Although they proved the importance of the head for recognizing the model as an owl, they found no evidence that the absence of merely the eyes decreases fear of the model. On the other hand, Smith and Graves (1978) showed that not only the absence of the head, but also the eyes on an Eurasian eagle-owl (*Bubo bubo*) mount greatly reduces the intensity of mobbing by barn swallows (*Hirundo rustica*). Similarly, the necessity of the eyes' presence was found in the reaction of pied flycatchers (*Ficedula hypoleuca*) to dummies of red-backed shrike (*Lanius collurio*) and pygmy owl (*Glaucidium passerinum*) (Curio 1975). The importance of the eyes in predator recognition was proved also in domestic chicken without any previous experience with raptors (Scaife 1976). A kestrel (*Falco tinnunculus*) dummy without eyes elicited a weaker response than an unmodified kestrel. Moreover, a brown kiwi (*Apteryx australis*) dummy with kestrel's eyes caused anti-predator behaviour (Scaife 1976).

In addition to the predator dummies, the importance of the eye has been tested for the nest parasite – common cuckoo (*Cuculus canorus*) that has a conspicuous yellow eye similar to that of the European sparrowhawk (*Accipiter nisus*). The cuckoo dummy with a black eye instead of a yellow one was not attacked by great reed warblers (*Acrocephalus arundinaceus*), although its colouration was not modified (Trnka et al. 2012). The importance of eye presence in the recognition process is also supported by studies that found that various birds can assess the direction of a predator's (human) gaze (Watve et al. 2002; Carter et al. 2008).

Beak

A hooked beak is another characteristic feature of raptors and owls, common for all members of the group. The shape and colour of the beak of owls and raptors is rather uniform compared to the eyes. Therefore, it could easily be considered a simple key feature defining this group of aerial predators but useless for more detailed distinction among different species.

Unnatural extension of the beak on a pygmy owl dummy partially reduced the mobbing reaction of flycatchers (Curio 1975). The complete absence of a beak on a great horned owl (*Bubo virginianus*) dummy caused a decline in the mobbing intensity of swallows (Smith and Graves 1978). Surprisingly, the importance of a beak as a key feature was found in nest parasite recognition as well. The beak on a brown-headed cowbird (*Molothrus ater*) dummy was replaced with the beak of a common starling (*Sturnus vulgaris*), which is longer and thinner. The response of yellow warblers (*Dendroica petechia*) to the modified dummy was much weaker than the response to the unmodified dummy with the original beak.

An interesting approach to test the importance of raptor local features is the presentation of a dummy Eurasian sparrowhawk and common cuckoo. They are very similar in colour, including conspicuous underpart barring and yellow eyes. The main difference is that the cuckoo lacks the features of a raptor – hooked beak and talons. The ability to distinguish between cuckoos and hawks despite their relative similarity was found in their potential hosts reed warblers (Duckworth 1991; Davies and Welbergen 2008), great reed warblers (Trnka and Grim 2013), and barn swallows (Liang and Møller 2015; Yu et al. 2016). Great tits (*Parus major*), an unsuitable host species for cuckoo, differed in their vocal response to the sparrowhawk and common cuckoo (Yu et al. 2017). However, their response to the cuckoo also differed from their reaction to a turtle dove, which implies that they still perceive it as a potential danger but probably less than the sparrowhawk.

Head

Manipulation of the whole head including local features can also be used. Usually, body/head chimeras are used. Such a chimera is not a simple 50% combination of two stimuli. The head part is smaller but contains more detailed features (for example already mentioned eye or beak). On the contrary, the body part largely influences the general shape of the chimera. This allows researchers to determine if the general appearance is more or less important than detailed local features.

Studies of chimera recognition were done largely on trained pigeons using artificial 2D pictures under laboratory conditions. Some of the stimuli were biologically irrelevant and probably unrecognizable for captive-bred pigeons – cat/dog chimeras (Ghosh et al. 2004) or black and white line drawings of birds and mammals (Cook et al. 2013). As a relevant stimulus, pictures of conspecifics were used (Nakamura et al. 2006; Patton et al. 2010). The results imply that pigeons prefer to categorize stimuli according to the body (Ghosh et al. 2004; Nakamura et al. 2006; Cook et al. 2013). However, a picture of just a female head can be enough to elicit courtship behaviour in male pigeons (Patton et al. 2010).

In untrained birds, the importance of just the head in predator recognition was studied only in the reaction of song sparrow to a cardboard dummy barred owl. The dummy with natural head and plain white body evoked a similar reaction to the model with natural colouration of the body (Nice and Ter Pelkwyk 1941). Nevertheless, the importance of the head was tested also in the context of nest parasite recognition. Willow warblers (*Phylloscopus trochilus*) did not attack a cuckoo torso deprived of its head. On the other hand, the separate head itself elicited an intensive mobbing reaction (Edwards et al. 1950). Surprisingly, there has been no study about the importance of the whole head or body in raptor recognition.

In our study, we investigated the importance of the raptor eye, beak and whole head as well. The reaction of great tits to dummies of pigeon and sparrowhawk with mutually exchanged eyes, beaks or heads was tested under laboratory conditions (Beránková et al. 2014). Laboratory conditions allowed us to study the reaction in detail. The tested tits showed three types of behaviour in the presence of the dummies. The fear reaction included the typical mobbing response – warning calls, feather cap raising and knee-bending. In contrast, feeding and pecking in the corn bedding was associated with the absence of fear. Interest in the dummy was manifested by approaching the dummy and a high frequency of movements. Dummies with interchanged heads confirmed the dominant role of the head part over the body in the process of predator recognition. The pigeon eyes on the sparrowhawk dummy reduced the level of fear it aroused. However, the presence of the sparrowhawk eyes did not increase the level of fear the pigeon dummy caused. On the contrary, the pigeon beak did not decrease the fear of the sparrowhawk dummy, but the presence of the sparrowhawk beak increased the fear of the pigeon dummy. Thus, the specific sparrowhawk feature (conspicuous yellow eye) is necessary for correct sparrowhawk dummy recognition but not enough to cause fear in combination with a pigeon dummy. On the other hand, the general raptor feature, a hooked beak, is not necessarily enough for correct sparrowhawk dummy recognition but it is enough to cause fear in combination with a pigeon dummy. These results imply that key features play an important, but not an exclusive, role in predator recognition.

Colouration

Another important cue used for predator recognition could be colouration, especially conspicuous colouration patterns. There are several studies testing the ability of birds to distinguish among real raptor species of similar size, differing only in colouration. Distinguishing between common kestrel and Eurasian sparrowhawk was studied in tits in feeder experiments (Tvardíková and Fuchs 2011, 2012), and in the context of nest-defence in shrikes (Strnad et al. 2012). Kestrel and sparrowhawk have similar body shape and size, and share typical raptor features (hooked beak, claws with long talons, and osseous ridge above the eyes). Therefore, it is probable that to distinguish them, the tested birds may use colouration. The colouration of these two species differs in many ways – colouration pattern, tone, ornament, and the colour of eyes and legs. Birds can perceive these elements of colouration as more or less equal and take them as a whole or just focus on a single conspicuous element, unique for the particular predator.

The first studies dealing with the role of colouration were rather unsystematic manipulations with various colouration patterns. Curio (1975) carried out an extensive study of the importance of the black eye stripe in shrikes mobbed by flycatchers. Naturally, an unmodified control mount of the shrike aroused the strongest alarm response among the flycatchers. The reaction to a mount with a red stripe through the eye did not significantly differ from the reaction to the control, while a mount with a green stripe caused a significant decrease in the reaction intensity. Reduction of the contrast between the stripe and the rest of the head did not cause a lessening of the flycatchers’ response, until the stripe merged with the background, then the flycatchers stopped emitting alarm calls (Curio 1975). However, the mere presence of an unmodified stripe was not sufficient and neither was a white rectangular bar with a black stripe. Nor did a uniformly white dummy with a stylized eye stripe elicit alarm responses from the flycatchers. The position of the eye stripe was important as well. Shifting the stripe from the forehead to the nape did not lower the response. Nevertheless, other modifications (stripe below the neck, on the abdomen or vertically on the nape) elicited only slight alarm responses. These results show that the eye stripe itself is not sufficient for recognition. It must be placed on the correct part of the body, and supplemented by other elements of colouration. On the other hand, the eye stripe is necessary for recognition. If the flycatcher encountered the shrike without the stripe, it caused no mobbing reaction.

The barred underpart that is quite conspicuous and common for the raptor genus *Accipiter* could play the same role in sparrowhawk recognition as the black stripe does in shrike recognition. However, the absence of underpart barring on a sparrowhawk dummy did not cause a reduction of fear reaction in great tits attending a winter feeder (Davies and Welbergen 2008). This result is therefore fundamentally different from that obtained in experiments with the red-backed shrike. While the eye-stripe is important for shrike recognition, the underpart barring is not essential for recognizing a sparrowhawk.

The explanation could be that the sparrowhawk without underpart barring is still recognizable as a raptor - other than a sparrowhawk but potentially dangerous. The modified dummy still offers a variety of features typical for birds of prey, like body shape, claws or hooked beak. Cautious behaviour towards an unknown predator also appears likely, since birds visiting a feeder are generally quite cautious (Hogstad 2017), with any suspicious object causing fear. If the starvation risk is not extremely high, it is more advantageous to hesitate with feeder attendance until the potential predator is gone.

The dispensability of underpart barring in the sparrowhawk dummy was found also in the reaction of reed warblers. They approached the sparrowhawk dummy without barred underparts with the same caution as an unmodified sparrowhawk (Welbergen and Davies 2011). This result corresponds with the above-described studies on tits, and the explanation will probably be similar. Reed warblers either recognize the sparrowhawk by other features or they fail to recognize the sparrowhawk, but are cautious towards the dummy as it bears all general raptor features, thus can be assessed as an unknown and potentially dangerous raptor species.

The majority of studies dealing with underpart barring were done with another enemy – the nest parasite. The grey morph of common cuckoo is conspicuously similar to the sparrowhawk, probably mimicking its colouration (Thorogood and Davies 2013; Gluckman and Mundy 2013). The advantage of experiments with nest-parasite recognition is the higher motivation of birds to react to the presented dummy not only with fear but also with active mobbing.

The experiments on great reed warblers that attacked the modified cuckoo dummy show that underpart barring is not necessary for proper cuckoo recognition (Trnka et al. 2012). Great reed warblers attacked a cuckoo dummy without underpart barring only slightly less than an unmodified cuckoo dummy, which suggests that recognition can be supported by another feature. The reed warblers (*Acrocephalus scirpaceus*) were even more active in mobbing a cuckoo dummy without underpart barring, probably because of its reduced similarity to the sparrowhawk (Welbergen and Davies 2011). On the contrary, a collared dove (*Streptopelia decaocto*) dummy with artificially added underpart barring was approached less than an unmodified dummy of the dove (Welbergen and Davies 2011).

Moreover, the brown morph of cuckoo was mobbed by great reed warblers less intensively than a grey morph but still more intensively than a harmless collared dove (Trnka and Grim 2013). This implies that they recognized it as dangerous but maybe with less certainty than the more common grey morph of cuckoo.

To sum up, birds undoubtedly use distinct particular elements of colouration in the process of recognition. However, they may not be necessary or sufficient, because if they are missing, the birds can use other less conspicuous features. It may depend on numerous circumstances – the uniqueness of particular features, the number of other features useful for recognition, but also the probability of encounter with the particular predator or the motivation of tested birds.

The above-mentioned studies deal only with the deletion or addition of a particular feature or colouration. However, valuable results can also be obtained by a complete change of overall colouration.

Such an experiment was done with the tits attending a winter feeder. They were presented with dummies of the European sparrowhawk with completely or partially modified colouration. The dummy without underpart barring, as well as the dummies coloured as a harmless great tit or robin, caused the same fear in the tits as the unmodified sparrowhawk dummy. Only the dummy with an artificial purple and white checkerboard pattern was not perceived as a greater threat than a harmless pigeon dummy (Veselý et al. 2016). These results imply that the presence of raptor features is enough to make tits more cautious, only highly unnatural colouration can overwhelm them and the tits probably perceive this dummy as a novel inanimate object. Nevertheless, the same problem as in the study of Welbergen and Davies (2011) applies here. A decrease in the number of birds attending the feeder was used as an estimate of fear reaction. However, the birds can evaluate the feeder as risky not only when the recognized sparrowhawk is present, but also when there is a “weird” bird carrying suspicious features.

The sensitivity of birds at a feeder can be seen when compared to my experiments under laboratory conditions where the manifestation of fear was measured directly. The great tits showed fear behaviour in the presence of a dummy with unmodified sparrowhawk colouration and a dummy with robin colouration. On the other hand, the presence of a sparrowhawk dummy with great tit and pigeon colouration caused no fear in the tested tits (Beránková et al. 2015). It seems that the colouration of familiar harmless birds can override the raptor features with the exception of robin colouration. The reason could be the relative similarity to sparrowhawk colouration and therefore a low efficiency in overriding the raptor features.

Size

Another significant factor in predator recognition could be size. Apel (1985) found that a dummy of the small sharp-shinned hawk (*Accipiter striatus*) results in a higher rate of calling than dummies of larger predators in black-capped chickadees (*Poecile atricapillus*). This finding was subsequently confirmed and further elaborated in several other studies on captive black-capped chickadees (Templeton et al. 2005), as well as on wild Carolina chickadees (*Poecile carolinensis*) (Soard and Ritchison 2009), and tufted titmice (*Baeolophus bicolor*) (Courter and Ritchison 2010). The chickadees and titmice responded to the presented predators of various size categories by uttering ‘chick-a-dee’ calls with different numbers and types of notes. Larger raptors (less dangerous for small songbirds) elicited calls with significantly more introductory ‘chick’ notes and fewer ‘dee’ notes, while smaller bird predators, more dangerous for small birds, elicited calls with few or no ‘chick’ notes and significantly more ‘dee’ notes (Soard and Ritchison 2009; Courter and Ritchison 2010). Likewise, Templeton et al. (2005) testing the vocal response of black-capped chickadees to different-sized ground and aerial predators found significant differences in the number of syllables according to the size of the predator.

Non-vocal response to variously sized predators was tested in great tits (Curio et al. 1983). Live owls were presented near to nest cavities and the distance of a great tit from the predator was measured. They dared to come relatively close to the tawny owl (*Strix aluco*), but they kept a greater distance from the pearl-spotted owlet (*Glaucidium perlatum*) considered to be the same as the pygmy owl. As opposed to the tawny owl, the pygmy owl is a specialized predator of small birds, which corresponds with the cautious behaviour of the tits.

The ability to discriminate predators similar in colour and differing essentially only in size was confirmed in experiments with birds reared in captivity (Palleroni et al. 2005). In this study, three trained raptors of different size categories (small-sized sharp-shinned hawk - *Accipiter striatus*, medium-sized Cooper's hawk - *Accipiter cooperii*; large-sized northern goshawk – *Accipiter gentilis*) flew over a paddock with free ranging fowls. Stronger reactions, such as sleeking and crouching, occurred most often in the presence of a large raptor, while displays of vigilance, like an erect posture with ruffling, constituted a more frequent response to a small bird of prey flying over. The fowls took up intermediate postures in the presence of a medium-sized raptor. In females, the intensity of their reaction was affected by whether they had chicks at the time of the experiment or not. Broody hens guarding chicks were more aggressive, especially toward the small-sized sharp-shinned hawk.

Although the hawks and owls used in the aforementioned experiments were very similar in colouration, we cannot exclude the possibility that the birds used some features of colouration in the process of recognition. Since the differences in a bird’s colouration that are indistinguishable for human eyes, can be obvious for birds (Eaton 2007).

The problem with colouration does not exist in experiments with silhouettes of flying raptors. Both captive domestic chickens (Evans et al. 1993) and wild-caught birds, namely blue tits (*Cyanistes caeruleus*) (Klump and Curio 1983) and the willow tits (*Poecile montanus*) (Alatalo and Helle 1990) underwent these experiments. As opposed to most of the experiments with mounted birds, or live birds mentioned hereinbefore, the trial birds responded to larger silhouettes more intensively than to smaller ones, specifically by reducing their motion and conversely by increasing the frequency or intensity of alarm calls in the studies (Klump and Curio 1983; Evans et al. 1993). The reason could be the fact that size provides information about the height of flight rather than the actual size of the raptor. A larger silhouette thus resulted in more fear since it presented a low-flying raptor, which was more dangerous for the potential prey. On the contrary, the tits called more intensively during a simulated flyover of a smaller silhouette in the study of Alatalo and Helle (1990). The authors explain this outcome by the fact that alarm calls are risky and therefore the tits prefer being silent, only calling when the risk of drawing attention to themselves is lower.

Nevertheless, the above mentioned and other similarly formulated studies with silhouettes cannot clearly provide evidence on the relevance of size for distinguishing various species. When presenting flying dummies, we can never unequivocally decide whether the size of the dummy refers to a body size or distance.

The solution is the presentation of the same dummies differing only in size. Curio (1975) found that a smaller red-backed shrike dummy with unchanged colouration elicited a similar reaction in the European pied flycatcher as an unmodified dummy. The same result was obtained in my study, there was no significant difference in the reaction of great tits to the dummy sparrowhawk in natural and reduced body size (Beránková et al. 2015). Body size was used as a cue only for discrimination of the robin-coloured dummies. The larger sparrowhawk dummy with robin colouration caused a fear reaction comparable to the unmodified sparrowhawk dummy, whereas the smaller dummy was treated as harmless.

Individual variability in the reaction

Most ethological studies include a lot of variability in behaviour. The individual behavioural differences within populations are usually assumed to be non-adaptive ‘noise’ around (possibly) adaptive average behaviour (Dall 2004). The situation has changed over the last decades and an effort has been made to explain the variability in the reaction of tested subjects. Consistent individual differences in behaviour have already been well described in numerous animal species and within various contexts (rev. in Gosling 2001). The terminology is highly variable in this field and numerous terms like personality, temperament, coping styles or strategies, and behavioural syndrome are used (Gosling 2001; Sih et al. 2004a, b; Groothuis and Carere 2005) for such differences.

Repeatedly a hypothetical link has been proposed between the well-documented personality traits and individual variation in cognition. Carere and Locurto (2011) suggested that personality profiles may be markers of different cognitive styles and conversely success or failure in cognitive tasks could affect different personalities diversely. Consequently, Sih and Del Giudice (2012) presented their hypothesis of complex connections among behavioural traits (fast-slow continuum), cognitive styles (speed-accuracy continuum), and risk-reward trade off. According to Griffin et al. (2015), behavioural traits such as boldness, activity, neophilia, and exploration might correlate statistically with cognitive abilities not only because they share a direct relationship but because they both are involved in some other process as well (Griffin et al. 2015). Nevertheless, the generally accepted idea is that differences in personalities cause the variation in perception of external stimuli and the consequent reaction, respectively cognitive abilities (Guillette et al. 2017).

In birds, studies relating to this question deal mainly with correlation of personality and learning abilities and/or problem solving. In great tits, exploratory behaviour does not correlate with spontaneous problem-solving (Cole et al. 2011) and general learning abilities (Amy et al. 2012). However, the slow male great tits (Amy et al. 2012) and slow black-capped chickadees (Guillette et al. 2011) react better to a change in the experimental setting, obtaining better results in reversal tasks, while the fast male great tits seem to be better at more complicated learning flexibility tasks (Titulaer et al. 2012).

The effect of personality in general learning abilities was found in fowls. Slow-exploring mallard ducks (*Anas platyrhynchos*) were better at finding the food in a maze (Bousquet et al. 2015). And reactive laying hens performed better in a colour-cue reward learning task, as proactive individuals tended to develop learning biases (de Haas et al. 2017).

Nevertheless, the correlation between personality traits and success in cognitive tasks can be less clear than was presented in the previous studies. Lermite et al. (2017) carried out a number of complex experiments testing the various dimensions of personality and cognitive abilities in common mynas (*Acridotheres tristis*). They found a number of correlations among different measured behavioural variables but no simply explainable correlation among the dimensions.

The correlation between personality and predator recognition has never been tested in birds. Nevertheless, studies aimed at the reaction to a predator in general imply that, not only the ability to recognize the predator can play the role, but the general differences in the risk assessment or risk-reward trade-off can play a role as well (Chittka et al. 2009; Sih and Del Giudice 2012). It was found out that the fast great tits are more willing to risk confrontation with a predator than the slow explorers (Quinn et al. 2012). Similarly, neophilic breeding pairs of great tits seem to be bolder, exhibiting stronger anti-predator mobbing responses than neophobic pairs (Vrublevska et al. 2015). Even though these studies show a correlation between personality and reaction to a predator, they fail to explain the mechanisms underlying the differences in behaviour (Beekman and Jordan 2017). The results of the aforementioned studies may mean that birds differ either in general boldness or the ability to recognize potential danger (predator). In the first case, the bolder birds are less careful in their reaction to all stimuli. In the second case, apparent boldness of some birds is the result of underestimation of danger due to insufficient inspection.

In my study, I compared the reaction of the slow and fast great tits to unmodified and modified dummies of a predator and non-predator to find out if the difference in the reaction is caused by the general fearfulness of slow birds or rather differences in cognitive abilities. On the one hand, slow birds were more cautious in the presence of an unmodified sparrowhawk. On the other hand, they tended to treat both chimaeras as less-threatening than fast individuals (Nácarová et al. in prep.). Since the slow birds are usually referred to as more sensitive to environmental cues (Sih and Del Giudice 2012), most of them correctly assessed the unmodified sparrowhawk as threatening, because they probably subjected the chimeras to a detailed inspection and were not confused by the presence of sparrowhawk features and assessed them as non-threatening.

This result implies that slow great tits are more fearful than fast birds only in the presence of an unambiguous danger, while the fast great tits seem to overestimate the danger posed by the chimera.

Conclusion

The complex study of the behavioural response of great tits (*Parus major*) to variously modified dummies of sparrowhawk (*Accipiter nisus*) and pigeon (*Columba livia* f. *domestica*) helped to reveal the cues that are necessary for predator recognition under controlled laboratory conditions.

The first study (Beránková et al. 2014) dealing with the role of key features found that the specific sparrowhawk yellow eye as well as the more general raptor hooked beak are necessary but not sufficient to induce fear reaction in the tested birds. This means that key features play an important but not an exclusive role in recognition and categorization.

The consecutive study was aimed at other possible cues involved in predator recognition, namely colour and size (Beránková et al. 2015). A strong effect to the proper sparrowhawk colouration was found, causing the fear reaction regardless of size. The size influenced the reaction only when the robin colouration was used.

The last study (Nácarová et al. in prep.) reveals the role of personality in the behavioural response of the tested great tits toward the highly modified predator dummies. Nevertheless, there is still a significant amount of unexplained variability. Its source should be the goal of following research.

References

Alatalo RV, Helle P (1990) Alarm calling by individual willow tits, *Parus montanus*. Anim Behav 40:437–442.

Allen C, Bekoff M (1997) Species of mind: The philosophy and biology of cognitive ethology. MIT Press

Amo L, Galván I, Tomás G, Sanz JJ (2008) Predator odour recognition and avoidance in a songbird. Funct Ecol 22:289–293. doi: 10.1111/j.1365-2435.2007.01361.x

Amo L, López-Rull I, Pagán I, García CM (2015) Evidence that the house finch (*Carpodacus mexicanus*) uses scent to avoid omnivore mammals. Rev Chil Hist Nat. doi: 10.1186/s40693-015-0036-4

Amy M, Oers K, Naguib M (2012) Worms under cover: relationships between performance in learning tasks and personality in great tits (*Parus major*). Anim Cogn 15:763–770. doi: 10.1007/s10071-012-0500-3

Apel KM (1985) Antipredator behavior in the Black-capped Chickadee (*Parus atricapillus*). Dissertation, University of Wisconsin

Barnett C, Salter M, Chevallier C, et al (2013) The Ability of North Island Robins to Discriminate between Humans Is Related to Their Behavioural Type. PLOS ONE 8:e64487. doi: 10.1371/journal.pone.0064487

Beekman M, Jordan LA (2017) Does the field of animal personality provide any new insights for behavioral ecology? Behav Ecol. doi: 10.1093/beheco/arx022

Beránková J, Veselý P, Fuchs R (2015) The role of body size in predator recognition by untrained birds. Behav Processes 120:128–134. doi: 10.1016/j.beproc.2015.09.015

Beránková J, Veselý P, Sýkorová J, Fuchs R (2014) The role of key features in predator recognition by untrained birds. Anim Cogn 17:963–971. doi: 10.1007/s10071-014-0728-1

Blaser R, Heyser C (2015) Spontaneous object recognition: a promising approach to the comparative study of memory. Front Behav Neurosci. doi: 10.3389/fnbeh.2015.00183

Bousquet CAH, Petit O, Arrivé M, et al (2015) Personality tests predict responses to a spatial-learning task in mallards, *Anas platyrhynchos*. Anim Behav 110:145–154. doi: 10.1016/j.anbehav.2015.09.024

Butler SJ, Whittingham MJ, Quinn JL, Cresswell W (2006) Time in captivity, individual differences and foraging behaviour in wild-caught chaffinches. Behaviour 143:535–548.

Carere C, Locurto C (2011) Interaction between animal personality and animal cognition. Curr Zool 57:491−498.

Carlson NV, Pargeter HM, Templeton CN (2017) Sparrowhawk movement, calling, and presence of dead conspecifics differentially impact blue tit (*Cyanistes caeruleus*) vocal and behavioral mobbing responses. Behav Ecol Sociobiol 71:133. doi: 10.1007/s00265-017-2361-x

Caro T (2005) Antipredator Defenses in Birds and Mammals. University of Chicago Press

Carter J, Lyons NJ, Cole HL, Goldsmith AR (2008) Subtle cues of predation risk: starlings respond to a predator’s direction of eye-gaze. Proc R Soc B Biol Sci 275:1709–1715. doi: 10.1098/rspb.2008.0095

Chittka L, Skorupski P, Raine NE (2009) Speed–accuracy tradeoffs in animal decision making. Trends Ecol Evol 24:400–407. doi: 10.1016/j.tree.2009.02.010

Cole EF, Cram DL, Quinn JL (2011) Individual variation in spontaneous problem-solving performance among wild great tits. Anim Behav 81:491–498.

Cook RG, Wright AA, Drachman EE (2013) Categorization of birds, mammals, and chimeras by pigeons. Behav Processes 93:98–110. doi: 10.1016/j.beproc.2012.11.006

Cooper WE, Blumstein DT (2015) Escaping from predators: an integrative view of escape decisions.

Courter JR, Ritchison G (2010) Alarm calls of tufted titmice convey information about predator size and threat. Behav Ecol 21:936–942. doi: 10.1093/beheco/arq086

Curio E (1975) The functional organization of anti-predator behaviour in the pied flycatcher: A study of avian visual perception. Anim Behav 23:1–115. doi: 10.1016/0003-3472(75)90056-1

Curio E, Klump G, Regelmann K (1983) An anti-predator response in the great tit (*Parus major*): is it tuned to predator risk? Oecologia 60:83–88.

Dall SR. (2004) Behavioural Biology: Fortune Favours Bold and Shy Personalities. Curr Biol 14:R470–R472. doi: 10.1016/j.cub.2004.06.011

Davies N., Welbergen J. (2008) Cuckoo-hawk mimicry? An experimental test. Proc R Soc B Biol Sci 275:1817–1822. doi: 10.1098/rspb.2008.0331

Dawkins MS (2007) Observing Animal Behaviour: Design and analysis of quantitative data. OUP Oxford

de Haas EN, Lee C, Hernandez CE, et al (2017) Individual differences in personality in laying hens are related to learning a colour cue association. Behav Processes 134:37–42. doi: 10.1016/j.beproc.2016.11.001

Dickens MJ, Bentley GE (2014) Stress, captivity, and reproduction in a wild bird species. Horm Behav 66:685–693. doi: 10.1016/j.yhbeh.2014.09.011

Duckworth JW (1991) Responses of breeding reed warblers Acrocephalus scirpaceus to mounts of sparrowhawk *Accipiter nisus*, cuckoo *Cuculus canorus* and jay *Garrulus glandarius*. Ibis 133:68–74.

Eaton MD (2007) Avian visual perspective on plumage coloration confirms rarity of sexually monochromatic North American passerines. The Auk 124:155–161. doi: 10.1642/0004-8038(2007)124[155:AVPOPC]2.0.CO;2

Edwards G, Hosking E, Smith S (1950) Reactions of some passerine birds to a stuffed cuckoo. II. A detailed study of the willow-warbler. Brit Birds 43:144–150.

Emery NJ (2006) Cognitive ornithology: the evolution of avian intelligence. Philos Trans R Soc B Biol Sci 361:23–43. doi: 10.1098/rstb.2005.1736

Evans CS, Macedonia JM, Marler P (1993) Effects of apparent size and speed on the response of chickens, *Gallus gallus*, to computer-generated simulations of aerial predators. Anim Behav 46:1–11. doi: 10.1006/anbe.1993.1156

Ghosh N, Lea SE., Noury M (2004) Transfer to intermediate forms following concept discrimination by pigeons: chimeras and morphs. J Exp Anal Behav 82:125–141.

Gill SA, Neudorf DL, Sealy SG (1997) Host responses to cowbirds near the nest: cues for recognition. Anim Behav 53:1287–1293. doi: 10.1006/anbe.1996.0362

Gluckman T-L, Mundy NI (2013) Cuckoos in raptors’ clothing: barred plumage illuminates a fundamental principle of Batesian mimicry. Anim Behav 86:1165–1181. doi: 10.1016/j.anbehav.2013.09.020

Goethe F (1940) Beobachtungen und Versuche über angeborene Schreckreaktionen junger Auerhühner. [Observations and experiments on the innate fright reactions of young mountain cocks.]. Z Für Tierpsychol 4:165–167. doi: 10.1111/j.1439-0310.1940.tb00621.x

Gosling SD (2001) From Mice to Men: What Can We Learn About Personality From Animal Research? Psychol Bull 127:45–86.

Grether GF, Losin N, Anderson CN, Okamoto K (2009) The role of interspecific interference competition in character displacement and the evolution of competitor recognition. Biol Rev. doi: 10.1111/j.1469-185X.2009.00089.x

Griffin AS, Guillette LM, Healy SD (2015) Cognition and personality: an analysis of an emerging field. Trends Ecol Evol 30:207–214. doi: 10.1016/j.tree.2015.01.012

Griffin DR (1978) Prospects for a cognitive ethology. Behav Brain Sci 1:527–538.

Grim T (2005) Host recognition of brood parasites: Implications for methodology in studies of enemy recognition. The Auk 122:530. doi: 10.1642/0004-8038(2005)122[0530:HROBPI]2.0.CO;2

Groothuis TGG, Carere C (2005) Avian personalities: characterization and epigenesis. Neurosci Biobehav Rev 29:137–150. doi: 10.1016/j.neubiorev.2004.06.010

Guillette LM, Reddon AR, Hoeschele M, Sturdy CB (2011) Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task. Proc R Soc B Biol Sci 278:767–773. doi: 10.1098/rspb.2010.1669

Guillette LM, Naguib M, Griffin AS (2017) Individual differences in cognition and personality. Behav Processes 134:1–3. doi: 10.1016/j.beproc.2016.12.001

Hogstad O (2017) Predator discrimination and anti-predator behaviour by wintering parids: an experimental study. Ornis Nor 40:39–44. doi: 10.15845/on.v40i0.1320

Huntingford F (1984) The Study of Animal Behaviour. Springer Netherlands, Dordrecht

Jennions MD, Petrie M (1997) Variation in mate choice and mating preferences: a review of causes and consequences. Biol Rev 72:283–327.

Klump GM, Curio E (1983) Reactions of Blue Tits *Parus caeruleus* to Hawk Models of Different Sizes. Bird Behav 4:78–81.

Krebs JR, Davies NB (2009) Behavioural Ecology: An Evolutionary Approach. John Wiley & Sons

Lermite F, Peneaux C, Griffin AS (2017) Personality and problem-solving in common mynas (*Acridotheres tristis*). Behav Processes 134:87–94. doi: 10.1016/j.beproc.2016.09.013

Liang W, Møller AP (2015) Hawk mimicry in cuckoos and anti-parasitic aggressive behavior of barn swallows in Denmark and China. J Avian Biol 46:216–223. doi: 10.1111/jav.00515

Lorenz K (1937a) The Companion in the Bird's World. The Auk 54:245–273. doi: 10.2307/4078077

Lorenz K (1937b) Über die Bildung des Instinktbegriffes. Naturwissenschaften 25:289–300. doi: 10.1007/BF01492648

Lorenz K (1939) Vergleichende Verhaltensforschung. Verhandlungen Dtsch Zool Ges 12:69–102.

Marr D, Nishihara HK (1978) Representation and recognition of the spatial organization of three-dimensional shapes. Proc R Soc Lond B Biol Sci 200:269–294.

Nácarová J, Veselý P, Fuchs R (in prep.) Effect of behavioural syndrome on a bird's ability to categorize a predator.

Nakamura T, Ito M, Croft DB, Frederick Westbrook R (2006) Domestic pigeons (*Columba livia*) discriminate between photographs of male and female pigeons. Learn Behav 34:327–339.

Nice MM, Ter Pelkwyk J (1941) Enemy Recognition by the Song Sparrow. The Auk 58:195–214. doi: 10.2307/4079104

Palleroni A, Hauser M, Marler P (2005) Do responses of galliform birds vary adaptively with predator size? Anim Cogn 8:200–210. doi: 10.1007/s10071-004-0250-y

Patton TB, Szafranski G, Shimizu T (2010) Male pigeons react differentially to altered facial features of female pigeons. Behaviour 147:757–773. doi: 10.1163/000579510X491090

Quinn JL, Cole EF, Bates J, et al (2012) Personality predicts individual responsiveness to the risks of starvation and predation. Proc R Soc B Biol Sci 279:1919–1926.

Scaife M (1976) The response to eye-like shapes by birds. I. The effect of context: A predator and a strange bird. Anim Behav 24:195–199. doi: 10.1016/S0003-3472(76)80115-7

Schleidt W, Shalter MD, Moura-Neto H (2011) The hawk/goose story: The classical ethological experiments of Lorenz and Tinbergen, revisited. J Comp Psychol 125:121–133. doi: 10.1037/a0022068

Shettleworth SJ (2010) Cognition, evolution, and behavior, 2nd ed. Oxford University Press, Oxford ; New York

Sih A, Bell A, Johnson JC (2004a) Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol Evol 19:372–378. doi: 10.1016/j.tree.2004.04.009

Sih A, Bell AM, Johnson JC, Ziemba RE (2004b) Behavioral syndromes: an integrative overview. Q Rev Biol 79:241–277.

Sih A, Del Giudice M (2012) Linking behavioural syndromes and cognition: a behavioural ecology perspective. Philos Trans R Soc B Biol Sci 367:2762–2772. doi: 10.1098/rstb.2012.0216

Smith MJ, Graves HB (1978) Some factors influencing mobbing behavior in barn swallows (*Hirundo rustica*). Behav Biol 23:355–372.

Soard CM, Ritchison G (2009) "Chick-a-dee" calls of Carolina chickadees convey information about degree of threat posed by avian predators. Anim Behav 78:1447–1453. doi: 10.1016/j.anbehav.2009.09.026

Strnad M, Nemec M, Vesely 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.

Templeton CN, Greene E, Davis K (2005) Allometry of Alarm Calls: Black-Capped Chickadees Encode Information About Predator Size. Science 308:1934–1937. doi: 10.1126/science.1108841

Thorogood R, Davies NB (2013) Hawk mimicry and the evolution of polymorphic cuckoos. Chin Birds 4:39–50. doi: 10.5122/cbirds.2013.0002

Tinbergen N (1963) On aims and methods of Ethology. Z Für Tierpsychol 20:410–433. doi: 10.1111/j.1439-0310.1963.tb01161.x

Tinbergen N (1948) Social releasers and the experimental method required for their study. Wilson Bull 60:6–51.

Titulaer M, van Oers K, Naguib M (2012) Personality affects learning performance in difficult tasks in a sex-dependent way. Anim Behav 83:723–730. doi: 10.1016/j.anbehav.2011.12.020

Trnka A, Grim T (2013) Color plumage polymorphism and predator mimicry in brood parasites. Front Zool 10:25.

Trnka A, Prokop P, Grim T (2012) Uncovering dangerous cheats: how do avian hosts recognize adult brood parasites? PloS One 7:e37445.

Tvardíková K, Fuchs R (2011) Do birds behave according to dynamic risk assessment theory? A feeder experiment. Behav Ecol Sociobiol 65:727–733. doi: 10.1007/s00265-010-1075-0

Tvardíková K, Fuchs R (2012) Tits recognize the potential dangers of predators and harmless birds in feeder experiments. J Ethol 30:157–165. doi: 10.1007/s10164-011-0310-0

Veselý P, Buršíková M, Fuchs R (2016) Birds at the Winter Feeder do not Recognize an Artificially Coloured Predator. Ethology 122:937–944. doi: 10.1111/eth.12565

Vrublevska J, Krama T, Rantala MJ, et al (2015) Personality and density affect nest defence and nest survival in the great tit. Acta Ethologica 18:111–120. doi: 10.1007/s10211-014-0191-7

Watve M, Thakar J, Kale A, et al (2002) Bee-eaters (*Merops orientalis*) respond to what a predator can see. Anim Cogn 5:253–259. doi: 10.1007/s10071-002-0155-6

Welbergen JA, Davies NB (2011) A parasite in wolf's clothing: hawk mimicry reduces mobbing of cuckoos by hosts. Behav Ecol 22:574–579. doi: 10.1093/beheco/arr008

Yu J, Wang L, Xing X, et al (2016) Barn swallows (*Hirundo rustica*) differentiate between common cuckoo and sparrowhawk in China: alarm calls convey information on threat. Behav Ecol Sociobiol 70:171–178. doi: 10.1007/s00265-015-2036-4

Yu J, Xing X, Jiang Y, et al (2017) Alarm call-based discrimination between common cuckoo and Eurasian sparrowhawk in a Chinese population of great tits. Ethology 123:542–550. doi: 10.1111/eth.12624

Chapter I

The role of key features in predator recognition by untrained birds

Jana Beránková, Petr Veselý, Jana Sýkorová, Roman Fuchs

Animal Cognition 17:963–971

The role of key features in predator recognition by untrained birds

Jana Beránková*, Petr Veselý, Jana Sýkorová, Roman Fuchs

Faculty of Science, University of South Bohemia,
Branišovská 31a, 37005 České Budějovice, Czech Republic
**Corresponding autor, e-mail: jaja.berankova@gmail.com*

Abstract

The most important role in the recognition and categorization of predators (as well as other animals) is usually attributed to so-called key features. Under laboratory conditions, we tested the role of yellow eyes (specific for the genus Accipiter in European raptors) and hooked beak (common for all European birds of prey) in the recognition of the sparrowhawk (*Accipiter nisus*) by untrained great tits (*Parus major*) caught in the wild. Using wooden dummies, we interchanged either one of these potential key features or the body of the sparrowhawk (predator) and domestic pigeon (harmless bird). The tested tits showed three types of behaviour in the presence of the dummies: fear, interest without fear, and lack of interest. Eye interchange lowered fear of the sparrowhawk, but did not cause fear of the pigeon. Beak interchange did not lower fear of the sparrowhawk. Eye interchange caused increased interest in both species. Thus, a specific sparrowhawk feature is necessary for correct sparrowhawk dummy recognition but a general raptor feature is not. On the other hand, a specific sparrowhawk feature on a pigeon dummy is not enough to prompt sparrowhawk recognition. Thus, key features play an important, but not exclusive, role in predator recognition. An increased interest in some of the modified dummies implies that the tits have a general concept of a sparrowhawk. The individual variability in behaviour of tits is discussed.

Keywords: Key features, Recognition, Categorization, Concept, Untrained birds

Introduction

Almost any aspect of animal decision-making (from foraging behaviour to mate choice) can be influenced by the risk of predation (Lima and Dill 1990). Only fast and accurate predator recognition gives prey a chance to choose the right anti-predator behaviour and escape tactic (Curio 1976).

If all types of predator pose the same threat and require the same response, then there is no need to distinguish among them (Kullberg and Lind 2002). For example, the mouth size and distance between eyes are sufficient for predator recognition in piscivorous fish, and no further cues are needed (Karplus and Algom 1981; Karplus et al. 1982). However, when different types of predator represent different levels or kinds of threat, then selection of the appropriate response requires their more specific recognition and categorization (McLean and Rhodes 1991). It is obvious that birds are able to distinguish between predators of different taxa (Curio et al. 1983; Suzuki 2012; Strnad et al. 2012) or size (Klump and Curio 1983; Palleroni et al. 2005), but the mechanisms that facilitate recognition are poorly understood.

The most important role in the recognition and categorization of predators (as well as other animals) is usually attributed to so-called key features. The origin of this idea dates to 1935 when Konrad Lorenz defined the term "releaser" (Auslöser) as an acoustic or visual stimulus causing a specific reaction (Lorenz 1937). Later on, different terms, such as "sign stimuli", were used (Tinbergen 1948), but the central idea remained the same. The term "key feature" comes from feature theory (Bruner et al. 1956; Marr and Nishihara 1978; Smith and Medin 1981). According to this theory, objects are assigned to categories on the basis of the features of which they are composed (Pearce 2008).

The role of key features in predator recognition has been only rarely tested. The first studies focused on the "short neck" in the silhouettes of birds of prey. It was found that even a cardboard dummy that has a short neck prompts an escape response independently of the colour or shape of the wings and tail (Krätzig 1940; Lorenz 1940; Tinbergen 1948). The first more complex study was carried out by Curio (1975) who tested the reaction of the pied flycatcher (*Ficedula hypoleuca*) to the modified dummies of two similar-sized predators, the pygmy owl (*Glaucidium passerinum*), and the male red-backed shrike (*Lanius collurio*). Several further studies aimed at the recognition of predators (Scaife 1976; Watve et al. 2002; Davies and Welbergen 2008), nest parasites (Gill et al. 1997; Welbergen and Davies 2011; Trnka et al. 2012), or sexual partners (Burley and Coopersmith 1987; Pincemy et al. 2009) followed. They confirmed the importance of eyes (Scaife 1976; Watve et al. 2002; Trnka et al. 2012), beak (Burley and Coopersmith 1987; Gill et al. 1997), and coloration patterns (Davies and Welbergen 2008; Pincemy et al. 2009; Welbergen and Davies 2011) for recognition of tested stimuli.

Key feature theory (Marr and Nishihara 1978) has also been repeatedly tested under laboratory condition by training birds (most often the domestic pigeon) to respond to drawings or photographs with key features present/absent (Kirkpatrick-Steger et al. 1998; Huber 2001; Matsukawa et al. 2004) or to objects composed of several previously learnt stimuli (Cerella 1980; Aust and Huber 2001; Werner et al. 2004). The results imply that pigeons are able to use local features for categorization, but their importance depends largely on the stimuli used. Moreover, most of the tested stimuli were unrelated to the real life of birds. Animal reactions to relevant and irrelevant stimuli may be different, and therefore, the categorization mechanism may also be different (Pashler 2002).

The reactions of untrained birds to natural stimuli have only occasionally been tested under laboratory conditions. Patton et al. (2010) examined the reaction of male pigeons to an altered picture of a female using their tendency to perform courtship behaviour in the presence of a relevant sexual partner. He proved that the beak and eyes are important features for mate recognition because pigeons showed no reaction to a pigeon head without these features.

In birds in general, some of the potential key features are species specific, while others characterize whole taxonomical and/or ecological groups of species. One example is the yellow eyes and hooked beak in birds of prey in Central Europe. Conspicuous yellow eyes are specific for the genus Accipiter, while a hooked beak characterizes all members of Falconiformes (and Strigiformes as well).

We tested the role of these features in the recognition of the sparrowhawk (*Accipiter nisus*). The replacement of key features on predator dummies applied in all the studies mentioned above tests whether those features are necessary, but not whether they are in themselves sufficient for proper recognition. Therefore, in our study, we interchanged either eye or beak of a sparrowhawk (predator) and a domestic pigeon (harmless bird). However, the sparrowhawk possesses potential key features on the body as well (especially the coloration pattern or claws). Therefore, we interchanged also the whole body of sparrowhawk and pigeon.

The great tit (*Parus major*) was chosen as a model species as we know that tits are able to recognize pigeons and sparrowhawks from our previous field study (Tvardíková and Fuchs 2012). The amount of stress in this experiment was measured by the number of arrivals at the feeder with the presented dummy. Our current experiments were carried out in the laboratory which facilitated more detailed behavioural analysis and discrimination among stress response and other relevant reactions (e.g. stimulus exploration).

We tested five hypotheses:

(1) The presence of the sparrowhawk eyes on the sparrowhawk dummy is necessary for the recognition of the dummy as a sparrowhawk (the sparrowhawk dummy without sparrowhawk eyes will be treated as less dangerous than the unmodified sparrowhawk dummy).

(2) The presence of the sparrowhawk eyes on the pigeon dummy is sufficient for its recognition as a sparrowhawk (the pigeon dummy with sparrowhawk eyes will not be treated as less dangerous than the unmodified sparrowhawk dummy).

(3) The presence of the raptor beak on the sparrowhawk dummy is not necessary for the recognition of the dummy as a sparrowhawk (the sparrowhawk dummy without raptor beak will not be treated as less dangerous than the unmodified sparrowhawk dummy).

(4) The presence of the raptor beak on the pigeon dummy is sufficient for its recognition as a raptor (the pigeon dummy with raptor beak will be treated as more dangerous than the unmodified pigeon dummy).

(5) Change of the body does not influence the recognition of pigeon and sparrowhawk (the sparrowhawk dummy with pigeon body will not be treated as less dangerous than the unmodified sparrowhawk, and the pigeon dummy with sparrowhawk body will not be treated as more dangerous than the unmodified pigeon).

Materials and methods

Subjects

The great tit (*Parus major*) was chosen as a model species. Great tits are very adaptable to laboratory conditions (e.g. Dingemanse 2002). Moreover, no neophobic reaction that could negatively influence their behaviour in the presence of an unfamiliar stimulus has been confirmed in them (Cole et al. 2011). Birds were trapped in mist-nets in the suburban areas of České Budějovice (Czech Republic) during the winter seasons of the years 2008–2011. Tits were ringed after capturing to avoid testing individuals repeatedly. After that, the birds were held in cages and provided with water and sunflower seeds ad libitum. Each bird was tested only once. Altogether we used 160 individuals for all the experiments (20 birds to each presented dummy).

Experimental stimuli

A sparrowhawk dummy was used as a predator because it is a specialized predator of small birds in Europe (Zawadzka and Zawadzki 2001; Bujoczek and Ciach 2009; Chamberlain et al. 2009). Wild great tits strictly avoid the sparrowhawk and are able to recognize and distinguish it from other predator species (Tvardíková and Fuchs 2011). The domestic pigeon dummy was used as a harmless species because its size is comparable to the sparrowhawk. Great tits living in suburban areas encounter it commonly, and they do not express any fear in the presence of a pigeon dummy (Tvardíková and Fuchs 2012).

We assumed that if there is no difference in reaction to the chimera (a dummy with changed key feature) and to the unmodified sparrowhawk, the tits recognize the dummy as a sparrowhawk. If they are afraid of the chimera less than the unmodified sparrowhawk, but more than the unmodified pigeon, it may be concluded that they recognize the dummy as a raptor (but not sparrowhawk). If the stress reaction does not differ from the reaction to the unmodified pigeon dummy, it may be concluded that tits do not recognize the dummy as any raptor.

Both dummies consisted of carved wood with detachable and interchangeable parts (beak, eyes, and the whole body including the trunk, folded wings, tail, and legs). In preliminary studies, we found that there is no difference in the reaction to a wooden and a stuffed sparrowhawk dummy (Poláková et al in prep.). In our study, we used 8 types of dummies: unmodified sparrowhawk (HHH), sparrowhawk with pigeon eyes (PHH), sparrowhawk with pigeon beak (HPH), sparrowhawk with pigeon body (HHP), unmodified pigeon (PPP), pigeon with sparrowhawk eyes (HPP), pigeon with sparrowhawk beak (PHP), and pigeon with sparrowhawk body (PPH). For coding explanation, see Table 1.

Table 1 Abbreviations of dummy types

Eye	Beak	Body	Code
Hawk	Hawk	Hawk	HHH
Pigeon	Hawk	Hawk	PHH
Hawk	Pigeon	Hawk	HPH
Hawk	Hawk	Pigeon	HHP
Pigeon	Pigeon	Pigeon	PPP
Hawk	Pigeon	Pigeon	HPP
Pigeon	Hawk	Pigeon	PHP
Pigeon	Pigeon	Hawk	PPH

The eye, beak, and body features are represented by the first, second, and third alphabets

Experimental design

Before the experiment, the birds were deprived of food for 1.5 h. Afterwards they were released into an experimental cage (2 x 1 x 0.5 m). The cage was equipped with corn bedding, perches, a nesting box, and a dish with sunflower seeds in the front part. The dummy was placed in front of the cage above the dish with food. The experiment started after the removal of a wooden barrier between the tested bird and the dummy. The behaviour of the birds during their exposure to the dummies was recorded on video for 10 min.

The video was analysed in Observer XT 6.1 (Noldus Information Technology 1990–2006) by a single observer. The following behaviours were quantified: total occurrence of raising feathers on head (cap), knee bending (knee), warning calls (warn), approach of the dummy to less than 1 m away (approach), movement from one perch to another (move), pecking the equipment in the cage (peck), total duration of scanning the dummy from less than 1 m away (scan), surveying the corn bedding for food (bedding), feeding on the provided sunflower seeds (feeding), sitting still (sit). The inter-rater reliability was estimated by analysing all recorded experiments by another rater. The correlations between the two sets of behavioural measures were calculated using Correlation matrices in STATISTICA 9.1 (StatSoft Inc. 2009). The results show significant correlations ($p < 0.05$) in most of the observed behaviours (warn, $r = 0.99$; knee, $r = 0.61$; cap, $r = 0.51$; move, $r = 0.90$; peck, $r = 0.57$; feeding, $r = 0.93$; bedding, $r = 0.98$; sit, $r = 0.71$).

The behavioural elements mentioned above have been already used in various behavioural studies on birds (e.g. Kullberg and Lind 2002; Stuber and Bartell 2013). Studies on tits' personality established that individual birds are consistent in such behavioural traits as exploratory behaviour, risk taking, fearfulness, and reactivity (see Groothuis and Carere 2005 for review).

Statistical analysis

Tit behaviour (all the activities mentioned above) was analysed using the multivariate technique - the principal component analysis (PCA) in Canoco 4.5 (ter Braak and Šmilauer 1998) to find out whether there was a consistent reaction to the dummies. Thus, the dummies were used as supplementary environmental data in PCA. PCA scores of the first and second axis were used as synthetic dependent variables in ANOVA in STATISTICA 9.1 (StatSoft Inc. 2009) to test the effect of the dummies on the tits' behaviour. Differences among the individual dummies were consequently compared using the Tukey's HSD test. We also used redundancy analysis (RDA) in Canoco 4.5 with the dummies as environmental data to compare behaviour of individual tits toward tested dummies. Data for PCA and RDA analysis were logarithmically adjusted and centred.

Results

Principal component analysis shows that there are consistent reactions to presented dummies (Fig. 1). The first PCA axis explains 39.4 % of variability and separates stress behaviour (knee bending, warning calls, raised feathers on the head) from other behavioural types (exploration or feeding). The second PCA axis explains 17.7 % of variability and divides exploration of the dummy (approaching and scanning the dummy) or displacement activity (moving and pecking of the cage equipment) from other behaviours (stress or feeding).

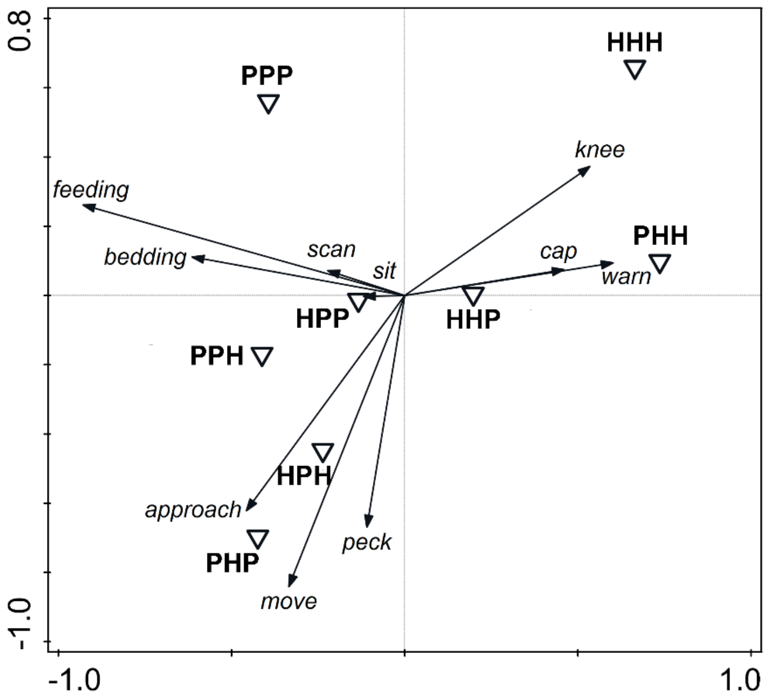

Fig. 1 Behaviour of tested tits in the presence of individual dummies visualized on the first and second axis of PCA. For explanations of behavioural types, see ''Materials and methods''. For explaining the abbreviations of dummy types, see Table 1

The particular dummy presented significantly influences the tested birds' PCA scores on the first axis (ANOVA, F = 5.430, p <0.001) and the second axis (ANOVA, F = 4.901, p <0.001). The following p values refer to post hoc Tukey's HSD test. The tits showed more stress behaviour (first PCA axis) in the presence of the dummy HHH and HPH than in the presence of PHH (p = 0.040, p = 0.018) HPP (p = 0.004, p = 0.002), PPH (p = 0.005, 0.002), and PPP (p = 0.007, 0.003). The dummies HHP and PHP differ from neither group (Fig. 2). Effects of the key features manipulation are summarized in Table 2.

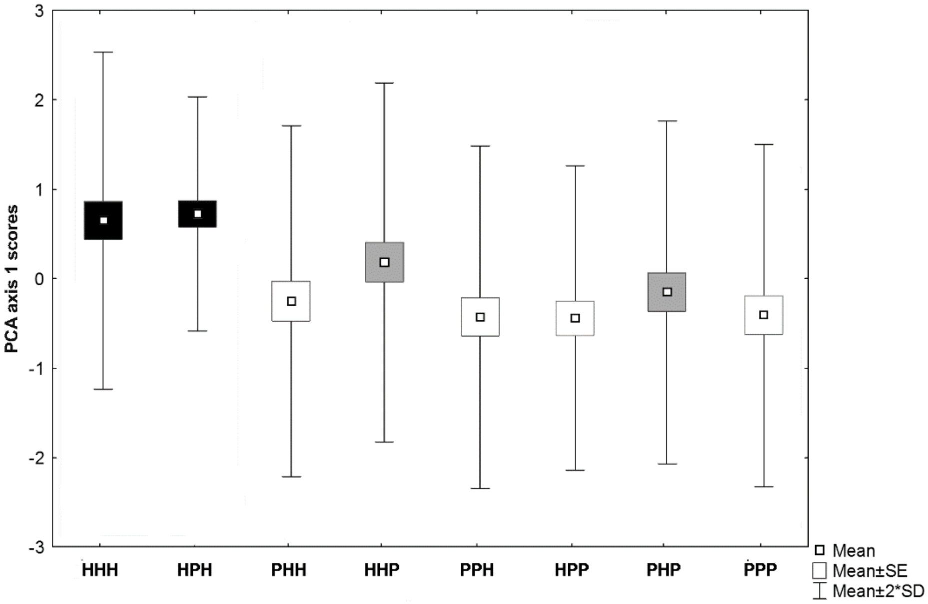

Fig. 2 The effect of the presence of individual dummies on the behaviour of tested tits (first PCA axis scores). *Positive values* indicate the stress behaviour (feather cap, knee bending, and warn calls). For explaining the abbreviations of dummy types, see Table 1. *Black* and *white boxes* differ significantly from each other. *Grey boxes* do not differ from any other

Table 2 Comparison of responses of great tits to various presented dummies on the first PCA axis

Dummies in comparison		Post hoc Tukey's HSD test, p value
Effect of the eye		
PHH	HHH	**0.040**
HPP	PPP	1.000
Effect of the beak		
HPH	HHH	1.000
PHP	PPP	0.987
Effect of the body		
HHP	HHH	0.746
PPH	PPP	1.000

Significant differences in bold. For explaining the abbreviations of dummy types, see Table 1

More intense exploration (second PCA axis) was observed in the presence of dummies with interchanged eyes (PHH, HPP) than unmodified dummies HHH (p = 0.004, p<0.001) and PPP (p = 0.014, p<0.001). Other dummies (PPH, HHP, PHP, and HPH) differ from neither group (Fig. 3).

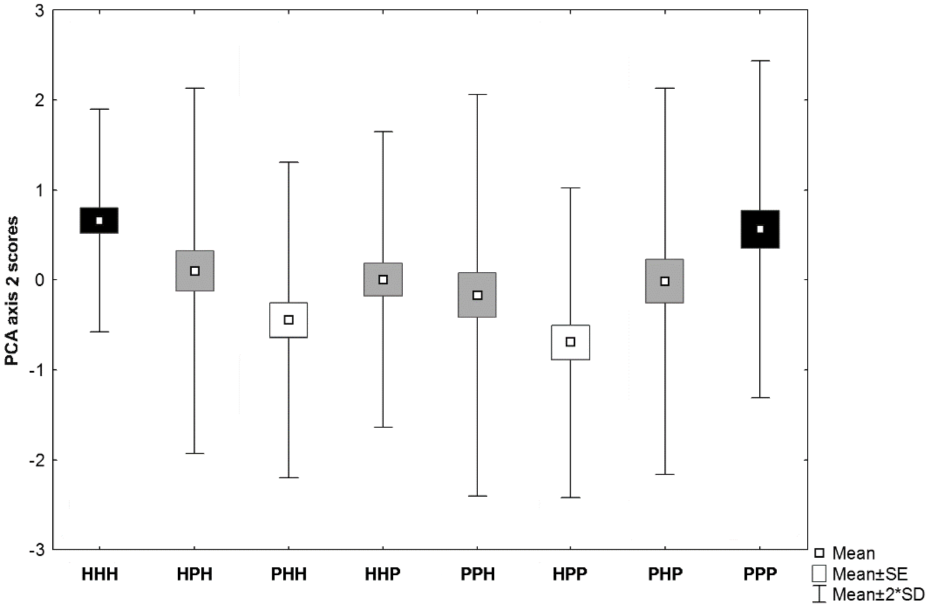

Fig. 3 The effect of the presence of individual dummies on the behaviour of tested tits (second PCA axis scores). Negative values indicate interest in the dummy (scanning and approaching it). For explaining the abbreviations of dummy types, see Table 1. *Black* and *white boxes* differ significantly from each other. *Grey boxes* do not differ from any other

Redundancy analysis also showed that there are significant differences in the tits' behaviour in the presence of individual dummies (Monte Carlo permutation test, F = 4.886, p = 0.002). The first RDA axis explains 11.0 %; the second axis explains 3.8 % of variability. The marginal effects of all the dummies besides HHP are significant (Table 3). The size of the effect was the largest for HHH and HPH. However, projection of scores of individual tits on RDA axes (Fig. 4) shows that there is great interindividual variability in behaviour toward most of the dummies. The behaviour of the individual birds was rather consistent during the experiment. The most of the birds are located further from the intersection of the RDA axes (in the positive as well as negative values). It means that behavioural elements correlated with either the first or the second axis prevailed in their behaviour. There was only a minority of the birds with balanced representation of antagonistic types of behaviour during the experiment. These birds are located near the intersection of the RDA axes.

Table 3 Marginal effects of presence of individual dummies on tested tits behaviour (RDA)

Dummy type	Explained variability (%)	Pseudo-F	p value
HPH	4.4	7.2	0.002
HHH	4.3	7.1	0.002
PPP	2.9	4.8	0.002
HPP	2.8	4.5	0.006
PHH	2.2	3.5	0.006
PPH	1.9	3.1	0.028
PHP	1.6	2.6	0.022
HHP	0.9	1.5	0.202

For explaining the abbreviations of dummy types, see Table 1

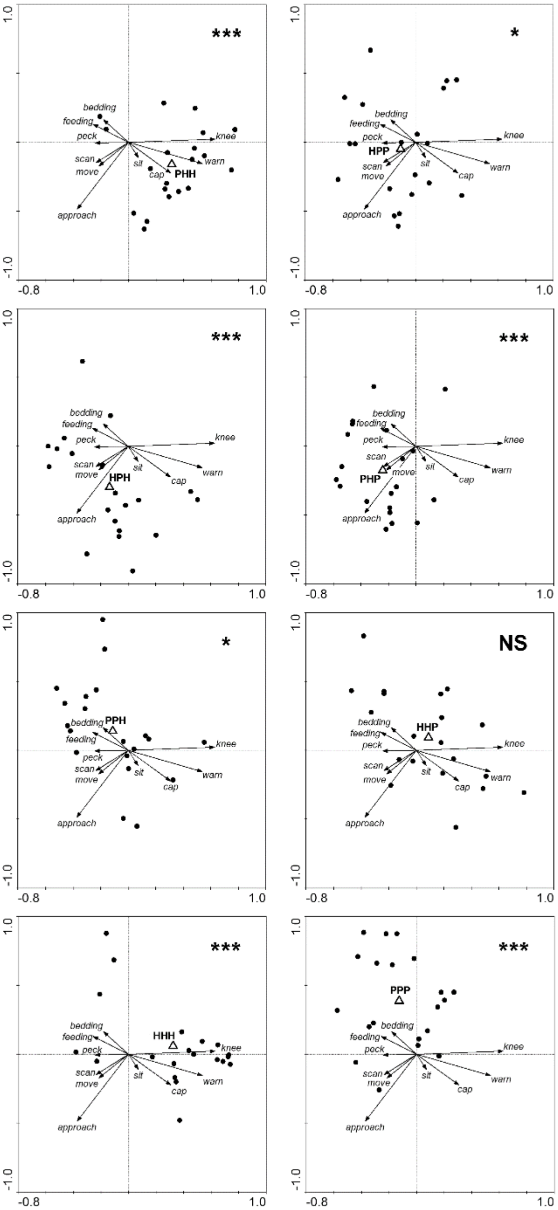

Fig. 4 Scores of individual tits on the first and second RDA axis in the presence of individual dummies. For explanations of behavioural types, see ''Materials and methods''. For explaining the abbreviations of dummy types, see Table 1. *Triple asterisk* indicates the dummies with very significant effect on behaviour of tits ($p<0.01$). *Asterisk* indicates the dummies with significant effect on behaviour of tits ($p<0.05$). NS indicates the dummy with no significant effect on the behaviour of tits ($p>0.05$)

Discussion

The hypotheses that the presence of the sparrowhawk eyes is necessary and also sufficient for the recognition the dummy as a sparrowhawk were confirmed only partially. Pigeon eyes on the sparrowhawk dummy (PHH) make the dummy less dangerous than the unmodified sparrowhawk dummy (HHH). However, the sparrowhawk eyes on the pigeon dummy (HPP) do not make the dummy as dangerous as the HHH. It means that the mere yellow eyes are necessary but not sufficient for sparrowhawk recognition and another cue is therefore needed for the correct recognition. This is not surprising because yellow eyes are a unique for the genus *Accipiter* within the birds of prey in Central Europe but they occur also in other harmless bird species (e.g. tufted duck *Aythya fuligula*, common cuckoo *Cuculus canorus*, or barred warbler *Sylvia nisoria*).

The hypotheses that the presence of the raptor beak is not necessary for the dummy recognition as a sparrowhawk but sufficient for recognition as a raptor in general were confirmed in part. The pigeon beak on sparrowhawk dummy (HPH) does not lower the fear of the dummy significantly as compared to the HHH. It means that the wrong beak does not influence the recognition when the appropriate sparrowhawk eye and body are present. The pigeon dummy with raptor beak (PHP) is not treated as more dangerous than the unmodified pigeon dummy (PPP) but also not less dangerous than HHH. It means that PHP is not conclusively treated as harmless or as dangerous. It seems that individual birds are not uniform in the reaction to it but at least a portion of the tits recognized the dummy as a raptor due to the hooked beak although the other features belonged to the pigeon (see below). Raptor recognition based on a single feature would be useful in the categorization of unfamiliar bird species, and a hooked beak is appropriate for this purpose because this feature is unique for birds of prey in Central Europe, where parrots do not occur.

In accordance with the hypothesis that change of the body does not influence the recognition, the sparrowhawk with pigeon body (HHP) is not treated as less dangerous than HHH, and the pigeon with sparrowhawk body (PPH) is not more dangerous than the PPP. However, the HHP is also not treated as more dangerous than PPP. It implies that some of the cues usable for recognition of sparrowhawk are present on its body.

Based on these results, we may rule out the theory that any of the typical predator features (general - hooked beak, or species specific - yellow eye) acts as a universal key feature for predator recognition in untrained birds as proposed by the classical ethological school (Tinbergen 1948). Moreover, the behaviour reflected by the second PCA axis implies that tits have a complex image of how the pigeon and sparrowhawk should appear. Tits showed interest in the modified dummies, and it seems that they are aware of any strangeness in the chimeras. Tits were the most interested in the dummies with interchanged eyes (PHH and HPP). Thus, it seems that tits use both key features and more complex concepts for predator recognition and categorization. Local key features allow the fast and simple recognition and categorization of familiar species which is necessary for effective anti-predatory behaviour. On the other hand, complex concepts may be used for the discrimination of unfamiliar species that must be further examined.

The importance of local key features for recognition and categorization in untrained birds has been tested rather rarely. Several studies show that the absence or replacement of appropriate eyes (Scaife 1976; Trnka et al. 2012) or beak (Gill et al. 1997; Patton et al. 2010) results in a decrease in the ability to recognize a predator (Scaife 1976), nest parasite (Gill et al. 1997; Trnka et al. 2012), or sexual partner (Patton et al. 2010). Only (Patton et al. 2010) compared the effect of eye and beak removal. In contrast to our results, he found that the beak is more important than the eye for recognition. Male pigeons showed more courtship behaviour to the image of female pigeon without eyes than to the one without a beak. The author hypothesizes that the beak provides useful information about the quality of a sexual partner such as efficacy of feeding and parasite control (Patton et al. 2010). The reason why the eye was a more important feature in our study could be that it allows the recognition of a specific (and extremely dangerous) predator species while the beak allows only the recognition of raptors in general. Therefore, it seems that the importance of key features is context dependent.

Scaife (1976), Davies and Welbergen (2008), and Trnka et al. (2012) compared the effect of the absence of key features on the dummy of a harmful species and their presence on harmless birds. Scaife (1976) found that a European kestrel with covered eyes caused less stress reaction in chickens than a kestrel with conspicuous yellow eyes (inappropriate for European kestrel) visible, whereas the presence of yellow eyes on a harmless kiwi increased the stress reaction significantly. In our study, a similar effect of mere yellow eyes on the pigeon dummy was not significant. The reason could be that Scaife (1976) tested a captive, naïve chicken whose ability to recognize a predator could differ from our experienced wild great tits (Kullberg and Lind 2002, see below). Davies and Welbergen (2008) tested the importance of hawk-like underparts for cuckoo and sparrowhawk recognition. They found that the absence of this coloration pattern in a cuckoo lowers fear of the dummy and the presence of it in a dove increases fear of that dummy in tits on winter feeders. On the other hand, the absence of barring did not lower the ability of the tested tits to recognize the dummy as a sparrowhawk. It seems that the manipulation with underpart barring in this study influenced the dummies' recognition more than the body manipulation in our experiments. The explanation could be in the different experimental design. The tits in the experiment at winter feeder (Davies and Welbergen 2008) observed the presented dummies from a further distance, while in our experiments, they could see them at close range. Extensive and contrast barring should be visible and recognizable from further distance than the detailed features like eyes or beak. Trnka et al. (2012) found that the reaction of great reed warblers was not aggressive to an unmodified dove and to the dove with cuckoo body. Thus, contrary to the experiments of Davies and Welbergen (2008), the mere barred underparts did not cause aversion to the dummy. The reaction to the dummy of the cuckoo with a dove body did not differ from the reaction to the unmodified cuckoo. These results are in better agreement with ours than the results of Davies and Welbergen (2008). The explanation may be that the great reed warblers were physically attacking the dummies and so they could assess all the potential key features from proximity.

Categorization processes have also been intensively studied in pigeons under laboratory condition using operational conditioning. Discrimination between the chimeras of cats and dogs (Ghosh et al. 2004) or mammals and birds (Cook et al. 2013) has been tested. Contrary to our results, the chimeras' discrimination was based rather on the body than on the head. The main difference between their and our experiments is that pigeons were presented two dimensional images which may not be relevant to them (see Weisman and Spetch 2010 for review). We may hypothesize that our tits were searching for key features on the head part, because they were aware of the stimulus being an animal. Pigeons confronted with non-relevant stimuli search for the features usable for categorization on the greatest part of the stimulus, which is the body.

Our results can be compared with the experiments aimed at human face recognition as well. Matsukawa et al. (2004) examined the effect of deletion of individual elements of line drawings. Deletion of eyes and eyebrows considerably suppressed responding, while the deletion of the other parts (nose and mouth, ears, and head contours) did not. It is in accordance with our results about the importance of the eyes. However, the pigeons' discriminative performance was substantially impaired by fragmentation. It suggests that the pigeons use both global and local features for discrimination. Jitsumori and Yoshihara (1997) trained pigeons to discriminate between happy and angry human faces. The pigeons directed their pecks predominantly to the mouth or eyes, eventually the area between them, which implies that these features were important for face recognition. The pigeons were subsequently tested with stimuli manipulated by substitution or removal of facial features. The importance of particular features differed considerably among the birds but generally, the pigeons did not perform as single-feature detectors because no feature was dominant over the others and discrimination was based on an additive integration of individual features. Both studies imply that the pigeon is able to adjust the discrimination depending on the particular perceptual context and it is possible that untrained tits can also adapt the choice of the cues for recognition to the situation they are just facing.

As previously mentioned, the reaction to the dummies was not unequivocal. There was a fluid gradient of the tits' responses both in stress (first PCA axis) and interest (second PCA axis) to particular tested dummies, more significant in the case of the interest in chimeras. These results may have been caused either by inconsistency in the behaviour of individual tits or by differences in behaviour among the individual tits. The results of RDA with the depicted reactions of individual tits show that their behaviour is rather consistent during the experiment but there is a great variability among individuals. The tits were mostly scared in the presence of the sparrowhawk and mostly calm (feeding) in the presence of the pigeon, while in the presence of some chimeras, a portion of the tits were scared while others were calm (Fig. 4). It seems that individual tits evaluate the cues provided by the chimeras in different ways.

The reason for individual differences in behaviour toward the chimeras may be the different experience or personality of the tested birds. We are not able to gauge these differences because we have no prior knowledge of the experience or personality of the tested tits before they are caught in the wild. Great tits are one of the first birds whose personality has been tested and shown. There are consistent behavioural differences among individual tits, which are usually referred as “fast” or “slow” (e.g. Verbeek et al 1994; Dingemanse 2002). Quinn et al. (2012) tested and showed that personality influences the resolution of trade-off between foraging and anti-predatory behaviour. Slow females and juveniles were less responsive to increasing predation risk than fast females and juveniles. Another possibility could be that the individual birds differ in their cognitive style which could influence their ability or propensity to see the stimuli as not real (Carere and Locurto 2011; Sih and Del Giudice 2012).

The importance of experience in predator recognition has also been tested. A comparison between naïve 30-dayold great tit fledglings and wild-caught 4-month old tits showed that the naïve tits were not able to discriminate the predator from a harmless species but the wild-caught tits were (Kullberg and Lind 2002). Studies with birds from areas without the presence of predator also confirm the importance of experience. Birds from areas without predators are not able to recognize a predator, but one-event learning is enough for proper later recognition (Maloney and McLean 1995; McLean et al. 1999). Our tits come from Central and Eastern Europe (Cepák et al. 2008), and so, all of them have had the opportunity to encounter resident sparrowhawks (Cramp et al. 1994). However, a significant portion of the birds are yearlings (Cepák et al. 2008) in which we can assume lesser experience with predators than in older individuals.

Acknowledgments: We thank B. A. Christopher Mark Steer for the language improvement. We thank the Grant agency of the University of South Bohemia (159/2013/P) for financial support.

Ethical standard: Experiments carried out in this research comply with the current laws of the Czech Republic. Authors are licensed for catching and ringing birds (Bird Ringing Centre Prague No. 1004 and 1159), 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).

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

References

Aust U, Huber L (2009) Representational insight in pigeons: comparing subjects with and without real-life experience. Anim Cogn 13:207–218

Bruner JS, Goodnow JJ, Austin GA (1956) A study of thinking. Wiley, New York

Bujoczek M, Ciach M (2009) Seasonal changes in the avian diet of breeding sparrow hawks *Accipiter nisus*: how to fulfil the offspring's food demands? Zool Stud 48:215–222

Burley N, Coopersmith C (1987) Bill color preferences of zebra finches. Ethology 76:133–151

Carere C, Locurto C (2011) Interaction between animal personality and animal cognition. Curr Zool 57:491–498

Cepák J, Klvaňa P, Škopek J, Schröpfer L, Jelínek M, Hořák D, Formánek J, Zárybnický J (2008) Atlas migrace ptáků České republiky a Slovenska. Aventinum, Praha (in Czech with English summaries)

Cerella J (1980) The pigeon's analysis of pictures. Pattern Recogn 12:1–6

Chamberlain DE, Glue DE, Toms MP (2009) Sparrowhawk *Accipiter nisus* presence and winter bird abundance. J Ornithol 150:247–254

Cole EF, Cram DL, Quinn JL (2011) Individual variation in spontaneous problem-solving performance among wild great tits. Anim Behav 81:491–498

Cook RG, Wright AA, Drachman EE (2013) Categorization of birds, mammals, and chimeras by pigeons. Behav Process 93:98–110

Cramp S, Perrins CM, Brooks DJ et al (1994) Handbook of the birds of Europe the Middle East and North Africa. Oxford University Press, Oxford, New York

Curio E (1975) The functional organization of anti-predator behaviour in the pied flycatcher: a study of avian visual perception. Anim Behav 23:1–115

Curio E (1976) The ethology of predation. Springer, Berlin

Curio E, Klump G, Regelmann K (1983) An anti-predator response in the great tit (*Parus major*): Is it tuned to predator risk? Oecologia 60:83–88

Davies NB, Welbergen JA (2008) Cuckoo–hawk mimicry? An experimental test. Proc R Soc B 275:1817–1822

Dingemanse N (2002) Repeatability and heritability of exploratory behaviour in great tits from the wild. Anim Behav 64:929–938

Ghosh N, Lea SE, Noury M (2004) Transfer to intermediate forms following concept discrimination by pigeons: chimeras and morphs. J Exp Anal Behav 82:125

Gill SA, Neudorf DL, Sealy SG (1997) Host responses to cowbirds near the nest: cues for recognition. Anim Behav 53:1287–1293

Groothuis TGG, Carere C (2005) Avian personalities: characterization and epigenesis. Neurosci Biobehav R 29:137–150

Huber L (2001) Visual categorization in pigeons. In: Cook RG (ed) Avian visual cognition. http://www.pigeon.psy.tufts.edu/avc/huber/. Accessed 24 Feb 2013

Jitsumori M, Yoshihara M (1997) Categorical discrimination of human facial expressions by pigeons: a test of the linear feature model. Q J Exp Psychol-B 50:253–268

Karplus I, Algom D (1981) Visual cues for predator face recognition by reef fishes. Z Tierpsychol 55:343–364

Karplus I, Goren M, Algom D (1982) A preliminary experimental analysis of predator face recognition by *Chromis caeruleus* (Pisces, Pomacentridae). Z Tierpsychol 58:53–65

Kirkpatrick-Steger K, Wasserman EA, Biederman I (1998) Effects of geon deletion, scrambling, and movement on picture recognition in pigeons. J Exp Psychol Anim Behav Process 24:34–46

Klump GM, Curio E (1983) Reactions of blue tits *Parus caeruleus* to hawk models of different sizes. Bird Behav 4:78–81

Krätzig H (1940) Untersuchungen zur Lebensweise des Moorschneehuhns (*Lagopus l. lagopus* L.) während der Jugendentwicklung. J Ornithol 88:139–165

Kullberg C, Lind J (2002) An experimental study of predator recognition in great tit fledglings. Ethology 108:429–441

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Lorenz K (1937) The companion in the bird's world. Auk 54:245–273

Lorenz K (1940) Vergleichende Verhaltensforschung. Verh deutsch Zool Gesellsch 1939:69–102

Maloney RF, McLean IG (1995) Historical and experimental learned predator recognition in free-living New-Zealand robins. Anim Behav 50:1193–1201

Marr D, Nishihara HK (1978) Representation and recognition of the spatial organization of three dimensional shapes. Proc R Soc Lond B 200:269–294

Matsukawa A, Inoue S, Jitsumori M (2004) Pigeon's recognition of cartoons: effects of fragmentation, scrambling, and deletion of elements. Behav Process 65:25–34

McLean IG, Rhodes G (1991) Enemy recognition and response in birds. Current Ornithol 8(173–211):1

McLean IG, Hölzer C, Studholme JS (1999) Teaching predator recognition to a naive bird: implications for management. Biol Cons 87:123–130

Palleroni A, Hauser M, Marler P (2005) Do responses of galliform birds vary adaptively with predator size? Anim Cogn 8:200–210

Pashler H (2002) Stevens' handbook of experimental psychology I: sensation and perception. Wiley, New York

Patton TB, Szafranski G, Shimizu T (2010) Male pigeons react differentially to altered facial features of female pigeons. Behaviour 147:757–773

Pearce JM (2008) Animal learning and cognition: an introduction. Psychology Press, New York

Pincemy G, Dobson FS, Jouventin P (2009) Experiments on colour ornaments and mate choice in king penguins. Anim Behav 78:1247–1253

Quinn JL, Cole EF, Bates J, Payne RW, Cresswell W (2012) Personality predicts individual responsiveness to the risks of starvation and predation. Proc R Soc B 279:1919–1926

Scaife M (1976) The response to eye-like shapes by birds. I. The effect of context: a predator and a strange bird. Anim Behav 24:195–199

Sih A, Del Giudice M (2012) Linking behavioural syndromes and cognition: a behavioural ecology perspective. Philos Trans R Soc B 367:2762–2772

Smith EE, Medin DL (1981) Categories and concepts. Harvard University Press, Cambridge

StatSoft Inc (2009) STATISTICA, version 9.1. http://www.statsoft.com

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

Stuber EF, Bartell PA (2013) Seasonal differences in behaviour patterns of the migratory white-throated sparrow. J Ethol 31:151–158

Suzuki TN (2012) Referential mobbing calls elicit different predator searching behaviours in Japanese great tits. Anim Behav 84:53–57

ter Braak CJF, Šmilauer P (1998) CANOCO reference manual and user's guide to Canoco for windows: software for canonical community ordination (version 4). Microcomputer Power, Ithaca, NY

Tinbergen N (1948) Social releasers and the experimental method required for their study. Wilson Bull 60:6–51

Trnka A, Prokop P, Grim T (2012) Uncovering dangerous cheats: how do avian hosts recognize adult brood parasites? PLoS ONE 7:e37445

Tvardíková K, Fuchs R (2011) Do birds behave according to dynamic risk assessment theory? A feeder experiment. Behav Ecol Sociobiol 65:727–733

Tvardíková K, Fuchs R (2012) Tits recognize the potential dangers of predators and harmless birds in feeder experiments. J Ethol 30:157–165

Verbeek M, Drent PJ, Wiepkema P (1994) Consistent individual differences in early exploratory behaviour of male great tits. Anim Behav 48:1113–1121

Watve M, Thakar J, Kale A, Puntambekar S, Shaikh I, Vaze K, Jog M, Paranjape S (2002) Bee-eaters (*Merops orientalis*) respond to what a predator can see. Anim Cogn 5:253–259

Weisman R, Spetch M (2010) Determining when birds perceive correspondence between pictures and objects: a critique. Comp Cogn Behav Rev 5:117–131

Welbergen JA, Davies NB (2011) A parasite in wolf’s clothing: hawk mimicry reduces mobbing of cuckoos by hosts. Behav Ecol 22:574–579

Werner CW, Tiemann I, Cnotka J, Rehkämper G (2004) Do chickens (*Gallus gallus* f. *domestica*) decompose visual figures? Anim Cogn 8:129–140

Zawadzka D, Zawadzki J (2001) Breeding populations and diets of the Sparrowhawk *Accipiter nisus* and the Hobby *Falco Subbuteo* in the Wigry National Park (NE Poland). Acta Ornithol 36:25–31

Chapter II

The role of body size in predator recognition by untrained birds

Jana Beránková, Petr Veselý, Roman Fuchs

Behavioural Processes 120:128–134

The role of body size in predator recognition by untrained birds

Jana Beránková, Petr Veselý[*], Roman Fuchs

Faculty of Science, University of South Bohemia,
Branišovská 31a, 37005 České Budějovice, Czech Republic
[*] *Corresponding autor, e-mail: petr-vesely@seznam.cz*

Abstract

It is supposed that body size serves as an important cue in the recognition of relevant stimuli in nature. As predators of varying body size pose differing levels of threat, their potential prey should be able to discriminate between them. We tested the reaction of great tits (*Parus major*) to the dummies of their common predator (the European sparrowhawk - *Accipiter nisus*) in natural and reduced body sizes under laboratory conditions. All of the tested dummies possessed local raptor-specific features (hooked beak, claws with talons, and conspicuous eyes), but differed in global species-specific features: body size (large – the size of a sparrowhawk, small – the size of a great tit) and colouration (sparrowhawk, great tit, robin, and pigeon). The sparrowhawk-coloured dummies evoked fear regardless of their size while both great tit- and pigeon-coloured dummies evoked no fear reaction. The body size was used as the cue only for the discrimination of the robin-coloured dummies. The differences in reactions to the dummies with robin colouration (species unimportant to the great tits) could be explained as that the tits are able to recognize these birds in nature, but not so undoubtedly as the predator or the conspecific.

Keywords: Predator, Body size, Colouration, Recognition, Categorization, Untrained birds

1. Introduction

Object recognition and categorization play an important role in animal life as it allows for an effective, fast, and appropriate reaction to objects (Shettleworth, 1993, 2010). Animals in the wild possess the ability to recognize objects that are in some way relevant to them (Shettleworth, 2010). Such objects usually represent food, sexual partners, or predators (Strnad et al., 2012; Veselý and Fuchs,2009; Veselý et al., 2013). The animals can use either local or global features for precise object recognition (Jitsumori and Delius, 2001).

The largest portion of our knowledge on the usage of these two types of features comes from experiments with captive animals that were trained to discriminate modified pictures of conspecifics (e.g. Marsh and MacDonald, 2008), humans (e.g. Aust and Huber,2002), or other objects (e.g. Kirkpatrick-Steger et al., 1998; Goto et al., 2004; Matsukawa et al., 2004). Partial local features typical for natural stimuli (e.g. eyes, head, or hands of animals or humans) were shown to play an important role in natural stimuli recognition, whereas more conspicuous, global features (such as overall body shape) were important for artificial stimuli recognition. However, it seems that animals are able to use both local and global features and switch between them when needed (Fremouw et al., 1998; Fremouw et al., 2002).

Some experiments were also conducted with untrained animals, either in natural (e.g. Curio, 1975; Gill et al., 1997; Thorogood and Davies, 2012; Trnka et al., 2012), or laboratory conditions (e.g. Karplus and Algom, 1981; Patton et al., 2010; Beránková et al.,2014).

These studies found that local features like the colour of eyes, shape of beak and mouth, or conspicuous components in colouration are essential for the proper recognition of a predator (e.g. Curio,1975; Karplus and Algom, 1981; Gill et al., 1997; Beránková et al.,2014), nest parasite (e.g Thorogood and Davies, 2012; Trnka et al.,2012) or conspecific (e.g. Patton et al., 2010). Moreover, some studies imply that birds are able to use a combination of features in object recognition (e.g. Trnka and Prokop, 2012;

Beránková et al.,2014). If the local features are not available for recognition, birds can do without them and use only global features. An example is the recognition of raptor silhouettes (e.g. Evans et al., 1993).

Another possible global feature used in predator recognition is body size. Predators of different body size should be discriminated between because they can pose different levels of threat to the potential prey in invertebrates (e.g. Binz et al., 2014) as well as vertebrates (e.g. Swaisgood et al., 1999). Body size is especially important in birds of prey because they are quite similar in overall appearance as well as body shape, but their size provides a reliable indicator of the level of threat they pose to the potential prey. A small raptor is more dangerous for small prey, while a large raptor is a greater threat to large prey.

It has been repeatedly showed that various bird species can distinguish between raptors differing in size. Domestic hens (*Gallus gallus* f. *domestica*) react differently to the variously sized trained live raptors (Palleroni et al., 2005). Wild Carolina chickadees (*Poecile carolinensis*), tufted titmice (*Baeolophus bicolor*), and captive black-capped chickadees (*Poecile atricapilla*) react differently to stuffed raptors of various sizes via differing the intensity of their warning calls (Soard and Ritchison, 2009; Courter and Ritchison, 2010; Templeton et al., 2005). Chickens (*Gallus gallus* f. *domestica*) as well as blue tits (*Cyanistes caeruleus*) can even recognize differences in the size of flying silhouettes (Evans et al., 1993; Klump and Curio,1983).

All of the stimuli used in the studies mentioned above were either real or created to simulate real raptors. These results show that birds are able to distinguish between raptors differing in size, but they do not answer the question of whether size is an important feature in the recognition of particular raptor species. In other words, if the particular raptor species can be recognized in its “proper” as well as its “wrong” size.

The fact that birds are able to use size as a cue in object recognition was supported by experiments testing trained animals. It was shown that European starlings (*Sturnus vulgaris*) can perceive a difference of as little as 5% in size asymmetry (Swaddle and Johnson,2007). Pigeons (*Columba livia* f. *domestica*) are also able to notice a size change in the stimuli. On the other hand, this change does not disrupt the birds' ability of discriminate regarding the sameness or differentness of the multi-item array (Castro and Wasserman,2010). Pigeons are also able to generalize their object discrimination of smaller and larger versions of objects familiar to them through training, but their performance drops as the size increases or decreases relatively to the trained size (Peissig et al., 2006).

We decided to test how untrained birds (great tits) generalize the most dangerous predator of small passerines in Europe (the European sparrowhawk, *Accipiter nisus*) using a smaller dummy of the species, which they have no experience of. The sparrowhawk is characterized not only by raptor specific features (eye, beak and claws) but by species-specific features (size, overall colouration) as well. Raptor specific features are typical local features. On the other hand, overall colouration pattern composed of the set of the partial local features (e.g. barred under-part, greyish back) can be considered as a global feature (Aust and Huber, 2001) the same way as the size. Therefore, we used dummies with the colouration of three harmless birds: a pigeon (comparable in body size to the sparrowhawk), robin (comparable in body size to the great tit) and great tit (conspecific colouration) as well as the dummies with sparrowhawk colouration. The dummies possessing the above-mentioned colourations were made in the sizes of a sparrowhawk as well as in the size of a great tit. Behaviour of the tits without the presence of any dummy was used as a control condition.

Null hypothesis of our experiments states that recognition is based on the raptor specific features and all of the dummies would induce fear (the same amount) in the tits. Falsification of this hypothesis means that recognition is based also on the col-oration and/or size. Then we can predict that: (1)

only larger dummies would induce fear in the tits - the recognition is based on the presence of raptor-specific features on the dummy of the size of a sparrowhawk, (2) only the dummies with the sparrowhawk colouration would induce fear in the tits - the recognition is based on the presence of raptor-specific features and sparrowhawk colouration, (3) only the unmodified, realistic sparrowhawk dummy would induce fear - the recognition is based on the presence of raptor-specific features and body size as well as the colouration of the sparrowhawk, (4) all but the dummies with con-specific (great tit) colouration would induce fear - the recognition is based only on the presence of raptor-specific features, but the conspicuous conspecific colouration cancels out their effect.

1.1. Terminological comment

We often use a term "recognition" that unfortunately has no unambiguous meaning. It is the term connected to the memory in psychological research and refers to the successful recalling of the previously learnt stimuli. However, recognition can also refer to classifying objects or other animals appropriately on the first encounter by means of some distinctive feature (Shettelworth, 2010). This meaning is common in behavioural ecology and we use it for purposes of our study. The reason is that experiments with untrained animals do not allow testing the recognition based on previous learning. The ability to recognize presented stimuli in behavioural studies is evaluated on the basis of appropriate reaction to the biologically meaningful stimulus (Krebs and Davies, 2009).

2. Methods

2.1. Subjects

The great tit was chosen as a model species. Great tits are very adaptable to laboratory conditions (e.g. Dingemanse et al., 2002). Moreover, no neophobic reaction that could negatively influence their behaviour in the presence of an unfamiliar stimulus has been found in this species (Cole et al., 2011).

The birds were trapped in mist-nets in the suburban areas of České Budějovice (Czech Republic) during the winter seasons of the years 2011–2012 using the same procedure as in Beránková et al. (2014). Experiments conducted during the winter season ensure that yearlings are already able to recognize the sparrowhawk properly (Kullberg and Lind, 2002). Each bird was tested only once. One hundred eighty individuals were used for all the experiments (20tits for each dummy, with eight dummies presented and 20 control tits). Sex ratio in our experiments was balanced and had no significant effect on great tits reactions to the presented dummies ($p = 0.677$).

Authors have complied with APA ethical standards. Experiments carried out in this research comply with the current laws of the Czech Republic.

2.2. Experimental stimuli

The European sparrowhawk is the main predator of small passerines in Europe (Zawadzka and Zawadzki, 2001; Bujoczek and Ciach, 2009; Chamberlain et al., 2009). It has already been established that wild great tits are able to recognize a sparrowhawk and distinguish it from less dangerous raptor species (Tvardíková and Fuchs, 2011).

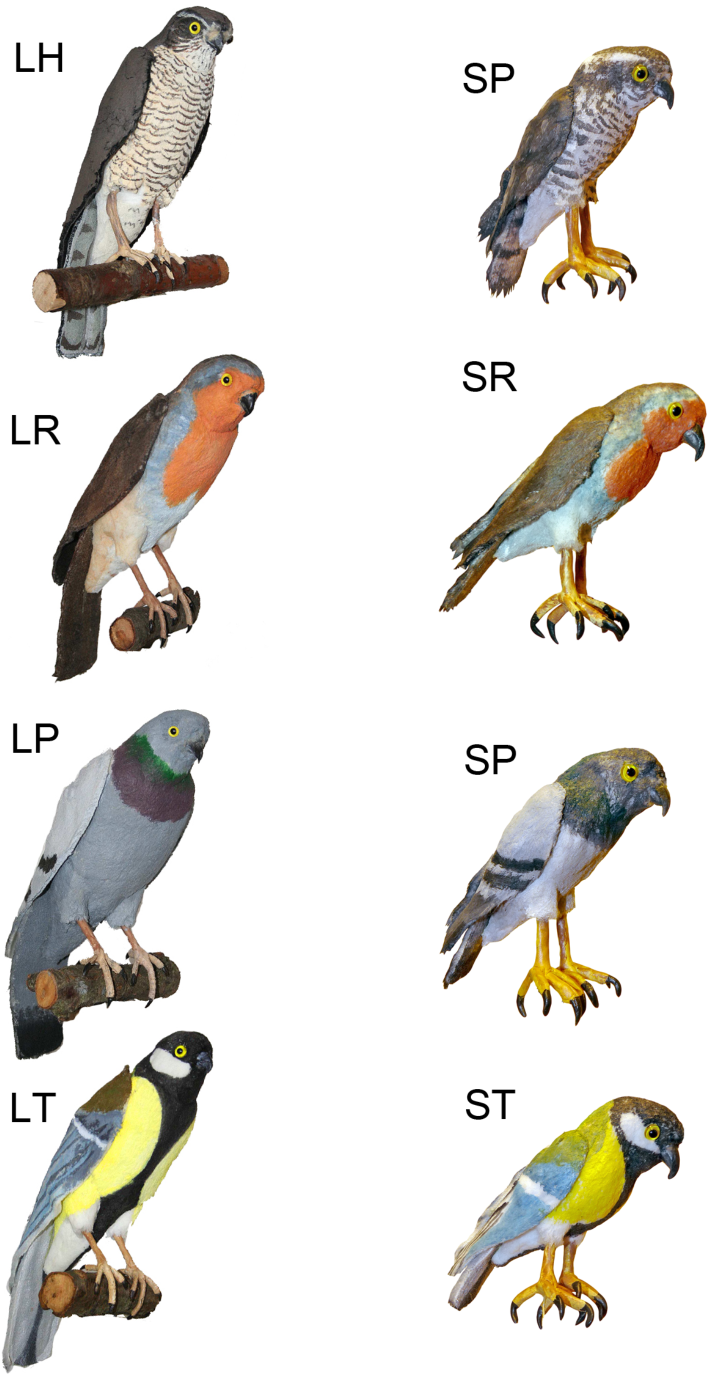

Fig. 1. Presented dummies. LH - large hawk, SH - small hawk, LR - large robin, SR - small robin, LP - large pigeon, SP - small pigeon, LT - large tit, ST - small tit.

Plush dummies were made of hollow textile fibres on a wire skeleton. The plush surface was painted with acrylic colours to imitate the bird's feathers. The beak and claws were made from modelling clay; the eyes were made of glass. The efficiency of such dummies in experiments with passerines has already been demonstrated by Němec et al. (2015). In our study, we used four different colour modifications of the sparrowhawk (Fig. 1). As well as for the unmodified, realistic sparrowhawk colouration (indexed as H), we used the colourations of a pigeon (P) and a robin (R) as they are harmless birds approximately of the same body sizes of a sparrowhawk and a great tit respectively. The last colouration used was that of a conspecific great tit (T). One set of dummies was larger (indexed as L - LH, LP, LR, LT) - the size of a female sparrowhawk (body length 35 cm), and the second set was smaller (indexed as S - SH, SP, SR, ST) - the size of a great tit (body length 15 cm). All of the dummies we made to imitate a sparrowhawk resting on a perch. There is no raptor with a body size similar to that of the great tit in Europe; thus, the smaller sparrowhawk dummies could not be familiar to great tits.

2.3. Experimental design

Before the experiment started, the birds had been deprived of food for 1.5 h to gain motivation. Afterwards, they were released into an experimental cage (2×1×0.5 m). The cage was equipped with corn bedding, perches, a nesting box and a dish with sunflower seeds in the front part. The dummy was positioned in front of the experimental cage so that it was facing toward the subject. In the case of the control sessions, only an empty perch was presented in front of the cage. The experiment started after the removal of a wooden barrier between the tested bird and the rest of the cage, including the dummy. The behaviour of the birds during their exposure to the dummies was recorded on video for 10 min.

The video was analysed in Observer XT 6.1 (Noldus Information Technology, 1990–2006). The total occurrence of the following behaviours was recorded: raising feathers on head (cap), knee bending (knee), warning calls (warn), approaching the dummy up to a distance of less than 1 m (approach), movement from one perch to another (move), scanning the dummy from a distance of less than 1 m (scan). The total duration of the following behaviours was recorded: surveying the corn bedding for food (bedding), feeding on the provided sunflower seeds (feeding), sitting still (sit), and pecking the equipment in the cage (peck). The inter-rater reliability was estimated by analysing experiments by two raters (J.B. and P.V.). The correlations between the two sets of behavioural measures were calculated using correlation matrices (package Hmisc) in R 2.12.2 (R Development Core Team, 2011). The results show significant correlations ($p < 0.01$) in all of the observed behaviours (cap, $r = 0.73$; knee, $r = 0.83$; warn, $r = 0.99$; approach, $r = 0.80$; move, $r = 0.95$; scan, $r = 0.32$; bedding, $r = 0.92$; feeding, $r = 0.99$; sit, $r = 0.87$; peck, $r = 0.79$).

2.4. Statistical analysis

The tit behaviour (including all of the activities mentioned above) was analysed using the multivariate technique - the principal component analysis (PCA) using Canoco 5 software (ter Braak and Šmilauer, 1998) to find out if there was a consistent reaction to the dummies. The dummies were used as supplementary environmental data in PCA. PCA scores on the first and second axis were of a Gaussian distribution and were subsequently used as synthetic dependent variables in ANOVA using STATISTICA 9.1 software (StatSoft Inc., 2009) to test the effect of particular parameters of the tested dummies (the size, colour, and their interaction) on the tits' behaviour. The differences among the individual dummies were consequently compared using the Tukey HSD post hoc test (again in STATISTICA 9.1 software). We also ran a redundancy analysis (RDA) in Canoco 5 software with the dummies as environmental data to compare the behaviour of individual tits towards the tested dummies. The data for PCA and RDA analysis were logarithmically adjusted and centred.

Results

Principal component analysis (PCA) shows that there are consistent reactions to the presented dummies (Fig. 2). The first PCA axis explains 44.6% of the variability of the birds' behaviour and separates the stress behaviour (knee-bending, warning calls, raised feathers on the head) from other behavioural types (cage exploration or feeding). The second PCA axis explains 27.0% of the variability. Negative values on this axis correlate with an increased movement of the tits in the cage (flying and approaching the dummy).

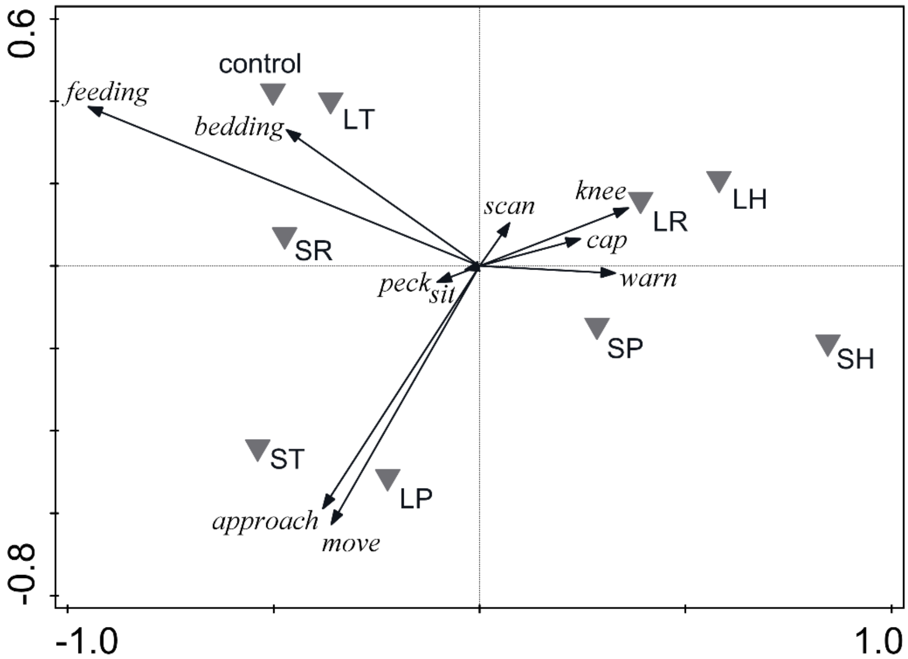

Fig. 2. Position of particular dummies on the first and second canonical axis of the principal component analysis created on the basis of particular behavioural responses of the birds performed towards these dummies. The first axis explains 44.6% of variability; the second axis explains 27.0% of variability. Control = no dummy, ST - small tit, SR - small robin, LT - large tit, LP - large pigeon, SP - small pigeon, LR - large robin, LH - large hawk, SH - small hawk.

The type of dummy influences the position of the tested birds on the first PCA axis (one-way ANOVA, $F_{8,171} = 7.047$, $p < 0.001$). The tits showed higher amounts of stress-induced behaviour (positive values on the first PCA axis) in the presence of both sparrowhawk dummies (LH and SH) and the large dummy with robin colouration (LR) than during the control trial. The behaviour of tits in the presence of the great tit dummies (LT, ST), pigeon dummies (LP and SP) and the small dummy with robin colouration (SR) did not differ from behaviour during the control trial. (Tukey HSD test, Table 1, Fig. 3). The type of dummy influenced the position of the tits on the second PCA axis as well (one-way ANOVA, $F_{8,171} = 2.459$, $p = 0.015$). However, none of the pot-hoc tests testing the differences among individual dummies was significant.

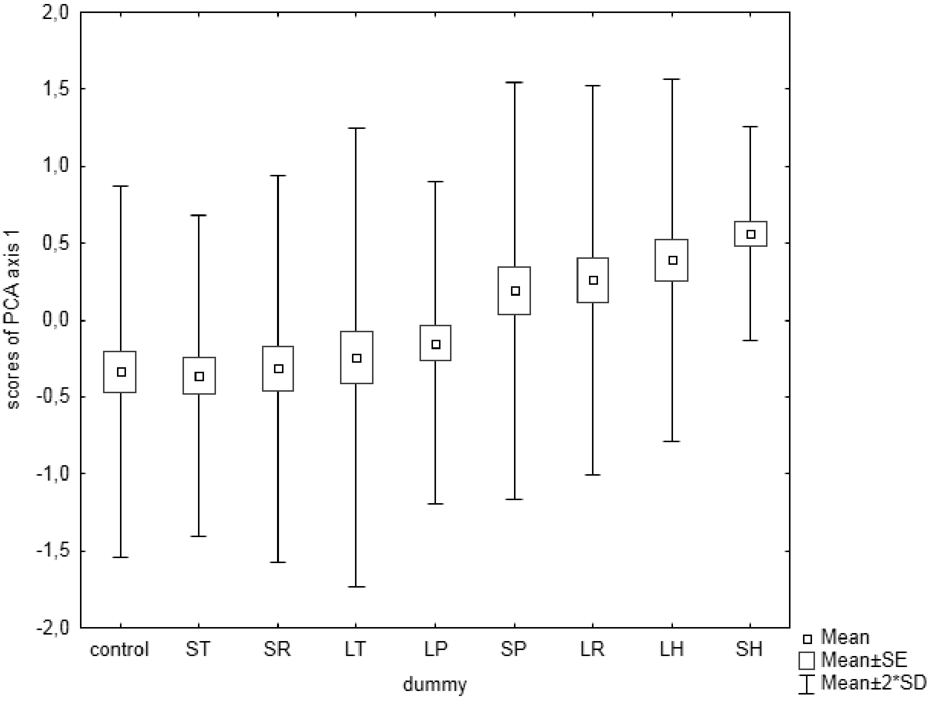

Fig. 3. Position of the birds confronted with particular dummies on the first canonical axis of the principal component analysis (PCA scores). Positive values reflect the stress behaviour; negative values reflect the interest in dummies or comfort behaviour. Control = no dummy, ST - small tit, SR - small robin, LT - large tit, LP - large pigeon, SP - small pigeon, LR - large robin, LH - large hawk, SH - small hawk.

Table 1

Differences in the reaction to individual dummies on the base of scores on the first canonical axis of the principle component analysis (PCA), Tukey HSD test, p-values. Significant p values indicated in bold.

Dummy	LH	LT	LR	LP	SH	ST	SR	SP
LH		-	-	-	-	-	-	-
LT	**0.023**		-	-	-	-	-	-
LR	0.999	0.157		-	-	-	-	-
LP	0.099	1.000	0.417		-	-	-	-
SH	0.991	**<0.001**	0.797	**0.005**		-	-	-
ST	**0.002**	0.999	**0.027**	0.971	**<0.001**		-	-
SR	**0.006**	1.000	0.055	0.994	**<0.001**	1.000		-
SP	0.981	0.344	1.000	0.679	0.550	0.082	0.150	
Control	**0.004**	1.000	**0.040**	0.987	**<0.001**	1.000	1.000	0.117

LH - large hawk, LT - large tit, LR - large robin, LP - large pigeon; SH - small hawk, ST - small tit, SR - small robin, SP - small pigeon, control = no dummy.

RDA confirmed that there were significant differences in the tits' behaviour in the presence of most of the individual dummies (Monte Carlo permutation test, F = 4.616, p = 0.002; Fig. 4). The first RDA axis explains 12.9%; the second axis explains 3.0% of the variability of the birds' behaviour. The marginal effects of all the dummies besides SP and LR are significant (Table 2). The RDA scores for most of the individual tits for the first as well as second canonical axes are far from the zero value in the case of all the dummies. This means that there was always a consistent response by individual birds to them. In most of the dummies, this response was predominantly stress, unconcern, or interest. Nevertheless, in the case of SP and LR, particular birds occur evenly on opposite positions on both axes. This means that some birds considered these dummies to be dangerous, other observed them and behaved as if there was no relevant stimulus.

Table 2

Marginal effects of individual dummies in redundancy analysis (RDA).

Dummy	Explains %	F-values	p-values
SH	5.2	9.8	**0.002**
Control	3.1	5.7	**0.002**
LH	2.7	5.0	**0.004**
ST	2.4	4.4	**0.004**
SR	1.6	3.0	**0.026**
LT	1.4	2.6	**0.048**
LP	1.4	2.6	**0.050**
LR	1.0	1.9	0.116
SP	0.9	1.7	0.116

Significant p values indicated in bold.

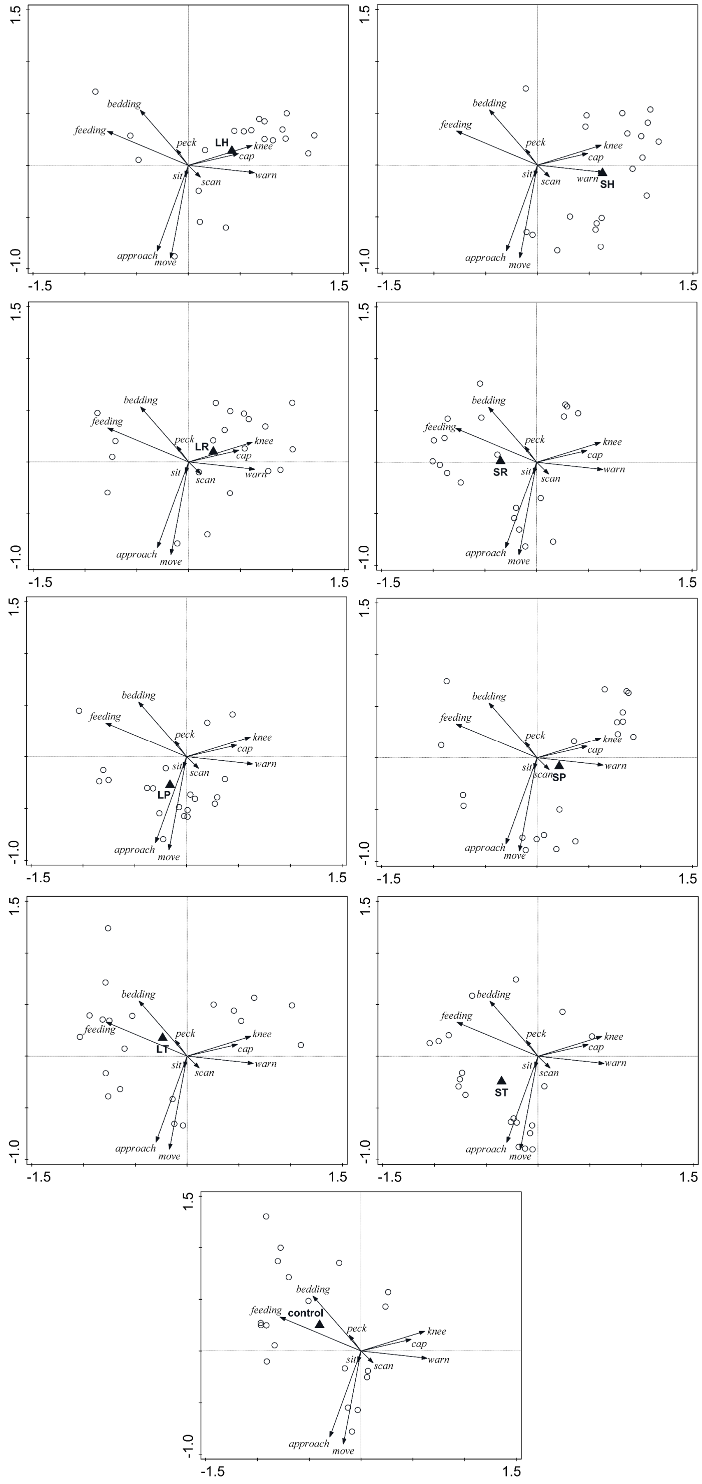

Fig. 4. Position of particular birds on the first and second canonical axis of the redundancy analysis (RDA) created on the basis of behavioural responses of the birds performed towards particular dummies. The first axis explains 12.9% of variability; the second axis explains 3.0% of variability.

LH - large hawk,
SH - small hawk,
LR - large robin,
SR – small robin,
LP - large pigeon,
SP - small pigeon,
LT - large tit,
ST - small tit,
control = no dummy.

Discussion

None of our predictions was fully supported by our results. The reason is that the great tits probably combined local raptor-specific features (hooked beak, claws with talons, conspicuous eye with prominent eyebrow) and species-specific global features (colouration and size) in the process of predator recognition. Their actual importance probably depends on the whole context of the other stimulus properties, especially their relevance to the tested tits. The presence of key features by itself is not enough for tits to recognize the dummy as a sparrowhawk, or raptor. Neither the great tit dummies (LT and ST), pigeon dummies (LP and SP), nor the small dummy with robin colouration (SR) were considered dangerous, regardless of the presence of conspicuous raptor features. On the other hand, a combination of raptor features and appropriate colouration was certainly enough, but not necessary, for the tested birds to recognize a predator in the presented dummy because besides both sparrowhawk dummies (LH and SH), the large dummy with robin colouration (LR) was considered dangerous as well.

Also, according to our results, size does not play a simple role in raptor recognition. Two of the large dummies (LH and LR) were treated as dangerous while the other large dummies (LT and LP) were treated as harmless. Most of the small dummies were treated as harmless. However, the reaction to the small sparrowhawk dummy (SH) was as strong as to the unmodified sparrowhawk (LH) regardless of its improper size. It is supposed that the typical colouration pattern overwhelmed the effect of the improper body size in this case. Similarly, sparrowhawk-like colouration increases fear of the grey form of the cuckoo (*Cuculus canorus*) (Welbergen and Davies, 2011) or modified dove dummy (Trnka et al., 2012). In concordance with our fourth prediction, conspecific (great tit) colouration in the dummies (LT and ST) really does eliminate fear of those dummies. However, pigeon (LP and SP) and partially also robin colouration (SR) eliminates fear as well.

Unlike the other studies testing the role of predator size in recognition, we found no difference in the reaction to the small and large sparrowhawk dummies unmodified in colour. The reason could be that the colouration of both of our dummies was identical whereas the other studies used stuffed (Soard and Ritchison, 2009; Courter and Ritchison, 2010; Templeton et al., 2005) or living (Palleroni et al., 2005) birds of prey (raptors and owls) of different species. Pronounced differences in colouration—e.g. sharp-shinned hawk (*Accipiter striatus*) vs. red-tailed hawk (*Buteo jamaicensis*) in Soard and Ritchison (2009) or northern pygmy-owl (*Glaucidium gnoma*) vs. short-eared owl (*Asio flammeus*) in Templeton et al. (2005) might serve as a cue for the discrimination of species varying in body size. The use of colouration in raptor recognition was confirmed by different responses towards equally sized raptors - sharp-shinned hawk vs. American kestrel (*Falco sparverius*) in Soard and Ritchison (2009) or prairie falcon (*Falco mexicanus*) vs. peregrine falcon (*Falco peregrinus*) in Templeton et al. (2005). All of the studies mentioned above used real raptors or owls. Tested birds therefore may have some experience of them, and they also pose some, varying, level of threat to them. For example, in the study of Courter and Ritchison (2010), tufted titmice are less threatened by the larger red-tailed hawk (hunting mostly squirrels and gophers, Fitch et al., 1946) than by the smaller sharp-shinned hawk (preferring small passerines, Mueller and Berger, 1970).

Similarly, birds were able to react differently to variously sized raptor silhouettes (Evans et al., 1993; Klump and Curio, 1983). The amount of fear induced by the silhouettes increases with size in both of the studies. The reason is that the size of the silhouette provides more information about the height of the flying raptor above the ground than the actual body size, and thus, warns about the danger presented by the raptor at that moment (Evans et al., 1993).

A raptor with a body size comparable to that of our SH does not occur in Europe and thus tits had no pre-formed ability to differentiate between SH and LH. Therefore, we tested only the importance of size as a feature for raptor recognition and we showed that size plays no role when appropriate key features and colouration is present.

Experiments with artificial stimuli under laboratory conditions showed that the birds are able to perceive negligible differences in the stimulus size (e.g. Swaddle and Johnson, 2007). On the other hand, they are able to treat the stimuli differing in size as equal, when they are trained to do so (Castro and Wasserman, 2010; Peissig et al., 2006). It means that under some conditions they are able to use other determining features and ignore the stimulus size.

The inappropriate size of the dummies seems to play no role in discrimination in the case of the dummies carrying great tit colouration, similarly as in the dummies carrying sparrowhawk colouration. The conspecific colouration is such a strong cue that even the presence of raptor-specific features cannot make the dummy dangerous for great tits. It is understandable that conspecific colouration is such a strong cue because all of the individuals must know it thoroughly to recognize an appropriate mate, competitor, etc.

In a concordance with our first prediction that the larger dummies would cause more fear than the smaller dummies, the dummy size influenced only the reaction to the dummies carrying robin colouration. Unlike the sparrowhawk and conspecifics, the robin is definitely a less important bird species for great tits because it is neither a predator nor a competitor for them. Therefore, we can assume that great tits have no motivation to learn how to recognize them. However, both dummies were treated as harmless in the case of pigeon colouration and the pigeon is as unimportant as the robin for great tits at the same time. Of course, the difference between the pigeon and the robin relies on the fact that the improper size is the smaller one in the case of the pigeon, and the larger one in the case of the robin.

Therefore, differences in the reactions to the dummies with pigeon and robin colouration may be explained by tits being able to recognize these birds in nature but not so undoubtedly as predator or conspecifics. A large pigeon and a small robin would then be recognized as familiar harmless birds regardless of raptor-specific features. A small pigeon may be perceived as an unfamiliar bird species, but because of his size probably a harmless one. To the contrary, a large robin may be perceived as unfamiliar and a potentially dangerous bird species because of its large size and the presence of raptor features. Such a conclusion may seem to be rather speculative, but it is supported by the overall reaction to the small dummy with the pigeon colouration and the large dummy with robin colouration. In the presence of both of these dummies, the significant part of the tested birds reacted conversely to the rest (see later). This fact indicates that these dummies carry conflicting features for great tits.

It is certain that wild living great tits repeatedly meet both pigeons and robins. Despite the fact that they are not biologically relevant to them, the ability to recognize them could probably help tits to quickly discriminate between novel and potentially relevant stimuli, e.g. an unfamiliar predator. Our results actually suggest that the birds are able to discriminate between more objects in the nature than might be expected based on their basic need to feed, avoid predation, and successfully reproduce. Indeed, experiments based on operant conditioning showed that trained pigeons under laboratory conditions are able to learn to discriminate between as many as 320 particular photographs of non-relevant stimuli and remember them for at least two years (Vaughan and Greene, 1984).

Our results could seem too complicated at the first sight but we can assume one general conclusion. There is a lot of studies showing the ability of untrained birds to distinguish among various predator species, but only a little is known about the process of predator recognition. Strong emphasis was put on the role of the key features in predator recognition since the time of experiments conducted by founders of classical ethology (Lorenz, 1937; Tinbergen, 1948). However, the laboratory experiments with trained birds imply that object recognition is a complex process based on more than a few local features (Huber, 2001).

Our study using untrained birds and altered naturally relevant stimuli under controlled laboratory conditions demonstrate that even the untrained bird spontaneously use rather a complex approach to the recognition and do not rely on a simple presence or absence of partial key features.

The results of the redundancy analysis showed that the behaviour of the individual tits was rather consistent during the experiment which further shows absence of habituation. However, there was a great variability among the tested individuals. Especially in the case of SP and LR dummies, various attitudes were adopted by various birds. It means that a portion of the birds used rather the harmless features in recognizing the ambiguous dummies while the other portion of the birds used rather the predator-specific features. Similarly to our previous study (Beránková et al., 2014) we can see that reaction to the ambiguous stimuli varies highly according to the individual, probably because of either different experience or personality.

Acknowledgments: We thank Silvie Lišková and Christopher Mark Steer for the language improvement. We thank the Grant agency of the University of South Bohemia (159/2013/P) for financial support.

References

Aust, U., Huber, L., 2002. Target-defining features in a people-present/people-absent discrimination task by pigeons. Learn. Behav. 30, 165–176.

Beránková, J., Veselý, P., Sýkorová, J., Fuchs, R., 2014. The role of key features in predator recognition by untrained birds. Anim. Cogn. 17, 963–971, http://dx.doi.org/10.1007/s10071-014-0728-1.

Binz, H., Bucher, R., Entling, M.H., Menzel, F., 2014. Knowing the risk: crickets distinguish between spider predators of different size and commonness. Ethology 120, 99–110, http://dx.doi.org/10.1111/eth.12183.

Bujoczek, M., Ciach, M., 2009. Seasonal changes in the avian diet of breeding sparrowhawks *Accipiter nisus*: how to fulfil the offspring's food demands? Zool. Study 48, 215–222.

Castro, L., Wasserman, E.A., 2010. Effects of stimulus size and spatial organization on pigeons' conditional same–different discrimination. Behav. Process. 83, 162–171, http://dx.doi.org/10.1016/j.beproc.2009.10.007.

Chamberlain, D.E., Glue, D.E., Toms, M.P., 2009. Sparrowhawk *Accipiter nisus* presence and winter bird abundance. J. Ornithol. 150, 247–254, http://dx.doi.org/10.1007/s10336-008-0344-4.

Cole, E.F., Cram, D.L., Quinn, J.L., 2011. Individual variation in spontaneous problem-solving performance among wild great tits. Anim. Behav. 81, 491–498.

Courter, J.R., Ritchison, G., 2010. Alarm calls of tufted titmice convey information about predator size and threat. Behav. Ecol. 21, 936–942, http://dx.doi.org/10.1093/beheco/arq086.

Curio, E., 1975. The functional organization of anti-predator behaviour in the pied flycatcher: a study of avian visual perception. Anim. Behav. 23, 1–115.

Dingemanse, N., Both, C., Drent, P.J., Van Oers, K., van Noordwijk, A.J., 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. Anim. Behav. 64, 929–938, http://dx.doi.org/10.1006/anbe.2002.2006.

Evans, C., Macedonia, J., Marler, P., 1993. Effects of apparent size and speed on the response of chickens, *Gallus gallus*, to computer-generated simulations of aerial predators. Anim. Behav. 46, 1–11, http://dx.doi.org/10.1006/anbe.1993.1156.

Fitch, H.S., Swenson, F., Tillotson, D.F., 1946. Behavior and food habits of the red-tailed Hawk. Condor 48, 205–237.

Fremouw, T., Herbranson, W.T., Shimp, C.P., 1998. Priming of attention to local or global levels of visual analysis. J. Exp. Psychol. Anim. Learn. Cogn. 24, 278–290.

Fremouw, T., Herbranson, W.T., Shimp, C.P., 2002. Dynamic shifts of pigeon local/global attention. Anim. Cogn. 5, 233–243, http://dx.doi.org/10.1007/s10071-002-0152-9.

Gill, S.A., Neudorf, D.L., Sealy, S.G., 1997. Host responses to cowbirds near the nest: cues for recognition. Anim. Behav. 53, 1287–1293.

Goto, K., Wills, A.J., Lea, S.E.G., 2004. Global-feature classification can be acquired more rapidly than local-feature classification in both humans and pigeons. Anim. Cogn. 7, 109–113, http://dx.doi.org/10.1007/s10071-003-0193-8.

Huber, L., 2001. Visual categorization in pigeons. In: R.G. Cook (Ed.), Avian visual cognition [on-line]. Available: www.pigeon.psy.tufts.edu/avc/huber/.

Jitsumori, M., Delius, J.D., 2001. Object recognition and object categorization in animals. In: Matsuzawa, T. (Ed.), Primate Origins of Human Cognition and Behavior. Springer, Berlin, pp. 269–293.

Karplus, I., Algom, D., 1981. Visual cues for predator face recognition by reef fishes. Z. Tierpsychol. 55, 343–364, http://dx.doi.org/10.1111/j.1439-0310.1981.tb01277.x.

Kirkpatrick-Steger, K., Wasserman, E.A., Biederman, I., 1998. Effects of geon deletion, scrambling, and movement on picture recognition in pigeons. J. Exp. Psychol. Anim. Learn. Cogn. 24, 34–46.

Klump, G.M., Curio, E., 1983. Reactions of blue tits Parus caeruleus to hawk models of different sizes. Bird Behav. 4, 78–81.

Krebs, J.R., Davies, N.B., 2009. Behavioural Ecology: An Evolutionary Approach. Blackwell Publishing, Oxford.

Kullberg, C., Lind, J., 2002. An experimental study of predator recognition in great tit fledglings. Ethology 108, 429–441.

Lorenz, K., 1937. The companion in the bird’s world. Auk 54, 245–273.

Marsh, H.L., MacDonald, S.E., 2008. The use of perceptual features in categorization by orangutans (*Pongo abelli*). Anim. Cogn. 11, 569–585, http://dx.doi.org/10.1007/s10071-008-0148-1.

Matsukawa, A., Inoue, S., Jitsumori, M., 2004. Pigeon’s recognition of cartoons: effects of fragmentation, scrambling, and deletion of elements. Behav. Process. 65, 25–34, http://dx.doi.org/10.1016/s0376-6357(03)00147-5.

Mueller, H.C., Berger, D.D., 1970. Prey preferences in the sharp-shinned hawk: the roles of sex, experience, and motivation. Auk 87, 452–457.

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, 259–268.

Palleroni, A., Hauser, M., Marler, P., 2005. Do responses of galliform birds vary adaptively with predator size? Anim. Cogn. 8, 200–210, http://dx.doi.org/10.1007/s10071-004-0250-y.

Patton, T.B., Szafranski, G., Shimizu, T., 2010. Male pigeons react differentially to altered facial features of female pigeons. Behaviour 147, 757–773, http://dx.doi.org/10.1163/000579510X491090.

Peissig, J.J., Kirkpatrick, K., Young, M.E., Wasserman, E.E., Biederman, I., 2006. Effects of varying stimulus size on object recognition in pigeons. J. Exp. Psychol.: Anim. Learn. Cogn. 32, 419–430, http://dx.doi.org/10.1037/0097-7403.32.4.419.

R Development Core Team, 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Shettleworth, S.J., 1993. Where is the comparison in comparative cognition? Alternative research programs. Psychol. Sci. 4, 179–184, http://dx.doi.org/10.1111/j.1467-9280.1993.tb00484.x.

Shettleworth, S.J., 2010. Cognition, Evolution, and Behavior, 2nd ed. Oxford University Press, New York.

Soard, C.M., Ritchison, G., 2009. Chick-a-dee calls of Carolina chickadees convey information about degree of threat posed by avian predators. Anim. Behav. 78, 1447–1453.

StatSoft Inc. (2009) STATISTICA, version 9.1. www.statsoft.com.

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 Fennica 89, 206–215.

Swaddle, J.P., Johnson, C.W., 2007. European starlings are capable of discriminating subtle size asymmetries in paired stimuli. J. Exp. Anal. Behav. 87, 39–49, http://dx.doi.org/10.1901/jeab.2007.103-05.

Swaisgood, R.R., Owings, D.H., Rowe, M.P., 1999. Conflict and assessment in a predator–prey system: ground squirrels versus rattlesnakes. Anim. Behav. 57, 1033–1044, http://dx.doi.org/10.1006/anbe.1998.1069.

Templeton, C.N., Greene, E., Davis, K., 2005. Allometry of alarm calls: black-capped chickadees encode information about predator size. Science 308, 1934–1937, http://dx.doi.org/10.1126/science.1108841.

ter Braak, C.J.F., Šmilauer, P., 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca, NY.

Thorogood, R., Davies, N.B., 2012. Cuckoos combat socially transmitted defenses of reed warbler hosts with a plumage polymorphism. Science 337, 578–580, http://dx.doi.org/10.1126/science.1220759.

Tinbergen, N., 1948. Social releasers and the experimental method required for their study. Wilson Bull. 60, 6–51.

Trnka, A., Prokop, P., 2012. The effectiveness of hawk mimicry in protecting cuckoos from aggressive hosts. Anim. Behav. 83, 263–268, http://dx.doi.org/10.1016/j.anbehav.2011.10.036.

Trnka, A., Prokop, P., Grim, T., 2012. Uncovering dangerous cheats: how do avian hosts recognize adult brood parasites? PloS One 7, e37445.

Tvardíková, K., Fuchs, R., 2011. Do birds behave according to dynamic risk assessment theory? A feeder experiment. Behav. Ecol. Sociobiol. 65, 727–733, http://dx.doi.org/10.1007/s00265-010-1075-0.

Vaughan, W., Greene, S.L., 1984. Pigeon visual memory capacity. J. Exp. Psychol.: Anim. Learn. Cogn. 10, 256–271, http://dx.doi.org/10.1037/0097-7403.10.2.256.

Veselý, P., Fuchs, R., 2009. Newly emerged Batesian mimicry protects only unfamiliar prey. Evol. Ecol. 23, 919–929.

Veselý, P., Luhanová, D., Prášková, M., Fuchs, R., 2013. Generalization of mimics imperfect in colour patterns: the point of view of wild avian predators. Ethology 119, 138–145.

Welbergen, J.A., Davies, N.B., 2011. A parasite in Wolf's clothing: hawk mimicry reduces mobbing of cuckoos by hosts. Behav. Ecol. 22, 574–579.

Zawadzka, D., Zawadzki, J., 2001. Breeding populations and diets of the Sparrowhawk *Accipiter nisus* and the Hobby *Falco subbuteo* in the Wigry National Park (NE Poland). Acta Ornithol. 36, 25–31.

Chapter III

Effect of behavioural syndrome on a bird's ability to categorize a predator

Jana Beránková, Petr Veselý, Roman Fuchs

Effect of behavioural syndrome on a bird's ability to categorize a predator

Jana Beránková, Petr Veselý*, Roman Fuchs

Faculty of Science, University of South Bohemia,
Branišovská 31a, 37005 České Budějovice, Czech Republic
**Corresponding autor, e-mail: petr-vesely@seznam.cz*

Abstract

Behavioural syndromes and individual personality traits have a strong influence on the way animals deal with the trade-off between the risk of predation and starvation. Despite the encountering of a predator always being extremely threatening, there is a significant plasticity among individuals in how they cope with such a situation. In laboratory experiments with wild-caught great tits (*Parus major*), we tested the effect of personality (on a fast-slow continuum) on the ability of individual birds to assess the threat represented by a predator. We presented a wooden dummy of the European sparrowhawk (*Accipiter nisus*), an extremely dangerous predator, and its visual modifications (chimeras), changing the beak or head to be non-threatening (those of a pigeon – *Columba livia* f. *domestica*). We showed that the differences between 'slow' and 'fast' great tits are not very distinct, but that 'slow' birds generally tended to be more cautious in the presence of an unmodified sparrowhawk dummy, but, on the contrary, they tended to treat both chimaeras (and the pigeon dummy as well) as less-threatening than 'fast' individuals. Since slow birds are usually considered to be more sensitive to environmental cues, it came as no surprise that most of them correctly assessed the unmodified sparrowhawk dummy as threatening, while they probably subjected the chimeras to a detailed inspection and were not confused by the presence of sparrowhawk features and assessed them as non-threatening.

Keywords: Personality, Fast-slow continuum, Risk taking, Predator categorization

1. Introduction

Animal personality and behavioural syndromes have been well-studied phenomena during the last decade with an exponentially increasing number of studies being published. Inter-individual differences stable in time and across situations have been subjected to investigation in numerous animal species and the interest in the ecological importance of these differences is growing (Roche et al., 2016). The variability in individual personality traits influences (or at least correlates with) survival, reproductive success, social status, dispersal, or parasitic load (Réale et al., 2007). Experimental studies have found correlations between personality and exploratory behaviour (e.g. Dingemanse et al., 2002; van Oers et al., 2005), which may, among others, result in a varying ability to correctly assess the threat, and take risk when a predator is encountered (Jones and Godin, 2010; Quinn and Cresswell, 2005; Van Oers et al., 2004).

The question of how different behavioural types cope with the predator encounter has been studied in detail especially in fish model species. The boldness of the stickleback (*Gasterosteus aculeatus*) under predatory risk was positively correlated with aggression toward a conspecific and active exploration of the unfamiliar environment (Bell, 2005). This correlation was significantly tighter in populations living in sympatry with piscivorous predators than in predator-naïve populations of stickleback (Dingemanse et al., 2007). Similarly, a strong positive correlation between exploration and the time taken to respond to the predator model was also found in the convict cichlid (*Amatitlania nigrofasciata*). Fish that were fast to explore the novel environment were slower to respond to the predator (Jones and Godin, 2010).

Nevertheless, birds are probably the most common subjects in the study of behavioural syndromes. The most complete study of the ecological and evolutionary significance of personality involves research on great tits (*Parus major*). The first study found consistent individual differences in exploratory behaviour and therefore different personalities were labelled as

’fast’ and ’slow’ explorers (Verbeek et al., 1994). The succeeding studies found out that ’fast’ explorers were also more aggressive, less neophobic, and more likely to form routines. Using artificial selection, the lines of fast (bold, proactive) and slow (shy, reactive) birds were selected (rev. in Groothuis and Carere, 2005).

Despite the fact that the personality of the great tit has been so intensively studied, the effect of behavioural syndrome on the ability of birds to cope with the threat of predation has been tested only rarely. Quinn et al. (2012) showed that fast exploring great tits are more willing to visit a winter feeder with a high risk of predation than the slow explorers. Similarly, Vrublevska et al. (2015) showed that neophilic breeding pairs of great tits exhibited stronger antipredator mobbing responses than neophobic pairs. Both of these studies agree with the general understanding of the effect of behavioural syndromes, but the mechanisms underlying these differences in behaviour remain unknown (Beekman and Jordan, 2017).

Based on mathematical modelling, Sih and Del Giudice (2012) propose that differences between personalities are caused by different assessments of the risk–reward trade-off in general. This means that faster strategies tend to risk more but can result in more rewards. The higher willingness to risk can be caused by two principles. Firstly, animals possessing different personalities may substantially differ in the partition of their attention between foraging and anti-predator vigilance (Jones and Godin, 2010). Secondly, animals possessing different personalities may differ in their general ability to recognize a threat. It has been proposed that personality can influence cognitive abilities in many ways (Griffin et al., 2015). There could be a large difference in the speed and accuracy of a cognitive process caused by differences in sampling, learning, memory, sensitivity, impulsivity, neophilia, or choosiness (Sih and Del Giudice, 2012). Numerous studies have confirmed this in birds facing various learning and problem-solving tasks (Amy et al., 2012; Brust et al., 2013; Cole et al., 2011; Griffin et al., 2013; Guido et al., 2017; Guillette et al., 2009, 2011; Lermite et al., 2017; Titulaer et al., 2012; van Horik et al., 2017).

Generally, slow birds display longer latencies in approaching a task and solving it. Fast birds are therefore better at learning an initial discrimination. On the other hand, slow birds are more sensitive to changes in an already learned task and are therefore more flexible and better at reversible tasks.

Our previous experiments revealed distinctive inter-individual differences among the wild-caught great tits when facing variously modified predator dummies and when assessing the threat, they represent (Beránková et al., 2014, 2015). The dummy carrying a mixture of the features of predator and a non-threatening bird (hereafter referred to as chimera) caused a fear reaction only in a portion of the birds, while the majority did not consider such an object to be threatening. The level of fear caused by the chimeras depended on the level of conspicuousness of the change of the dummy. When the dummy had only the beak of a predator (a small change), it was generally considered to be non-threatening, when, though, it was augmented with the whole predator head (conspicuous change), it was considered to be threatening by a larger portion of birds. We propose that such differences are caused by the variability in the individual experience or personality. We may suggest that the conspicuous chimera is considered to be threatening by birds which are i) more experienced with predators, ii) more fearful, iii) more cautious about the predator features.

We tested the following hypotheses:

The response of tested birds to the presented dummies does not correlate with personality - the variability in previous experiences of birds with a sparrowhawk are responsible for differences in their behaviour rather than their personality.

Slow birds consider both chimaeras as more threatening than fast birds – slow birds are more cautious about predator features and/or are more fearful.

Only fast birds consider the more conspicuous chimera (with the predator head) as more threatening than the less conspicuous chimera (with the predator beak) – without a closer inspection, fast birds fail to notice the presence of a detailed predator feature.

2. Methods

2.1. Subjects

The great tit (*Parus major*) was chosen as a model species because it is a common subject in laboratory behavioural testing (Groothuis and Carere, 2005) and the behavioural syndromes of great tits have been well described and the procedure of their personality testing is well established (Carere et al., 2005).

Tested birds were trapped in mist-nets in the suburban areas of České Budějovice (Czech Republic, N 48°58.52473', E 14°27.21922') during the winter seasons (November to March) during the years 2013–2016. The tits were ringed after capturing to avoid testing individuals repeatedly. Consequently, the birds were held in commercially sold bird cages and provided with water and food (sunflower seeds, mealworms, and a mixture of dried insects) ad libitum. In sum, 76 individuals were used for all the experiments.

2.2. Experimental procedure

The experimental procedure consisted of personality testing and reaction to the dummies. The experimental setting had two modifications to avoid further individual experience biases. A subset of the birds was subjected to personality testing first, followed by the presentation of the dummy (52 birds). Another subset was presented with the dummy first, followed by personality testing (24 birds). Experiments started the day after the birds were brought to the laboratory from the wild and ended after four days, when the bird was released back into the wild.

2.2.1. Personality testing

Personality testing included four tests standardized for testing birds (namely great tits) in order to evaluate how quickly they respond to new situations. The novel environment test used was a modification of the procedure of free exploration in a novel environment defined for great tits by Verbeek et al. (1994). Great tits were released into a cage equipped with perches and small bushes (2 x 2 x 1 m) and their exploratory behaviour during the first 10 minutes was recorded (total number of movements, total duration of pecking in bedding and equipment in the cage). The startle test used was based on the procedure devised by Van Oers et al. (2004). The test was carried out in the same cage as the novel environment test. In contrast to the novel environment test, a feeder with mealworms was placed in the cage and the latency to visit the feeder and to return to it after being startled by an experimenter was measured. A novel food test and novel feeder test were carried out in the housing cages and the latency to approach novel objects was measured (Verbeek et al., 1994). During the novel food test, the novel object was represented by an unusual colour of food (violet sunflower seeds). During the novel feeder test, the standard black sunflower seeds were presented in a novel feeder (blue dish). The latency in collecting the first seed was measured in both cases. The experiments were conducted in the fixed order within three days starting the second day after the bird was brought into the lab or subjected to the dummy presentation. The novel environment test and startle test were conducted in the morning hours (9-10 AM) during the two subsequent days. The novel food test was conducted on the third day at 9 AM and the novel feeder test 2 hours after the end of the novel food test. 1.5 hours before the startle, novel food, and novel feeder tests the bird was deprived of food to encourage the motivation to forage. In between all tests the bird was housed in the commercially sold cages with food and water ad libitum.

2.2.2. Reaction to the dummies

Four wooden dummies were used to test the reaction of the great tits, a sparrowhawk dummy representing a highly dangerous raptor, a pigeon dummy as a neutral non-threatening bird the size of a sparrowhawk, and their chimeras – a pigeon dummy with a sparrowhawk head and a pigeon dummy with a sparrowhawk beak. Only one of the dummies was presented to each great tit to avoid bias due to the experimental experience.

Before the dummy presentation, the birds were deprived of food for 1.5 h to motivate foraging and exploration and then released into the experimental cage (2 x 1 x 0.5 m). The presented dummy was placed in front of the experimental cage (outside the cage) behind a wall made of plexiglass. Near this wall, but inside the cage, there was a feeder with sunflowers provided. The behaviour of the birds during their exposure to the dummies was video recorded for 10 minutes and analysed subsequently in ethological software (Observer XT 6.1, Noldus Information Technology 1990–2006) by a single observer (JN). We evaluated the feeding on the presented sunflower seeds and pecking in the corn bedding (both total duration in seconds) as a measure of exploration and foraging, and total numbers of feather cap raising, knee-bending, and warning calls as a measure of perceived threat.

2.3. Statistical analysis

2.3.1. Personality testing

Based on the activity during the novel environment test (sum of the number of movements and the total duration of pecking in bedding and equipment in the cage), the birds were separated into 10 groups, scoring 1 for the least active birds, 10 for the most active following van Oers et al. (2004). Based on the latencies during the startle test (latency to visit the feeder and to return to it after being startled), each bird was assigned another 1 to 10 points (1 for the longest latencies and 10 for shortest). Based on the latency levels in approaching novel food and novel feeder, the birds were assigned from 1 to 5 in each of the tests (van Oers et al. 2004). The total score for each bird was obtained by the sum of the partial scores (median ± SE = 15.5 ± 5). The median split separated the birds into two groups of 38 individuals each: fast (16 to 26) and slow (4 to 15) following Groothuis and Carere (2005), Barnett et al. (2013) and Vrublevska et al. (2015).

2.3.2. Reaction to the dummies

We created synthetic variables describing the observed bird behaviour in the presence of the dummy using the multivariate technique - the principal component analysis (PCA) was performed in Canoco 5 software (ter Braak and Šmilauer 1998). The data for PCA were logarithmically adjusted and centred. Based on the PCA, we obtained standardized component scores for each bird regardless of the scale on which the single behaviours were measured (Bell 2005).

PCA scores of the first and second axis (with residual variability following the Gaussian distribution) were used as synthetic response variables. The effect of the dummy type, personality, experimental setting (dummy or personality test first), sex, and age of the tested birds as predictor variables was assessed using linear models (command lm in R 3.2.3. - R Development Core Team, 2011). Akaike information criterion (command step in R 3.2.3.) was used to find the optimal models (Table 1). The selected model for the first PCA axis included experimental setting, dummy type, and their interaction. The model for the second PCA axis included dummy type, experimental setting, personality, sex, age, interaction of dummy type and experimental setting, and interaction of dummy type and personality. The effects of particular predictors were evaluated using a Likelihood ratio test following the Gaussian distribution (F test). Differences among the levels of categorical predictors were subsequently compared using the Tukey HSD post-hoc test (t test).

Table 1 Akaike information criteria (AIC) for possible models explaining the variability of the scores the birds obtained on the first (PCA 1) and the second (PCA 2) PCA axis of the multivariate analysis of the behaviour during the dummy presentation. The optimal models used for further analyses are stressed in bold.

response variable	predictor variables	AIC
PCA 1	dummy + setting + person + sex + dummy:setting	-6.23
PCA 1	dummy + setting + sex + dummy:setting	-7.28
PCA 1	**dummy + setting + dummy:setting**	**-7.97**
PCA 1	dummy + setting	-3.91
PCA 1	dummy	0.62
PCA 2	dummy*setting*person+sex+age	-35.60
PCA 2	dummy + setting + personality + sex + age + dummy:setting + dummy:personality + setting:personality	-38.51
PCA 2	**dummy + setting + personality + sex + age + dummy:setting + dummy:personality**	**-40.47**
PCA 2	dummy + setting + personality + age + dummy:setting + dummy:personality	-38.97
PCA 2	dummy + setting + personality + sex + dummy:setting + dummy:personality	-38.66

3. Results

3.1. Multivariate analysis of behaviour to dummies

The principal component analysis (PCA) of selected behavioural traits showed that explorative behaviour (feeding and exploration of bedding) correlated with the first PCA axis and is independent of fear-related behaviour (warning calls, raising feathers on the head, and knee-bending) correlating with the second PCA axis. The first PCA axis explained 54.6% of the variability of the birds' behaviour and the second PCA axis explained 29.0% of the variability (Fig. 1).

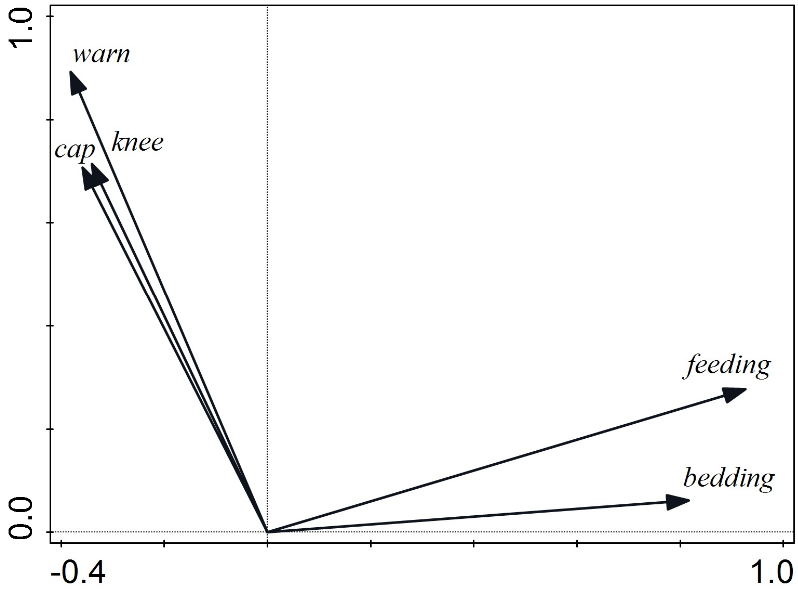

Fig. 1 Multivariate analysis of the behaviour of tested tits in the presence of all dummies visualized on the first and second axis of Principal Component Analysis (PCA). The first axis explains 54.6%; the second axis explains 29.0% of variability. Warn – number of alarm calls, knee – number of knee-bending, cap – number of rising feathers on the head, feeding – total time spent feeding on presented seeds, bedding – total time spent pecking into the bedding in the cage.

3.2. The first PCA axis – exploration and foraging behaviour

The birds without experience with personality testing had higher scores on the first PCA axis (Table 2) which means that that they displayed more exploration behaviour than the birds with experience with personality testing. The interaction of presented dummy and experimental setting was also significant (Table 2). The differences between experimental settings were significant only when the dummy of the pigeon with a sparrowhawk beak was presented (Tukey HSD post-hoc test, t=-3.184, p=0.041). In this case, the birds without experience with personality testing showed more feeding behaviour than the birds with the experience.

Table 2 Effect of particular predictors on the variability of the PCA scores (PCA 1 – first axis, PCA 2 – second axis) of the multivariate analysis of the bird behaviour in the presence of particular dummies. Colon indicates interaction of categorical factors, DFnum refers to the numerator degrees of freedom, DFden refers to the denominator degrees of freedom.

response	predictor	DFnum	DFden	F value	p value
PCA 1	dummy	3	75	2.875	**0.042**
PCA 1	setting	1	75	6.975	**0.010**
PCA 1	dummy:setting	3	75	3.206	**0.029**
PCA 2	dummy	3	75	22.230	**<0.001**
PCA 2	setting	1	75	0.094	0.761
PCA 2	personality	1	75	0.013	0.910
PCA 2	sex	1	75	2.769	0.101
PCA 2	age	1	75	2.111	0.151
PCA 2	dummy:setting	3	75	1.978	0.127
PCA 2	dummy:personality	3	75	4.341	**0.008**

3.3. The second PCA axis – fear-related behaviour

There was a significant effect regarding dummy type on the fear reaction of the tested great tits (Table 2). Fear-related behaviour was observed most often in the presence of the unmodified sparrowhawk dummy (Fig. 2). The modified dummy of the pigeon with a sparrowhawk head caused less fear and the minimum of the fear-related behaviour was observed in the presence of the unmodified pigeon dummy and the dummy of a sparrowhawk with a pigeon beak (Table 3).

Table 3 Differences in fear reaction (PCA axis 2 scores) to the particular dummies: t-values (bottom-left) and p-values (upper-right) of Tukey HSD post-hoc test. Significant differences in bold.

dummy	sparrowhawk	head chimera	beak chimera	pigeon
sparrowhawk		**0.009**	**<0.001**	**<0.001**
head chimera	**3.268**		**0.024**	**0.007**
beak chimera	**6.138**	**2.910**		0.971
pigeon	**6.649**	**-3.388**	-0.441	

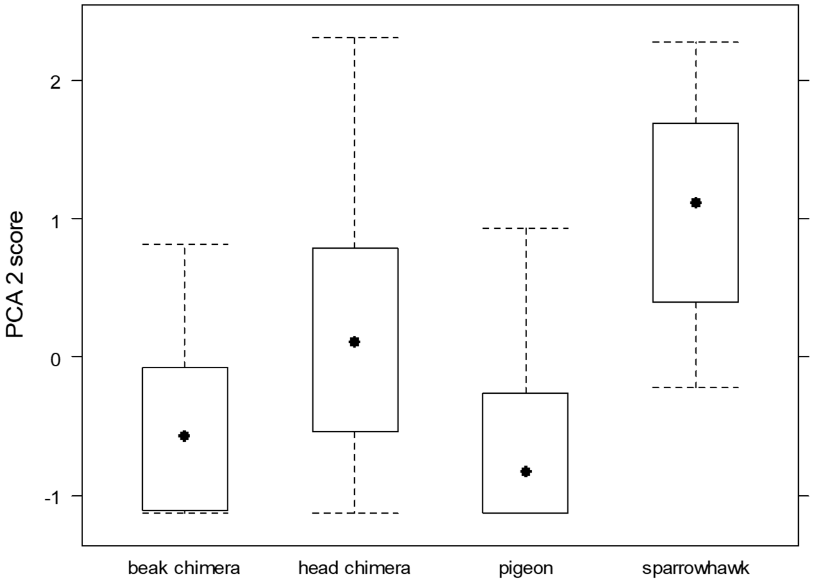

Fig. 2 Scores of the fear-related behaviour (the second PCA axis) of birds presented with particular dummies.

There was also a significant effect regarding the interaction of dummy type and personality (Table 2). Nevertheless, due to the Tukey correction of the significance level, we were not able to statistically corroborate any difference in the fear reactions between the fast and slow birds facing the same dummy – pigeon with sparrowhawk head (t=0.868, p=0.988), pigeon with sparrowhawk beak (t=1.189, p=0.932), and pigeon (t=0.832, p=0.990). There was a tendency for slow birds to show more fear reactions in the presence of the unmodified sparrowhawk dummy than fast birds (Fig. 3; t=-2.710, p=0.137).

Fast birds showed more fear reactions towards the unmodified dummy of the sparrowhawk than towards the unmodified dummy of the pigeon (Table 4; Fig. 2). Reaction to both chimeras was intermediate and did not differ from the reaction to the sparrowhawk nor the pigeon dummy (Table 4; Fig. 3). On the other hand, slow birds displayed a difference in reaction not only between the unmodified dummies but also between the unmodified sparrowhawk and both chimeras (Table 5; Fig. 3).

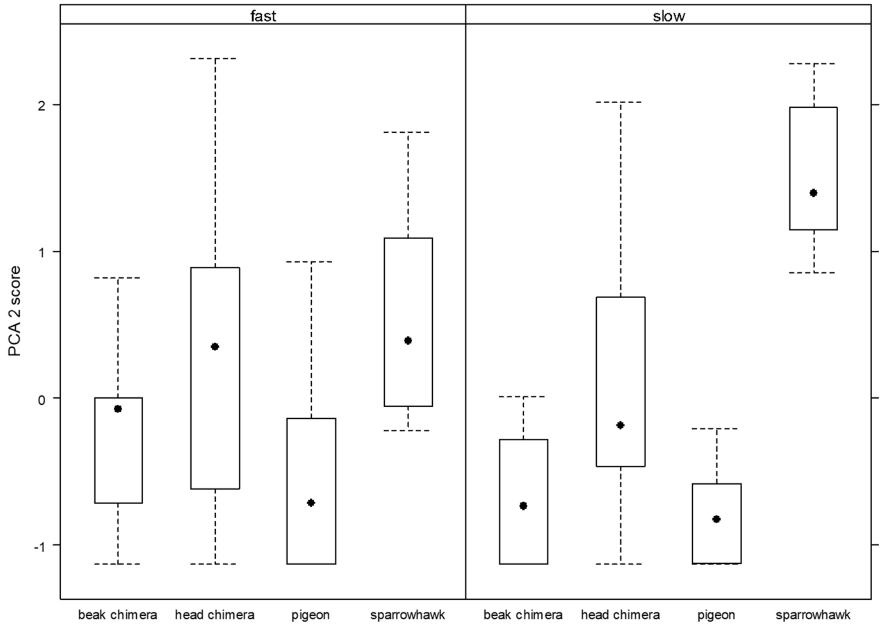

Fig. 3 Scores of the fear-related behaviour (the second PCA axis) of fast and slow birds presented with particular dummies.

Table 4 Differences in reaction of fast birds to particular dummies: t-values (bottom-left) and p-values (upper-right) of Tukey HSD post-hoc test. Significant differences in bold.

fast birds	sparrowhawk	head chimera	beak chimera	pigeon
sparrowhawk		0.998	0.364	**0.030**
head chimera	0.637		0.713	0.132
beak chimera	2.199	1.655		0.995
pigeon	3.313	-2.728	-0.741	

Table 5 Differences in reaction of slow birds to particular dummies: t-values (bottom-left) and p-values (upper-right) of Tukey HSD post-hoc test. Significant differences in bold.

slow birds	sparrowhawk	head chimera	beak chimera	pigeon
sparrowhawk		**0.002**	**<0.001**	**<0.001**
head chimera	4.177		0.347	0.274
beak chimera	6.693	2.228		0.999
pigeon	6.417	-2.365	-0.365	

4. Discussion

The measured level of explorative behaviour during the dummy presentation (first PCA axis) was independent of personality. On the other hand, fear-based behaviour (second PCA axis) was related to personality. The simple correlation between the scores on the second PCA axis and personality was not significant. There was no difference between the reaction of fast and slow birds to the same dummy, except for a non-significant tendency of slow birds to fear the sparrowhawk more than the fast birds. At first sight, this implies that individual experience with the sparrowhawk rather than personality is responsible for the variability in reaction to the presented dummies (as predicted by the first hypothesis).

Nevertheless, the effect of the interaction of personality and dummy type was significant. Both personalities differed in the categorization of particular dummies. The fast tits displayed a difference in behaviour only between the unmodified sparrowhawk and unmodified pigeon. The reaction to both chimeras was intermediate. On the other hand, the slow birds displayed a clearly different reaction to the sparrowhawk than to the rest of the dummies. These results show that personality somehow influences the reaction to the presented dummies. The differences in antipredator behaviour between fast and slow birds may be caused by different willingness to risk an encounter with a predator (Sih and Del Giudice, 2012). Experimental studies support the prediction that great tits of different personalities seem to differ in their risk-reward decisions. The exploratory behaviour of wild great tits was positively correlated with a tendency to feed on high quality food even though the predation risk was experimentally increased (Quinn et al., 2012). Neophilic great tits also approached the predator closer and producing more calls than neophobic individuals during their nest defence (Vrublevska et al., 2015). These results show that fast (neophilic) great tits are less fearful and therefore more willing to risk a confrontation with a predator regardless of the circumstances. However, there is no clear relationship caused by the generally lower level of fear in our results. The amount of fear does not significantly differ between slow and fast tits facing the same dummy. The tendency of fast birds to show lower fear was observed only in the reaction to the unmodified sparrowhawk.

The findings of experiments testing the differences in cognitive abilities of fast and slow birds seem to be in better agreement with our results. Since the slow birds are usually considered to be more sensitive to environmental cues, they probably categorized the chimeras as non-threatening after a closer inspection and revealed that they do not match the sparrowhawk category. On the other hand, the reaction of fast birds to the chimeras was rather confused. The reason for this can be found in the high variability in their reaction that is less uniform than in the slow birds. It could imply that some of the fast birds assessed the chimeras as threatening and some as non-threatening probably because they paid less attention to the details of the dummies. This suggests that another axis of the behavioural syndrome of the tits goes against the fast-slow continuum and causes another variability in threat perception.

Various behavioural syndromes may pay different amounts of attention to the environment and can therefore gain a different amount of information that they subsequently process (Fernández-Juricic et al. 2004). However, it is difficult to know if the fast birds really do not perceive a difference or if they ignore it (van Horik et al., 2017). The experiments with North Island robins (*Petroica longipes*), based on the discrimination between a familiar and unfamiliar human, imply that fast birds might pay less attention to the task and so learn fewer details associated with the experiment (Barnett et al., 2013). This result is in a concordance with our findings which means that the fast birds are less attentive not only while learning a new object but during the reaction to an already familiar predator as well.

The first PCA axis that is associated with explorative behaviour is not correlated with personality. However, there is an effect regarding experimental setting. The birds facing the dummy the next day after being kept in captivity showed significantly more feeding behaviour than the birds that underwent the procedure of personality testing at first. This means that personality testing and/or the stay in captivity had a considerable effect on behaviour during the experiment. We suppose that the reason could be the different risk of starvation, since the birds that spend a longer time in captivity with food ad libitum had less motivation to risk feeding during risky circumstances (Sih et al., 2015). Similarly, the experiments with chaffinches proved that individuals kept in captivity for longer periods were less likely to forage than the individuals that underwent the experiment soon after capture (Butler et al., 2006).

This result seems to be important from a methodological point of view. The habituation to captivity is usually considered as highly important in wild animals but there are some indices that long habituation may not always be beneficial before conducting the experiments (Butler et al., 2006). Moreover, theoretical studies also propose that individuals may converge to be relatively bold or relatively cautious under highly favourable or highly unfavourable conditions respectively (Luttbeg and Sih, 2010). Our results show that highly favourable conditions during captivity (ad libitum food source) had an effect only on the exploration-foraging behaviour during the experiment. The fear reaction seems to be influenced rather by personality and no significant effect of captivity was observed.

Conclusions

Recent studies dealing with the connection between personality and antipredator behaviour agree that slow birds rather avoid the risk of predation while fast birds are more willing to take the risk. We were not able to show any such strong signal. The birds in our study were not able to avoid the predator and were forced to face it in close proximity. As a result, the personality differences were weak and they were recognizable rather in the differences between both personalities in the evaluation of the confusing sparrowhawk-pigeon chimeras. This tells us something about the cognitive abilities of the birds rather than about the risk taking and perception of various personalities.

Acknowledgements

We thank Christopher Mark Steer for the language improvement. This work was supported by the Grant agency of the University of South Bohemia (04-151/2016/P).

References

Amy, M., Oers, K., Naguib, M., 2012. Worms under cover: relationships between performance in learning tasks and personality in great tits (*Parus major*). Anim. Cogn. 15, 763–770. doi:10.1007/s10071-012-0500-3

Barnett, C., Salter, M., Chevallier, C., Robertson, N., Berard, O., Burns, K.C., 2013. The Ability of North Island Robins to Discriminate between Humans Is Related to Their Behavioural Type. PLoS ONE 8, e64487. doi:10.1371/journal.pone.0064487

Beekman, M., Jordan, L.A., 2017. Does the field of animal personality provide any new insights for behavioral ecology? Behav. Ecol. doi:10.1093/beheco/arx022

Bell, A.M., 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*): Behavioural syndromes. J. Evol. Biol. 18, 464–473. doi:10.1111/j.1420-9101.2004.00817.x

Beránková, J., Veselý, P., Fuchs, R., 2015. The role of body size in predator recognition by untrained birds. Behav. Process. 120, 128–134. doi:10.1016/j.beproc.2015.09.015

Beránková, J., Veselý, P., Sýkorová, J., Fuchs, R., 2014. The role of key features in predator recognition by untrained birds. Anim. Cogn. 17, 963–971. doi:10.1007/s10071-014-0728-1

Brust, V., Wuerz, Y., Krüger, O., 2013. Behavioural Flexibility and Personality in Zebra Finches. Ethology 119, 559–569. doi:10.1111/eth.12095

Butler, S.J., Whittingham, M.J., Quinn, J.L., Cresswell, W., 2006. Time in captivity, individual differences and foraging behaviour in wild-caught chaffinches. Behaviour 143, 535–548.

Carere, C., Drent, P.J., Privitera, L., Koolhaas, J.M., Groothuis, T.G.., 2005. Personalities in great tits *Parus major*: stability and consistency. Anim. Behav. 70, 795–805.

Cole, E.F., Cram, D.L., Quinn, J.L., 2011. Individual variation in spontaneous problem-solving performance among wild great tits. Anim. Behav. 81, 491–498.

Dingemanse, N., Both, C., Drent, P.J., Van Oers, K., van Noordwijk, A.J., 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. Anim. Behav. 64, 929–938. doi:10.1006/anbe.2002.2006

Dingemanse, N.J., Wright, J., Kazem, A.J.N., Thomas, D.K., Hickling, R., Dawnay, N., 2007. Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. J. Anim. Ecol. 76, 1128–1138. doi:10.1111/j.1365-2656.2007.01284.x

Griffin, A.S., Guez, D., Lermite, F., Patience, M., 2013. Tracking Changing Environments: Innovators Are Fast, but Not Flexible Learners. PLoS ONE 8, e84907. doi:10.1371/journal.pone.0084907

Griffin, A.S., Guillette, L.M., Healy, S.D., 2015. Cognition and personality: an analysis of an emerging field. Trends Ecol. Evol. 30, 207–214. doi:10.1016/j.tree.2015.01.012

Groothuis, T.G.G., Carere, C., 2005. Avian personalities: characterization and epigenesis. Neurosci. Biobehav. Rev. 29, 137–150. doi:10.1016/j.neubiorev.2004.06.010

Guido, J.M., Biondi, L.M., Vasallo, A.I., Muzio, R.N., 2017. Neophobia is negatively related to reversal learning ability in females of a generalist bird of prey, the Chimango Caracara, *Milvago chimango*. Anim. Cogn. 20, 591–602. doi:10.1007/s10071-017-1083-9

Guillette, L.M., Reddon, A.R., Hoeschele, M., Sturdy, C.B., 2011. Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task. P. Roy. Soc. B-Biol. Sci. 278, 767–773. doi:10.1098/rspb.2010.1669

Guillette, L.M., Reddon, A.R., Hurd, P.L., Sturdy, C.B., 2009. Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, *Poecile atricapillus*. Behav. Process. 82, 265–270. doi:10.1016/j.beproc.2009.07.005

Jones, K.A., Godin, J.G.J., 2010. Are fast explorers slow reactors? Linking personality type and anti-predator behaviour. P. Roy. Soc. B-Biol. Sci. 277, 625–632.

Lermite, F., Peneaux, C., Griffin, A.S., 2017. Personality and problem-solving in common mynas (*Acridotheres tristis*). Behav. Process. 134, 87–94. doi:10.1016/j.beproc.2016.09.013

Luttbeg, B., Sih, A., 2010. Risk, resources and state-dependent adaptive behavioural syndromes. Phylos. T. Roy. Soc B 365, 3977–3990. doi:10.1098/rstb.2010.0207

Quinn, J.L., Cole, E.F., Bates, J., Payne, R.W., Cresswell, W., 2012. Personality predicts individual responsiveness to the risks of starvation and predation. P. Roy. Soc. B-Biol. Sci. 279, 1919–1926.

Quinn, J.L., Cresswell, W., 2005. Personality, anti-predation behaviour and behavioural plasticity in the chaffinch *Fringilla coelebs*. Behaviour 142, 1377–1402.

Réale, D., Reader, S.M., Sol, D., McDougall, P.T., Dingemanse, N.J., 2007. Integrating animal temperament within ecology and evolution. Biol. Rev. 82, 291–318. doi:10.1111/j.1469-185X.2007.00010.x

Roche, D.G., Careau, V., Binning, S.A., 2016. Demystifying animal “personality” (or not): why individual variation matters to experimental biologists. J. Exp. Biol. 219, 3832–3843. doi:10.1242/jeb.146712

Sih, A., Del Giudice, M., 2012. Linking behavioural syndromes and cognition: a behavioural ecology perspective. Phylos. T. Roy. Soc B 367, 2762–2772. doi:10.1098/rstb.2012.0216

Sih, A., Mathot, K.J., Moirón, M., Montiglio, P.-O., Wolf, M., Dingemanse, N.J., 2015. Animal personality and state–behaviour feedbacks: a review and guide for empiricists. Trends Ecol. Evol. 30, 50–60. doi:10.1016/j.tree.2014.11.004

Titulaer, M., van Oers, K., Naguib, M., 2012. Personality affects learning performance in difficult tasks in a sex-dependent way. Anim. Behav. 83, 723–730. doi:10.1016/j.anbehav.2011.12.020

van Horik, J.O., Langley, E.J.G., Whiteside, M.A., Madden, J.R., 2017. Differential participation in cognitive tests is driven by personality, sex, body condition and experience. Behav. Process., Individual differences in cognition and personality 134, 22–30. doi:10.1016/j.beproc.2016.07.001

van Oers, K., de Jong, G., van Noordwijk, A.J., Kempenaers, B., Drent, P.J., 2005. Contribution of genetics to the study of animal personalities: a review of case studies. Behaviour 142, 1191–1212.

Van Oers, K., Drent, P.J., De Goede, P., Van Noordwijk, A.J., 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. P. Roy. Soc. Lond. B Bio. 271, 65–73.

Verbeek, M., Drent, P.J., Wiepkema, P., 1994. Consistent individual differences in early exploratory behaviour of male great tits. Anim. Behav. 48, 1113–1121.

Vrublevska, J., Krama, T., Rantala, M.J., Mierauskas, P., Freeberg, T.M., Krams, I.A., 2015. Personality and density affect nest defence and nest survival in the great tit. Acta Ethol. 18, 111–120. doi:10.1007/s10211-014-0191-7

Curriculum Vitae

Date of birth: 09.04.1989
Place of birth: Chomutov, Czech Republic
Nationality: CZ

e-mail: jaja.nacarova@gmail.com

Education

– since 2013: Doctoral studies in Zoology, Faculty of Science, University of South Bohemia, Czech Republic

– 2011–2013: Master in Zoology, Faculty of Science, University of South Bohemia, Czech Republic

– 2008–2011: Bachelor in Biology, Faculty of Science, University of South Bohemia, Czech Republic

Study Stays

– 2017: Konrad Lorenz Forschungsstelle, Grünau im Almtal (Austria) – *Reaction of ravens to heterospecific alarm calls*

– 2016: Konrad Lorenz Forschungsstelle, Grünau im Almtal (Austria) – *Behavioural response of ravens to predator dummies posing different amount of threat*

– 2015: Konrad Lorenz Forschungsstelle, Grünau im Almtal (Austria) - *Ravens adjusting their antipredatory responses to con- and heterospecific alarms to the perceived threat*

– 2014: Department of Cognitive Biology, University of Vienna (Austria) - *Responses of urban crows to con- and hetero-specific alarm calls in predator and non-predator zoo enclosures*

Work Experience

– since 2014: Research assistant at Department of zoology, Faculty of Science, University of South Bohemia, Czech Republic

Teaching Experience

– Field presentation of birds and ringing:
Field Work (I), Vertebratological Excursions, Zoology of Higher Vertebrates

– Experimental work in lab and field:
Ecology, Animal Ecology, Practical Course in Ethology (II)

– Lectures:
Practicals in Vertebrate Zoology, Special Zoology (Faculty of Agriculture), Biology (Faculty of Agriculture)

International Conferences

– 8th European Conference of Behavioural Biology,
Vienna, Austria, July 12-15, 2016; *Personality and the reaction to predator in great tits (Parus major)*

– VII. European Conference on Behavioural Biology,
Praha, July 17-20, 2014; *The importance of key features, colour and size in predator recognition – cage experiments with great tits*

– 14th International Behavioral Ecology Congress,
Lund, Sweden, 12-17 August, 2012; *How to recognize a predator: key features, color or size?*

– ASAB summer meeting – “Understanding animal intelligence”,
St. Andrews, UK, 18-19 August, 2011; *How to recognize a predator: to use key features or concept?*

Publications

Nácarová J, Veselý P, Fuchs R (in prep.) Effect of behavioural syndrome on a bird's ability to categorize a predator.

Nácarová J, Veselý P, Bugnyar T (in prep.) Ravens adjust their antipredatory responses to con- and heterospecific alarms to the perceived threat.

Bílá K, **Beránková J**, Veselý P, Bugnyar T, Schwab C (2017) Responses of urban crows to con- and hetero-specific alarm calls in predator and non-predator zoo enclosures. Anim Cogn 20:43–51. doi: 10.1007/s10071-016-1047-5

Karlíková Z, Veselý P, **Beránková J**, Fuchs R (2016) Low Ability of Great Tits to Discriminate Similarly Inconspicuous Edible and Inedible Prey. Ethology 122:180–191. doi: 10.1111/eth.12454

Beránková J, Veselý P, Fuchs R (2015) The role of body size in predator recognition by untrained birds. Behavioural Processes 120:128–134. doi: 10.1016/j.beproc.2015.09.015

Beránková J, Veselý P, Sýkorová J, Fuchs R (2014) The role of key features in predator recognition by untrained birds. Animal Cognition 17:963–971. doi: 10.1007/s10071-014-0728-1

jaja.nacarova@gmail.com

Research on cognitive abilities in untrained birds
Ph.D. Thesis Series, 2017, No. 20

Printed in the Czech Republic by Typodesign
Edition of 20 copies

University of South Bohemia in České Budějovice
Faculty of Science
Branišovská 1760
CZ-37005 České Budějovice, Czech Republic

Phone: +420 387 776 201
www.prf.jcu.cz, e-mail: sekret-fpr@prf.jcu.cz