Antipredator behaviour of birds

Habilitation thesis

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Summary

To my wife Janča, thanks for being my best friend

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This work summarizes research of working group within the Department of Zoology, Faculty of Science, University of South Bohemia in České Budějovice, which I am honoured to be part of, and which we labelled Centre of Cognitive Ethology in 2005. This group have involved numerous people of all academic degrees during the last 20 years, and all of them contributed in some way to the origin of the research presented within this habilitation thesis.

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Introduction

Predation represents the main selective force that removes the individual from the population and sometimes even substantially affects the entire population and community (Taylor 2013). Therefore, the ability to avoid predation increases the individual fitness, in particular. There are multiple morphological, physiological and behavioural adaptations of animals that lead to their increased survival via two basic principles, avoiding predators (Ruxton et al. 2019) or surviving the encounter with predators (Caro 2005). Birds in particular are specific by several life history strategies with reference to predation. Some of their developmental stages (eggs and, very often, also chicks) are unable to perform behaviour and thus rely on the avoidance strategies. Adult birds, on the contrary, are very mobile to flee from predators, acoustically developed to perform a variety of sophisticated alarm calls, and very often also strong enough to fight the predators back (Caro 2005). As a result, birds show an incredibly diverse strategies securing their survival.

The strategies can generally be divided in passive and active. Passive strategies are based on not being revealed by the predator. This encompasses shifts in space and time (e.g., Turner and Montgomery 2003) but also development of specific body features, securing camouflage. Active defence presumes that some behaviour is triggered by the presence of the predator. As this review aims at behaviour, the active forms of defence will be described in detail. But the passive forms will also be mentioned in this chapter, as they often represent stunning natural phenomena.

Figure 1 – Clutch (above) and chick (below) of little ringed plover (*Charadrius hiaticula*). Examples of cryptic colouration using the disruptive colour pattern (Price et al. 2019, Rohr et al. 2021).

3

Passive antipredator strategies of birds

Crypsis and camouflage

Birds are very often textbook examples of adaptations to visual appearance to match their natural environments. Generations of students of ornithology were forced to learn very fine differences in warbler species that were very similar and inconspicuously coloured. Brownish, yellowish, and greenish shades are really very common in birds, and they represent a basic camouflage inventory for sure (Roulin 2004).

Eggs, chicks, and adults tend to develop cryptic colouration in some species to avoid predation. Usually, those stages of life and individuals threatened by visually orienting predators are selected for camouflage. The eggs of ground nesting bird species show more often a cryptic visual appearance with disruptive patterning and dull colours (Kilner 2006). On the contrary, eggs of nest hole breeders are usually white, because the eggs are quite safe in the cavity, but more importantly, their colours are usually invisible in the dark environment of the tree cavity (L'Herpiniere et al. 2021). Open nest breeders face multiple selective forces, not only predation, which results in stunning variability in bird eggshell colouration (Hanley et al. 2013). The most elaborate is the eggshell colouration in some ground nesters, namely shorebirds building their nests in sand and gravel with a complex structure (Skrade and Dinsmore 2013). These eggs use the principles of disruptive colouration, with contrasting patterns that make the outlines of the egg invisible on the structured background (Price et al. 2019; Figure 1).

Bird chicks very often show a similar strategy. The evolution of visual appearance of bird nestlings is usually driven by their parents to stimulate them to parental care (Avilés and Soler 2009). The conspicuous lining of the oral cavity is the best example (Kilner 1999). Nevertheless, once the nestlings get their first plumage, its colouration very often fulfils an antipredator function. Inexperienced young individuals after fledging, and very often even after reaching their sexual maturity (Hawkins et al. 2012), profit from possessing inconspicuous colouration, giving them advantage against predators.

In some specific cases, juvenile plumage may on the contrary handicap the individual. In the study Špička et al. (2024; Chapter 1), we tested the hypothesis that juvenile goshawk (*Accipiter gentilis*), which differs significantly from adults in its colouration, takes a profit from resembling a less powerful raptors (e.g., common buzzard – *Buteo buteo*) enabling it to approach its prey. In contrast to our prediction, we showed that Eurasian magpies (*Pica pica*) used the colouration of the inexperienced juvenile goshawk as a proxy of low threat and actively mobbed it, significantly more often than adult goshawk, which elicited fear in magpies. At the same time, magpies were able to recognise the juvenile goshawk from common buzzard, which elicited a zero response. Nevertheless, we cannot rule out the possibility that other prey species, e.g. pigeons cannot successfully differentiate juvenile goshawks from buzzards, giving the inexperienced juvenile goshawk some hunting advantage.

Similarly to eggs, the chicks of some shorebird species possess a complex colouration of their neoptile (Rohr et al. 2021; Figure 1). Some parts of their body are brownish, with a spotted pattern, others are white, and dark stripes are present between these parts. The overall appearance of the chick is broken, and its entire body is very hard to see in the matching background of gravel and stones.

Inconspicuous colouration is also specific for females of many species of birds. Badyaev and Hill (2003) showed in their phylogenetic analysis that sexual dichromatism in birds is an ancestral state, but at the same time, it is more common that females lose their conspicuous colouration rather than males develop their colouration as a result of sexual selection. This suggests the importance of crypsis in incubating females, especially in open nest breeders. In contrast, females tend to be conspicuously coloured in cavity-breeding species like tits (Paridae), where the advantage of camouflage is poor. In addition, the camouflage of incubating females may also include the olfactory sense. Females (or both sexes in the case of biparentally incubating species) of ground nesting birds change the composition of their preen oil produced by the uropygial gland in the period of incubation to less smelly substance to avoid predation by smell-oriented predator like mammals (Grieves et al. 2022).

The strategy to avoid predation is behaviourally pronounced in the case of nest concealment. As mentioned above, nest content is defenceless and extremely valuable to parents. The ability to hide the nest from predators seems to be an essential strategy that is important to increase the fitness of parents. However, there is surprisingly little evidence that nest concealment increases nest survival (Borgmann and Conway 2015). The authors suggest that in addition to methodological issues (e.g., measuring the concealment through foliage density in an inappropriate period), the main reason for this discrepancy resides in the fact that the parents, more than the nest, eggs, and nestlings themselves, are responsible for the visibility of the nest and thus the ability of predators to find it. The nesting site selection itself is of high importance, but even a well-hidden nest can be found by predators once the parents are conspicuously coloured or conspicuously behaving (Burhans and Thompson III 2001).

However, even well-hidden nests have their negatives. Götmark et al. (1995) showed that the view the incubating female has from the nest is at least similarly important as the nest concealment. Thus, there is a trade-off in nest site selection between hiding it in dense vegetation and having a good view on an approaching predator. Another factor is the phenology of the vegetation, as the visual conditions of the foliage may change over time. For example, rose shrubs (*Rosa* sp.) tend to lose and dry the leaves, resulting in nests being much better visible at the end of the breeding season, when the chicks are large (and thus of high evolutionary value) when compared to the period when the nest was built (5-6 weeks earlier; Burhans and Thompson III 1998).

Figure 2 – Above - Adult Eurasian hoopoe (*Upupa epops*) is showing the conspicuous white and black pattern on its wings and crest: This signal along with the smelly substance produced by its uropygial gland may suffice the definition of aposematism (Ruiz-Rodrígeuz et al. 2017).
Below - Eurasian wryneck (*Jynx torquilla*, left) performs twisting head movements, which may resemble snake movements. Along with specific pattern resembling common European viper (*Vipera berus*, right), this behaviour may discourage the predator from eating it (Brejcha 2019).

Warning signals

Another form of morphological adaptation is utilized once the predator reveals the prey. Multiple animals develop some quality making it inedible or even poisonous: chemicals, spikes, stings, or teeth and these qualities are advertised via so-called aposematic signals (Ruxton et al. 2019). In birds, there are few examples of smelly or even toxic species, utilizing these chemicals as protection from predators. E.g. Eurasian hoopoe (*Upupa epops*) nestlings are known to produce smelly substance from their uropygial gland. Tomás et al. (2020) showed that it has a repellent effect on blood-feeding insects like mosquitoes, but a similar effect is supposed also towards nest predators (Vaurie 1973). Repellent function of chemicals in faeces is also supposed in several duck species (Swennen 1968), wood hoopoes (Phoeniculidae, Vaurie 1973), and ground hornbills (*Bucorvus*, Marshall 1902).

The well-studied system represents the great spotted cuckoo (*Clamator glandarius*). As its Latin name suggests, its uropygial gland produces a smelly substance, which may deter predators from the nest (Röder et al. 2014). This is very interesting, as this cuckoo species is a brood parasite. Their chicks are raised by several corvid species, but they cause quite little harm to the hosts; as they do not attack their offspring, they just represent larger burden for the foster parents (Soler et al. 1999). Röder et al. (2014) showed that corvid nests containing the cuckoo nestling were significantly less predated than those without the cuckoo. This suggests that feeding a great spotted cuckoo represents rather an advantage than burden for the hosts, and that the relationship of a great spotted cuckoo and their hosts is rather mutualistic than parasitic. Chemical defence seems to be quite widespread in cuckoos (Trnka et al. 2016), as the cuckoo nestling is quite conspicuous in the host nest and needs an additive strategy to increase its survival. Of course, in the case of a common cuckoo (*Cuculus canorus*), which kills all host nestlings, there is no mutualism with hosts, just an effective parasitism.

Actually, pure aposematism presumes that the prey is toxic to predators, who in consequence learn to avoid eating it. This strategy was confirmed only in a handful of bird species, most of them occurring on the island of New Guinea. The content of batrachotoxins in the feathers and skin of the four species of genus *Pitohui* was first reported by Dumbacher et al. (1992). These birds have the ability to sequestrate these chemicals from their food (mainly beetles of the Lycidae family) and incorporate them into their body surface, resulting in a bitter taste perceived when the feather or skin is in the predator's mouth. Later on, a similar system was found in another passerine species from New Guinea, the blue-capped ifrit (*Ifrita kowaldi;* Dumbacher et al. 2000). The effect of these birds on predators is rather repellent, the levels of toxins in their tissues range significantly between individuals and populations, but usually do not meet concentrations that could threaten the life of their predators.

Along with development of chemical protection and distastefulness, an aposematic colouration developed in some bird species. The most pronounced example of aposematism is found in the hooded pitohui (*Pitohui dichrous*), which displays red and black colouration - colours usually utilized in aposematic signals (Harvey and Paxton 1981). The other toxic species are rather cryptic. Nevertheless, in many other bird species, we can see stunning variability in colour combination, which could also fulfil the criteria for aposematic signals. However, its antipredator meaning is suggested only in a handful of them though. The previously mentioned hoopoe possesses red-and-black stripped pattern on their back and wings, associated with a red-and-black stripped crest on the head, which is raised when the bird is alerted. This visual signal in combination with repellent smell of this species is supposed to fulfil the definition of aposematic signals (Ruiz-Rodrígeuz et al. 2017; Figure 2). Similarly, royal flycatcher (*Onychorhynchus coronatus*) possesses red, black and blue crest on its head, raised when captured by a predator (Rieveley 2010).

As the crest is raised actively when predator approaches and remains inconspicuous when bird is resting, we can treat this feature as a form of deimatic display (Umbers et al. 2015). This sudden display emphasizes the predators stress associated with such an encounter. However, in this case, there are very likely multiple functions of this structure, and the potential harm to the predator of this flycatcher species remains unrevealed.

Gelabert et al. (2020) suggest that the aposematic importance of colours applies even in such a colourful group of birds as the parrots and parakeets are. Their molecular analysis of the extinct Carolina parakeet (*Conuropsis carolinensis*) showed that this species had a mutation in several genes that allowed them to metabolise alkaloids ingested along with seeds of a highly toxic plant, cockleburs (*Xanthium strumarium*), which were commonly found in its diet. The authors speculate that the toxins were cumulated in the tissues in similar way as in pitohuis, ensuring their toxicity for predators, which was advertised by yellow and red colouration at the same time. However, evidence for these chemicals in parakeet tissue is lacking. Additionally, this adaptation to ingest toxins has not been shown in any other parrot species, but it definitely opens up to the possibility of aposematism.

Apart from toxicity, aposematic colouration is supposed to occur even in species that may cause another form of harm to the predator. For example, woodpeckers have a very strong bill adapted to digging in the wood, which is a powerful weapon against most predators. At the same time, many species possess very conspicuous colours, very often combining red, white, and black. Götmark and Unger (1994) showed that the mount of the great spotted woodpecker (*Dendrocopos major)* combining red, black, and white colours was attacked by raptors significantly less than the mount of the plain black of a blackbird (*Turdus merula*). This suggests that predators are aware of the risk associated with capturing the woodpecker, and the conspicuous colours advertise this risk on larger distance and secure the woodpecker from being hunted by raptors.

Lastly, I would like to mention one specific antipredator strategy of several bird species, which is snake mimicry. It does not represent a typical aposematic signal, as the birds are edible and are not colourful, but mimicking a snake is a strategy that may significantly increase the survival probability when captured by a predator, as there are very few snake-eating specialists (de Souza et al. 2022), and the fear of snakes is very widespread among animals (Hamm et al. 1997). Sibley (1955) suggested that tits and titmice (Passeriformes, Paridae) produce a hissing call resembling snakes when a predator enters their nesting hole. Subsequent studies showed that this specific call elicits vigilance in other animal species, including squirrels (Liu and Liang 2022) and mice (Zub et al. 2017), which may represent the predators of the tit nest. Krams et al. (2014) showed higher survival of nests where the female performed the strategy to produce hissing calls compared to nests where female was rather silent. On the contrary, Tilgar and Koosa (2019) showed a very opposite effect, suggesting that in some cases (populations, habitats), this strategy rather draws the attention of the predators to the nest presence.

However, the most spectacular snake mimicry is performed by Eurasian wryneck (*Jynx torquilla*). When captured by a predator, this bird starts twisting its neck and head, simulating snake movements. Additionally, the dark streaks on the head, neck and back of the bird emphasize the appearance of a snake, very likely some venomous viper species (genus *Vipera*; Brejcha 2019; Figure 2). It cannot be disentangled if this behaviour really aims to mimic a snake or just represents a very strange behaviour that discourages the predator from eating the wryneck. There are also no data on the survival of wrynecks compared to other birds. The general appearance of the wryneck is cryptic for sure, mimicking very elaborately the bark or broken branch. The more surprising is its behaviour when captured by a predator. There is no obvious quality, making the wryneck an unprofitable prey compared to other birds, but it is true that most of the species where snake mimicry occurred have strong bills (usually adapted to digging nesting cavities) and may cause some harm to the predators.

Figure 3 – Female killdeer (*Charadrius vociferus*) showing the distraction display, injury feigning, to make the predator focus on herself and chase it away from her nest (Grimes et al. 1936).

Fleeing

Most of bird species are very mobile, capable of flight, run, or diving. All these movements may secure fleeing from the threat, when a predator is encountered or already attacking (Caro 2005). Compared to other groups of vertebrates, birds are therefore the best in the "cut and run" strategy. Before a bird decides to fly away from the threat, the threat has to be revealed, and the bird has to assess that fleeing is the optimal strategy.

Vigilance

Revealing the threat is secured by vigilant behaviour. Each animal is adapted to scan its surroundings for an approaching threat permanently, and birds usually use the visual and acoustic sense to reveal an approaching predator (Fernández-Juricic 2012). As vision is an essential sense for birds, night (when the vision of birds is very limited, and they sleep) is the most challenging time for vigilance and predator detection. Lendrem (1983) showed that mallard ducks (*Anas platyrhynchos*) perform quick eye opening (peeking) when sleeping to scan their surroundings. It is interesting that this behaviour is more common when the bird sleeps further from the water surface and is more vulnerable to predation by terrestrial predators. Moreover, adult males, possessing conspicuous colouration, showed more peeks during sleep than dull females; and more interestingly, the males showed this behaviour more often when possessing this conspicuous plumage than when moulted into the eclipse, cryptic plumage.

There are multiple factors that affect the intensity of vigilance of an individual bird. The most pronounced and studied at the same time is the effect of sociality. One of the main forces pushing birds to form flock and spent time in societies is predatory pressure (Caro 2005). More eyes see more, and thus staying close to other birds endangered by the same predators (not necessarily the same species) bring profit and higher probability of survival (many eyes hypothesis – Pulliam 1973). There are numerous studies showing that the per capita time spent scanning the surrounding is disproportionate to the flock size (see Elgar 1989 for review). Another profit from aggregation is the so-called dilution effect, meaning that the per capita probability of being killed is reduced, once other individuals are in close proximity (Cresswell 1994). However, many other factors affect this relationship.

The most important is the perceived risk. Once the birds have recently encountered a predator (Lendrem 1984), are under regular predation pressure (Hilton et al. 1999) or are further from a cover (Whitfield 2003), their vigilance increases, despite the size of their social group. Another important factor is food availability and quality. Once the birds forage on a rich food source, their willingness to leave it, and thus the intensity of vigilance, decreases (Beauchamp 2009; Sansom 2010). This phenomenon is largely elaborated within the Optimal foraging theory (Bonter et al. 2013).

Various parameters of the bird itself also affect the level of vigilance and the associated flock size. Species body size is supposed to be very important, as larger species are not vulnerable to predation by a large array of predators (Cohen et al. 1993). However, Beauchamp (2010) showed in his phylogenetic analysis that this effect is significant only for vegetarian taxa. Larger vegetarian species have more non-foraging time, which can be devoted to vigilance. Furthermore, the effect of body size is pronounced only in social species, and the effect of flock size is significant only for rather vegetarian taxa. The individuality of each particular bird also importantly affects the level of vigilance it performs (Roche and Brown 2013). Vigilance may be understood as one dimension of personality (Mettke-Hoffman 2022), but experimental evidence shows that it is usually not correlated to other personality dimension like aggression or curiosity (Couchoux and Cresswell 2012).

The flock size is the result of a trade-off of several parameters. As mentioned above, the more individuals are present within the flock, the fewer time each individual devote to vigilant behaviour. On the contrary, this behaviour is rather affected by the number of birds in proximity than the total flock size, which may be scattered on a large area (Wickler 1985). The position of the vigilant individual within the flock is also very important. Individuals at the edge are more vulnerable and thus show higher vigilance than those in the flock centre, the so-called selfish herd hypothesis (Hamilton 1971; Proctor et al. 2006; Beauchamp and Ruxton 2008). However, the larger is the flock size, the more competition and aggression occurs (Metcalfe 1989; Sansom et al. 2008). In addition, information from other flock members (both useful and useless) might represent a disturbance to the vigilant behaviour of each particular bird, resulting in its low and delayed responses to threat - the so-called distracted prey hypothesis (Yee et al. 2013). Therefore, an optimal flock size can be calculated when finding the balance among all significant factors.

Flight Initiation Distance

When studying the willingness of birds to fly away from predators, a simple measure is usually utilized – the flight initiation distance (FID). It is the distance between the approaching predator and the bird at the moment when the bird decides to flee (Cooper and Frederick 2007). The distance can differ substantially between individuals and situations and gives a good proxy for individual threat and risk perception of the focal bird. The factors affecting the FID are usually very similar to what I mentioned generally in previous paragraphs. The social effect is very pronounced here, as one sensitive (hysterical) individual triggers the fleeing in the entire flock. This effect can be seen in shorebird flocks foraging on the seacoast (Mayer et al. 2019).

Recently, there has been a boom in studies focussing on FIDs, especially in response to human intruder. The reason is mainly in the high feasibility of the study, since the researcher simply walks towards birds and records the distance, when they flush. The other reason for the recent focus on this phenomenon is the human impact on nature, which is tested by means of FID. There are numerous studies showing that bird populations living in close proximity to humans decrease their FID, meaning that they got accustomed to disturbances from humans and do not consider humans as a big threat (e.g., Lin et al. 2012; Livezey et al. 2016; Hall et al. 2020). Møller et al. (2015) showed that one of the reasons could be food provisioning to birds, which substantially decreases their FID in urban habitats and that this effect is more pronounced in cold winters, when the food sources provided by people are more important for the birds (Møller et al. 2013). Similar effects can be seen even in relatively poorly urbanized tropical areas, where proximity to humans does not bring any direct profits to birds (Bjørvik et al. 2015; Braimoh et al. 2018). The habituation to human presence is obviously the main factor here. Most interesting is the finding that birds are sensitive even to the speed of cars driving on the streets and roads. Actually, Legagneux and Ducates (2013) showed that bird populations adjust their FIDs to the speed limits on the roads, rather than the speed particular cars are driving. On roads with higher speed limits, birds tend to fly sooner, to avoid collisions. This is one of the most pronounced examples of coevolution of birds and humans in human-dominated habitats. Contrary to these findings, Petrelli et al. (2017) surprisingly showed an increase in FIDs in urban populations of birds (especially ground foraging species). The reason was the urban noise, which prevented the birds (especially those positioned close to the noise sources, in undergrowth) to locate the threat in time.

There are also several characteristics of the focal bird that affect its FID. Møller et al. (2019) showed that conspicuously coloured species show larger FIDs and thus more vigilance than cryptic, dull coloured species. This effect can be seen even in dichromatic species, where colourful males have higher FIDs than dull females (Møller et al. 2016). Møller and Erritzøe (2014) showed that birds with relatively larger eyes show higher FIDs than smaller-eyed species, as they are capable of more accurate predator detection. On the contrary, birds with larger brains showed lower FIDs, because they were able to perform more accurate recognition and threat assessment (Møller and Erritzøe 2014). In a complex study on barn swallows (*Hirundo rustica*), Møller (2014) showed that young and very old individuals show higher FIDs, while individuals of reproductive age are less sensitive to the threat of predation. Furthermore, individuals (especially males) with higher fitness (preferred partners, with high reproductive success) also showed high FIDs. Those individuals showing low FID were shown to die from predation more likely. Of course, the causality in many of these aspects is not obvious, but FID was shown to be related to many life-history traits.

Some studies showed seemingly strange intercontinental differences in FIDs. Weston et al. (2021) showed that resident bird species from Africa had shorter FIDs than resident Australian birds. This difference was not proved in migratory species. Furthermore, longer FIDs were associated with a larger body mass in Australian bird species but not in African. The authors suggest that African birds in general may be more habituated to human presence than Australian species due to two factors: longer coevolution with humans as predators, and more likely higher human densities in Africa compared to Australia. Migratory species do not show this trend, as their FIDs are affected by mismatched experience with humans from multiple locations.

However, the results of a similar study cannot be explained as easily. Møller et al. (2014) showed a significant difference in FIDs between European and Australian birds on one side and North American birds on the other side. The population densities on their studied locations were similar on all three continents, and the evolutionary coexistence of birds and humans also does not differ substantially, at least not in the case of Australia and North America. Their main finding that bird species with higher FIDs face higher population declines was valid only for Europe and Australia, while in North America, the trend was very opposite. The authors did not explain this trend but they point out that declining species usually breed in farmland countryside, suggesting that differences in agriculture trends between the three continents are suspicious of affecting bird FIDs.

The characteristics of the approaching predator also substantially affect the decision of the bird to flee. The starting distance from which the experimenter started to approach the bird, is important to affect the FID. Bird can either continue its original activity (e.g. foraging), flee immediately, or watch the approaching intruder, once the experimenter starts to approach it. When the experimenter starts his experiment too close to the focal bird, the probability to flee earlier significantly increases when compared to situations when the experimenter starts its walk from larger distance (Blumstein 2003). This is of high importance when designing the study testing FID and the starting distance has to be included in the analyses along with the FID (Cooper 2005). The number of approaching intruders may also affect the FID, though only in some species (Geist et al. 2005). The most important may be the gaze of the intruder. Once the approaching human looks toward the focal bird, its FID increases (Bateman and Fleming 2011; Goumas et al. 2020). The speed of the approach plays also significant role, where faster approaches elicit longer FIDs (Cooper 2006).

Furthermore, some nectarivorous birds tend to show lower FIDs in the morning and in the evening as a result of higher energy demands and thus higher time which has to be devoted to foraging (Ferguson et al. 2019). Cooper et al. (2014) also showed that isolated island populations tend to show decreased FID and thus threat perception. This is a result of relaxed predation pressure on islands and may lead to higher vulnerability to introduced predators. This topic will be discussed in detail in the last chapter.

Fleeing vs. nesting

One of the last chapters of this work will focus on situations where there is a conflict in the motivation of the bird in response to a predator. Fleeing strategy is not optimal typically during nesting period, as the nest itself is defenceless, and once the parent decides to perform antipredator behaviour, fleeing makes the nest very vulnerable (Dowling and Bonier 2018). The fleeing parent, which had been incubating before, may even draw the attention to previously unseen nest. Dowling and Bonier (2018) performed a theoretical model showing the effect of multiple factors on the probability of the parent leaving the incubated nest. These factors included characteristics of the parent (reproductive values, detection distance, and cost of lost parental care), the nest (concealment and accessibility) and the approaching predator (detection capability and success of predation). Generally speaking, two extreme strategies are adopted: staying as long as possible or fleeing as early as possible.

There is one specific example when fleeing from the nest is an adaptive strategy securing a higher survival probability of the nest content, injury feigning. This strategy is utilized by several bird species, first described in plovers (Grimes et al. 1936), but occurs also in nighthawks (Tomkins 1942) and passerines (Liu et al. 2023). It usually encompasses pretending broken wings and slow and weird movements, leaving the impression that the parent bird is injured and thus easy to catch (Ristau 2013; Figure 3). The aim of this behaviour is to distract the predator's attention from the nest and draw it to the seemingly harmed parent. The parent bird continues its show and slowly moves away from the nest location. The predator usually follows the parent and thus gets further from the nest. Once the predator is far enough from the nest (or too close to the parent performer), the parent miraculously recovers and flies away. The nest remains uncovered.

Once the nest is abandoned, multiple factors may affect its survival. Besides predation itself, environmental conditions are the most important (Lord et al. 2001). In our study Syrová et al. (2020; Chapter 2), we tested the effect of climate and human disturbance on the willingness of parent Arctic terns (*Sterna paradisaea*) to return to the nest after being flushed. We conducted the experiments following the methodological paradigm, but instead of measuring the FID itself, we focused on the latency of the incubating parent to return to the nest and resume incubation. We conducted this research in extreme environment, in Svalbard, at 78° N latitude, where the temperatures in the nesting period (end of June and beginning of July) are very low (8.28 ± 1.58 °C) and the risk of cooling the abandoned eggs is extreme. Parent birds are usually forced to stay at the nest incubating as long as possible and when flushed, they aim to return as fast as possible (Díaz et al. 2013). In these weather conditions, our aim was to test the effect of habituation to human presence choosing two locations where terns bred. One colony was located within a human settlement, the Svalbard capital Longyearbyen, where the birds encounter people on a daily basis, and it is very common to be flushed when incubating (nests can be located at the very borders of pathways and roads within the town). The other colony was located in an abandoned location on a glacial foreland, where human visitors are very scarce. We showed that the terns breeding in town show high level of habituation, as they returned to the nest very quickly (tens of seconds), while birds from the glacier usually spent several minutes (mean 9 minutes) away from the nest. This finding may contribute to our knowledge on the potential threat because the tourism in locations where animals live in pristine habitats with zero experience with humans can result in lowered breeding success due to disturbing the parents.

Figure 4 – Fork-tailed drongo (*Dicrurus adsimilis*) produces a deceptive alarm call in the moment when meerkat (*Suricatta suricatta*) captured a scorpion, so that meerkat flees and drongo may steal the prey (Flower 2011).

Alarm calls

Apart from fleeing, birds may decide to use active defence against the predator, to stay at its post (at least until the predator attacks) and perform some behaviour increasing the probability of its survival. A very specific feature of antipredator behaviour of birds and mammals is the production of alarm calls. We can only seldom see usage of these signals in other animal groups (Hopkins and Folt 2019; Russell and Bauer 2021), especially because mammals and birds in particular are highly vocal. The basic function of alarm calls is to warn other individuals of the presence (Gill and Bierema 2013). However, the system is much more complex and draws a lot to attention of contemporary science.

Evolution of alarm calls

There is a fundamental discrepancy in understanding the evolution of alarm calls. The calling animal draws the predator's attention to itself and becomes thus very vulnerable to predation. How could this behaviour spread in the very first population, when it was likely that the first alarming individual was immediately eaten (Smith 1965)?

Alarm calls are usually understood as a textbook example of an altruistic behaviour (Charnov and Krebs 1975). In social species population, the usage of alarm calls spreads very quickly, because the benefit from performing it is very high, as it importantly increases the survival of other members of the society (Taylor et al. 1990). At the same time, it is supposed that the usage of the alarm calls is reciprocal (Krams et al. 2006a), that the individual that has been warned before also warns the others when necessary. Under such presumptions the system is working very well.

The important factor that affects the usage of alarm calls is the relationship between the caller and the receiver of the alarm call. Kin selection is understood as the main evolutionary principle securing the spread of the gene for alarm call behaviour in the population (Hollen and Radford 2009). When the very first alarming individual is eaten during his very first performance, its siblings are very likely to also carry the gene for this behaviour. More importantly, siblings were saved by the sacrifice of their alarming brother, which secured the survival of the gene and subsequently its spread in the population. This presumes that alarm calls occur more likely within relatives than nonrelatives. Krams et al. (2006b) showed that great tit (*Parus major*) males produce equal number of alarm calls when present close to their mates as when present close to other flock members. These flock members could not have and could have been related, but all were familiar with the focal male. This suggests that alarm calls are more likely to be presented to those individuals in which the probability of reciprocal alarming in the future is high. Kin selection should not be the main selective force here; reciprocal altruism seems to be more important.

Krams and Krama (2002) also confirmed the importance of the reciprocity of alarm calls in a smart experiment. Migratory Eurasian chaffinch males (*Fringilla coelebs*) made less alarm calls at the beginning of the breeding season, when they were new in the locality, and their social bonds were not well established. As the breeding season advanced and the male became familiar with the locals, his performance of alarm calls increased significantly because he could expect other to save his back in the future. The important thing in this study is that the male also showed similar alarm call intensity irrespective of who is present (not only his mate, but also other chaffinches and even other bird species).

Alarm call types and characteristics

We usually cannot speak about alarm calls as one type of acoustic communication, as there may be multiple alarm calls utilized by the same individual in different situations. Some of the alarm call types are very specific in terms of their acoustic characteristics, and multiple species are selected for using very similar alarms. Jurisevic and Sanderson (1994) identified in 30 Australian bird species two basic types of alarm calls. All species performed broad frequency calls, ranging from 0.6 to 10 kHz, which may be called mobbing calls. These calls were obviously not only at their allies but also to the predator itself. These calls might include harmonic or noisy structures and were generally very loud and harsh. Thus, experiencing these calls is unpleasant for the predator, which is already uncovered, and its probability of a successful hunt is very low. These calls are usually named mobbing calls and often represent a part of attacking the predator (see next chapter; Dutour et al. 2017). The very same calls may also act as recruitment calls, calling other society member for aid in fighting the predator back (Woods et al. 2018).

Second type of calls show usually narrow frequency bandwidth (1-5.5 kHz, Jurisevic and Sanderson 1994) and is addressed exclusively to other members of the society. The function of these calls is to warn others, which usually hide in the cover in response. These calls are usually given when an aerial predator, a raptor, is flying by, which represents an imminent threat. The calls have low frequency bandwidth to spread only on shorter distances (especially in shrubs and forests, where the frequencies are filtered out by the foliage) and thus are heard only by closely positioned allies, why the distant predator cannot hear it (Searcy and Yasukawa 2017). These calls are usually called seet calls and may be quite similar among different species (Gill and Sealy 2003). Due to their ecologically driven similarity, multiple species may also eavesdrop on these calls and respond to other species appropriately (Lawson et al. 2020).

Surprisingly, multiple raptors and owls perform quite badly in hearing the frequencies, which are specific for the seet calls (Jones and Hill 2001). The well-studied system is the communication between small passerines in Europe and their most common raptor predator, the Eurasian sparrowhawk (*Accipiter nisus*). Klump et al. (1986) showed that hearing of the sparrowhawk is quite similar to that of great tits. Both species can effectively detect two types of alarms produced by great tits – the mobbing call given when a sitting sparrowhawk is encountered, and the call given in response to a sparrowhawk flying in close proximity. However, sparrowhawks have a quite poor ability (compared to tits) to hear the seet call given when a sparrowhawk flies in larger distance. This is the situation where the seet call is of high importance to other birds, and they may hide in response. Multiple European passerine species were shown to respond to this call and to produce very similar seet calls (Marler 1955).

A very specific type of alarm is the so-called distress call. This call is produced specifically when the predator already captured the bird and represents the last call for help. The evolution and adaptive function of these calls have remained an enigma for decades (Inglis et al. 1982; Aubin 1991; Conover 1994a). As stated by Davis (1988), a person falling from a 20-floor building does not increase its survival probability when yelling compared to person falling quietly, yet they still yell. The distress calls have quite specific common acoustic characteristics, cover a wide range of frequencies (sound harsh), and are often repetitive. This results in their easy localisation, suggesting that their primary meaning is to make other individuals aware of the caller's presence. The calls are structurally quite similar across families, geographical areas, and bird evolutionary histories (Davis 1988).

The first adaptive function of distress calls is similar to mobbing calls. They are harsh and unpleasant; therefore, they make the struggle with the predator unpleasant to him (Marler 2004). Moreover, the distress call may encode information on the captured bird quality and strength, which may result in winning the fight and fleeing (Laiolo et al. 2004). More importantly, distress calls act as recruitment calls, calling others for help. The distress calls can usually be eavesdropped by other species (Aubin 1991; Conover 1994a,b; Wu et al. 2021), even bigger and stronger than the captured bird. This may result in predator seizing on the attack and fleeing (e.g. a cat chasing away a sparrowhawk that caught a starling).

Alarm calls may carry quite complex information on the predator. As mentioned previously, different alarm call types are used when the predator is perching and you aim to mob it, or when the predator is flying and potentially attacking, and you want to hide. North American titmice and chickadees (Passeriformes, Paridae) developed a very complex system of alarm calls, providing the receiver with detailed information on predator type, behaviour, and distance. Chickadees (especially *Poecile atricapillus* and *P. carolinensis*) are named according to their specific warning consisting of the syllables 'chick' followed by repeated syllable 'dee'. This alarm represents a mobbing call, is triggered by the presence of a perching raptor, and the response of others usually involves further alarm calling (Ficken 1990). Baker and Becker (2002) showed that black-capped chickadees are capable of encoding the distance of the predator in the call. When the predator is closer, the number of 'dee' syllables in a given time increases (they call it faster). Furthermore, Templeton et al. (2005) showed that the total number of 'dee' syllables within the alarm correlates significantly with the size of the predator encountered. Smaller predators, representing a higher level of threat for small passerines, elicit more syllables (3 or 4) than large rather harmless species (2 syllables). The same was shown in tufted titmice (*Baelophus bicolor* – Courter and Ritchison 2010) and Carolina chickadees (Soard and Ritchison 2009).

Further functions of alarm calls

Besides the information about the predator, alarm calls may carry much more information. As mentioned above, the calling individual puts itself at risk, which may be used as an advantage. In some mammal species, namely antelopes, it is notoriously known that some individuals, especially dominant males, tend to perform weird behaviour in the presence of their predators. For example, springboks (*Antidorcas marsupialis*) jump high with their legs stiff and with their dorsal fan of fur opened when encountering a cursorial predator like cheetah (*Acinonyx jubatus*, Bigalke 1972). The jumping individual puts itself at greater risk than when it opts for the strategy to simply run. The jumping individual is believed to show off its strength and qualities. The receiver of this signal is not only the predator, which may seize on the attack, but perhaps more importantly other springbok males and females, and this behaviour is utilised as a trait in sexual selection (West-Eberhard 1983).

In birds, this effect can also apply in general. Wilson et al. (2008) showed that in domestic fowl (*Gallus gallus* f. *domestica*) males are preferred by females when producing more alarm calls. In polygynous fowl, the main male function is to guard foraging hens and their chicks; therefore, the ability to actively warn them about approaching threat is likely to be a sexually preferred trait. However, Wilson and Evans (2008) further suggested that the causality in this relationship may be opposite. The males may rather perform more antipredator behaviour and give more alarm calls as a result of higher mating success, having sired more offspring in the flock.

A very special situation is using the deceptive calls, i.e., giving alarm calls, when there is no threat. There are several situations where this behaviour is adaptive, the foraging being the most common. Møller (1988) was probably the first to show that great tits visiting a winter feeder sometimes produce alarm calls despite no predator being present. The author also showed that these deceptive calls were made more often when tree sparrow (*Passer montanus*) monopolized the feeder. After the alarm, the sparrows flew away and the tits could attend it.

A similar strategy has been shown in fork-tailed drongos (*Dicrurus adsimilis*; Flower 2011; Figure 4). They cooperate with meerkats (*Suricatta suricatta*) during foraging, both gaining profit from mutual vigilance. Meerkats usually scan for ground predators while drongos scan the sky. Both eavesdrop each other's alarms and respond to them accordingly. However, drongos tend to produce false alarm calls also in situations without any threat. In addition, they tend to warn when a meerkat catches a food. Once the meerkats flee in response to the drongo's aerial alarm call, the drongo seizes the opportunity to steal their prey.

Another situation where deceptive calls are used adaptively is in nest defence. Igic et al. (2015) showed that brown thornbills (*Acanthiza pusilla*) can mimic aerial alarm calls of birds. They use this skill during nesting period, when a nest predator, e.g. pied currawongs (*Strepera graculina*), approaches their nest, the parents produce an alarm call, meaning a raptor is approaching. The currawong usually responds by scanning the sky and sometimes even fleeing, which can ensure the survival of the thornbill's nestlings.

I have already mentioned several times that alarm calls are used in inter-species communication. In some cases, like in the case of the seet calls (Jones and Hill 2001), this is simply a result of selective forces, forming the acoustic characteristics of aerial alarms to very similar values. The alarm calls of multiple species are very similar, and the species subsequently respond to them heterospecifically.

Another possibility that results in heterospecific eavesdropping is the formation of mixed flocks of several species. Goodale and Kotagama (2008) showed that some species in these flocks act as sentinels (e.g. greater racket–tailed drongo - *Dicrurus paradiseus*), being most vigilant and giving most alarm calls; others are the leading species determining the foraging and spatial activity (e.g. orange-billed babbler - *Turdoides rufescens*), while some species are freely associated with the flock (e.g. Malabar trogon – *Harpactes fasciatus*). Playback experiments showed that the leading species respond to alarm calls of the sentinel species, while the freely associated species respond quite ambiguously.

However, even nonsocial species often eavesdrop on alarm calls of social species, when associated in some situations. Winter feeders are the most common situation, where multiple species are encountered, and the mutual eavesdropping of alarm calls is of high profit. Templeton and Greene (2007) showed that otherwise territorial nuthatches (*Sitta canadensis*) respond adequately to detailed information on threat included in the alarm calls of black-capped chickadees. Nuthatches were able to respond to these calls even within their territories, when they were not involved in mixed flocks with chickadees, although they very likely learned to eavesdrop on these calls during foraging at winter feeders together with chickadees.

The eavesdropping on alarm calls may be successful even between different vertebrate classes. Communication between birds and mammals is quite common, as they both use similar acoustic channels (Lea et al. 2008; Flower et al. 2014; Hrouzková et al. 2020); however, Vitousek et al. (2007) showed that Galápagos marine iguanas (*Amblyrhynchus cristatus*), uncapable of voice production, can respond to alarms of Galápagos mockingbird (*Nesomimus parvulus*).

Some studies further suggest that eavesdropping on heterospecific alarm calls may occur not only outside the mixed flock, but also outside the area of occurrence. Johnston et al. (2004) showed that Australian apostlebird (*Struthidea cinerea*) responds to alarm calls of North American Carolina wren (*Thryothorus ludovicianus*). The responses to this allopatric alarm were weaker than to the conspecific alarm, though still stronger than responses to control stimulus. The authors discuss the importance of some acoustic characteristics of alarm calls (namely, the dominant frequency) in recognition. Similarly, Randler (2012) showed that European great tits are able to respond to alarm calls of North American black-capped chickadees. The authors discuss an evolutionary conserved type of alarm calls, intelligible to virtually all members of the Paridae family.

In three of our studies, we focused on heterospecific eavesdropping in corvids (Passeriformes, Corvidae). In the study Bílá et al. (2017; Chapter 3), we showed that carrion crows (*Corvus corone*) foraging within zoo enclosures respond equally to conspecific alarms and to alarms of jackdaws (*Coloeus monedula*). The reason for this eavesdropping very likely resides in a very similar spectrum of potential predators (besides wolfes and bears from the zoo, goshawk is regularly attacking both corvids). In addition, both corvids roam the area together, despite the fact that they do not form mixed flocks, they know each other well. In a follow-up study, we presented the alarm call playback of jackdaws to common ravens (*Corvus corax*), again foraging in zoo enclosures (Nácarová et al. 2018a; Chapter 4). Ravens are significantly larger than jackdaws and even crows, and subsequently face much narrower spectrum of predators. Only golden eagles (*Aquila chrysaetos*) and wolves (*Canis lupus*) regularly threaten adult ravens in the Alpes, where our experiments were conducted. Despite not sharing much of the predators, ravens responded to the jackdaw alarm very similarly as to their conspecific alarm. These results left us an impression that a specific acoustic characteristic can be included in alarms of all corvids in a similar way as Randler (2012) showed in tits.

To test this, we presented playbacks of four species to the same population of ravens in the Alps (Davídková et al. 2020; Chapter 5). All species were approximately the same size as the jackdaw but differed significantly in familiarity and relatedness to ravens. Eurasian jay (*Garrulus glandarius*) is a familiar corvid, blue jay (*Cyanocitta cristata*) is an unfamiliar corvid, black-headed gull (*Chroicocephalus ridibundus*) is a familiar non-corvid and the laughing gull (*Leucophaeus atricilla*) is an unfamiliar non-corvid. Our playback experiments showed that both corvids elicited equal responses as the conspecific alarm, while both gulls elicited only very weak responses. This suggests that ravens eavesdrop on alarms of all corvids, even unfamiliar. In future follow-up research, we plan to focus on identifying the acoustic characteristics responsible for this matching.

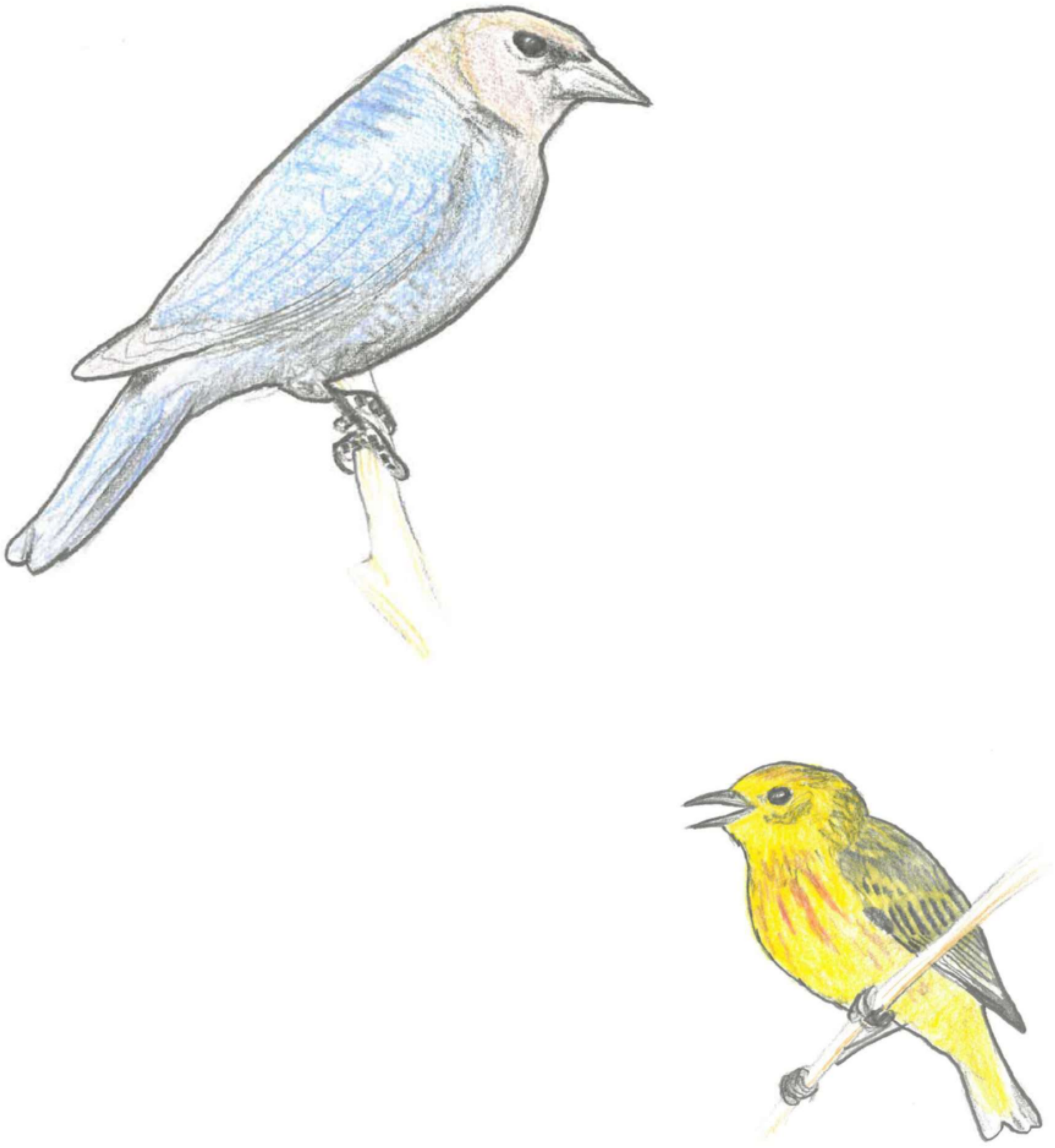

Figure 5 – Yellow warbler (*Setophaga petechia*) mobbing a brood parasite, brown-headed cowbird (*Molothrus ater*) at their nest (Gill and Sealy 1996).

Attack

The extreme form of antipredator behaviour is directly the predator. It is usually referred as mobbing; though, this term includes all active behaviours, attacks, alarming, and approaching, which are utilised in order to let the predator know, it was revealed, make its presence unpleasant for it, and chase it away (Altmann 1956). At first sight this behaviour seems unreasonable, as the prey puts itself to much higher risk than when it tries to flee; however, there are situations when this strategy is profitable and sometimes the only possible (Caro 2005). The most important parameter affecting the decision if to attack the predator or not is the motivation (Andrew 1961). During the clash itself, the attacking individual, no matter how strong and skilled, may win the fight, because its motivation is much stronger than that of the foraging predator (Carlson and Griesser 2022).

Multiple studies agree that the intensity and frequency of occurrence of predation in particular localities affect the willingness of local bird populations to perform mobbing (Sandoval and Wilson 2012; Tilgar and Moks 2015; Dutour et al. 2016). Birds perform mobbing usually only towards predators, which strongly threaten them (Cunha et al. 2017), and usually in time periods when the threat is the strongest (Nijman 2004; Dutour et al. 2019a). Put together, the most extreme strategies are chosen in situation of intensive predation pressure and in situation of no other possibility.

Nest defence

A textbook example of a situation where the predator attack is the best strategy is nest defence. For most birds, the nest content is defenceless (but see chapter Warning signals); therefore, active defence of the nest by the parents importantly increases the nest survival probability (McLean et al. 1986). The decision to engage in nest defence is affected by multiple trade-offs. The defending parents need to account for the threat, the predator represents for the nest content, itself, and other kin, and thus the probability of successful chasing it away.

Shields (1984) showed that barn swallows tend to perform active mobbing when their chicks or mates are nearby. Other flock members (juveniles and nonbreeders) were more passive during the predator presence. Their strategy obviously sufficed for protection for themselves, as the predator would not be able to catch them when flying around; nevertheless, they did not engage in attacking the predator, as their aim was not to chase the predator away. The parents present within the flock have completely different motivation and thus must be much more active.

A more elaborate example can be found in red-backed shrikes. Strnad et al. (2012) showed that the shrike parents perform very vigorous and aggressive defence against common kestrel, which represents rather a threat to their chicks, as it is not a specialized bird hunter. The presence of a mount of Eurasian sparrowhawk at their nest also elicits antipredator behaviour; however, its intensity is much weaker, and parents hesitate to engage in physical attacks on it. The Eurasian sparrowhawk also represents a threat to their chicks; nevertheless, it is also very dangerous to parents, as it is a specialized passerine hunter. Parents must solve the trade-off between protecting their chick and saving one’s own life. The result is to guard the predator, flying towards it, but avoid physical contact to the sparrowhawk.

However, the breeding season also brings other trade-off, which may affect the antipredator behaviour of birds. Bērziņš et al. (2010) showed that males Eurasian chaffinches may suffer higher extrapair mating intrusion during the time they spent chasing predators. Antipredator behaviour is energy and time-consuming, may draw the male attention and presence outside its territory, which is an opportunity for other males to mate with his female. Bērziņš et al. (2010) showed that chaffinches males hesitate to engage in antipredator behaviour during their female fertile period. The active predator attacking occurs much often when the female starts incubating the eggs.

Colonial breeding

During the breeding period, some birds also tend to form societies. The motivation for this behaviour is the same as described in the Vigilance chapter. On one side, aggregated nest may draw more attention of predators (Bellinato and Bogliani 1995); on the other hand, the per nest probability of being depredated decreases with the colony size (Hernández-Matiás et al. 2003). More importantly, colonially breeding birds are more effective in active nest defence. This is why coloniality usually occurs in species with higher capacity to fight back the predator such as gulls (Götmark and Andersson 1984), terns (Erwin 1978), herons (van Vessem and Draulans 1986), raptors (Arroyo et al. 2001), or thrushes (Hogstad 2004).

There are also obvious disadvantages to colonial breeding. One is the competition for food sources (Furness and Birkhead 1984). This is why coloniality occurs most often in seabirds, which often engage also in social foraging, because their food source is locally abundant (small fish – Kitaysky et al. 2000) and their foraging technique often involves cooperative hunting (e.g., pelicans of gannets – Wirtz 1986; Grémillet et al. 2004). Clode (1993) concluded that the sociality and colonial breeding in seabirds evolved as a result of aggregated and locally abundant prey, and the higher level of antipredator behaviour evolved as a necessity of highly vulnerable colonies. Another disadvantage is in competition for breeding sites (Ramos et al. 1997), especially in nest building species (Morandini et al. 2021). The trade-off between all these factors results in the optimal colony size in local situation (Sherley et al. 2014).

A very interesting phenomenon related to social breeding in relation to antipredator behaviour is forming nesting associations between species. We call a protective nesting association a situation when two species of birds breed very closely and show increased breeding success compared to non-associated pairs (Quinn and Ueta 2008). The most common situation is when a rather defenceless species seeks for company of a skilled nest defender, like grebes breeding within gull colonies (Burger 1984), pigeons breeding with kestrels (Bang et al. 2005), or goose breeding at owl nests (Bêty et al. 2001). In the tropics, eusocial hymenopterans like wasps and ants can also act as protective species to small birds (Dejean and Fotso 1995). At first sight, it is very contradictory to seek protection from a potential predator; nevertheless, the survival of protected species is not affected by the protectors and is increased in many examples (Quinn and Ueta 2008).

Sometimes it is very difficult to identify the adaptivity of such an association, as it may simply be a result of equal habitat preferences (Mouton and Martin 2018). For example, red-backed shrikes (*Lanius collurio*) very often breed close to barred warblers (*Curruca nisoria*). Both species inhabit mosaic agriculture land with scattered thorny bushes, especially rose (*Rosa*), hawthorn (*Crataegus*), prunes (*Prunus*) or berries (*Rubus*) – Polak (2012) and Pestka et al. (2018). Their nests are very often found very close even within the same shrub. Both species perform quite elaborate nest defence behaviour (Goławski and Mitrus 2008; Polak 2019), including physical attacks and vocalisation, which together can be highly effective against most predators. There is an evidence shows that red-backed shrikes breeding near the warbler nests experience higher breeding success (Goławski 2007), which suggests that this association is indeed adaptive.

Brood parasites

This entire text refers to the responses of birds to their predators. However, brood parasites represent a very similar threat to birds, especially during the breeding period. Many obligatory interspecific brood parasites destroy the entire clutch of their hosts to secure all the food brought by the foster parents to the parasitic chicks (Petrie and Møller 1991). Therefore, host parents tend to defend their nest from brood parasites in many ways (Soler 2017).

One of the most effective defences is the physical attack of the adults of brood parasite. However, since this behaviour is costly, parents engage in it only when profit outweighs the costs. Gill and Sealy (1996) showed that yellow warblers (*Setophaga petechia*) showed very intense and even specific antipredator behaviour towards the brood parasite, the brown-headed cowbird (*Molothrus ater*; Figure 5). However, compared to nest predator, common grackle (*Quiscalus quiscula*), warbler responses were stronger to cowbirds during the laying phase only, while weaker during the incubation period. This suggests that yellow warblers are able to differentiate the threat, brood parasite, and nest predator represent in particular breeding stages.

Lindholm and Thomas (2000) showed that different populations of reed warblers (*Acrocephalus scirpaceus)* vary in their responses to mounts of common cuckoos, the main European brood parasite. Populations suffering from cuckoo parasitism showed significantly stronger responses to cuckoos compared to populations where cuckoos do not occur. The non-parasited warblers responded to cuckoos similarly to how they respond to sparrowhawks and jays, i.e. they did perform some antipredator behaviour. However, the parasitized populations performed much stronger defensive behaviour against cuckoos.

Another strategy to reduce the costs of antiparasitic behaviour is the division of labour within the pair. Požgayová et al. (2009) showed that males of the great reed warbler (*Acrocephalus arundinaceus*) are more likely to attack adult cuckoo, while females focus on checking the clutch and removing the parasitic egg. The division of labour is since only females incubate the eggs in this passerine species. Consequently, the male has more time to search the surrounding of nest, while the female is primarily responsible for guarding the clutch.

Investment

Of the most prominent parameters affecting the parent decision if to attack the predator during nest defence or not is the amount of investments in it. The phenomenon that the defence of nests containing nestlings is more intense than the defence of nests containing eggs was observed many times in various passerine bird species (e.g. Burhans 2001, Weindinger 2002, Tryjanowski and Goławski 2004, D'Orazio and Neudorf 2008, Redmond et al. 2009). There are several hypotheses that explain the increased intensity of parental nest defence during the nesting period.

The 'reproductive value hypothesis' is based on parental investment theory (sensu Trivers 1985). It assumes that the intensity of nest defence increases during the breeding cycle due to the increasing value of offspring in terms of future gains. The larger value of older juveniles to parents can have various causes: older nestlings have greater chance of reaching maturity (Kleindorfer et al. 1996), they have higher reproductive potential (Redondo 1989), or older nestlings are more valuable in cases when there is a low possibility of re-nesting (Andersson et al. 1980; Montgomerie and Weatherhead 1988). There are alternative names describing this hypothesis, such as the offspring value hypothesis (Halupka 1999), brood-value hypothesis (Onnebrink and Curio 1991, Kleindorfer et al. 1996), or age investment hypotheses (Sproat and Ritchison 1993). This hypothesis predicts continuously increasing parental nest defence by both sexes equally (Brunton 1990).

The 'feedback hypothesis' (McLean and Rhodes 1991) assumes that the intensity of nest defence is directly proportional to the increased interaction between the young and each of the parents. It suggests that there are gender differences in nest defence in species where parents care for the nestlings is unequal. In bird species where the eggs are incubated by the female only, the female is expected to defend the nest more intensively than the male in the incubation period. But after the young hatch, male defence intensity should increase rapidly as both sexes participate in nestling feeding (Pavel and Bureš 2001).

The ‘vulnerability hypothesis’ formed by Skutch (1949) predicts that the intensity of parental nest defence increases dramatically after hatching (Brunton 1990; Onnebrink and Curio 1991) as the nest becomes more conspicuous to predators. Parents visit the nest more regularly, and the nestlings beg for food more intensively and become noisier, which is in sharp contrast to the usually camouflaged female incubating eggs (Redondo and Carranza 1989). The other cause of the sharp increase in nest defence could be the significantly higher profitability (nutritional value) of nestlings compared to eggs for the predators (Harvey and Greenwood 1978).

Our study of the antipredator behaviour of red-backed shrikes (Strnadová et al. 2018; Chapter 6) also focused on the effect of parental investment on the willingness to defend the nest. Only females incubate the eggs in red-backed shrikes, but both parents were shown to engage in nest defence behaviour, sometime with similar intensity (Strnad et al. 2012). We measured the intensity of antipredator behaviour of red-backed shrikes toward four avian predators varying in the threat they represent to eggs, nestlings, and adult shrikes. The mounts were presented at nests in two stages, during incubation and when the nestlings aged 5 to 10 days. We showed that the intensity of guarding the intruder, alarm calling and attacking it rapidly increased in most predators presented. In addition, this increase was the same for both sexes. Therefore, we conclude that the vulnerability hypothesis can be applied to red-backed shrikes. The shrike nests only partially rely on concealment, they can often be quite easily found, there the nests containing chick may become very vulnerable due to their activity. Therefore, parental effort is of high importance at this stage. Shrikes are equipped with tools securing the intruders to be chased away (high aggression in combination of hooked bill tip), the mobbing is thus very effective.

Figure 6 – Above - textile (plush) dummy combining beak and eye of feral pigeon (*Columba livia* f. *domestica*) and body shape and colouration of common kestrel female (*Falco tinnunculus*; Němec et al. 2021).
Below - textile (plush) dummy combining body shape and key features of the Eurasian sparrowhawk (*Accipiter nisus*) with colouration of European robin (*Erithacus rubecula*) presented at the winter feeder (Antonová et al. 2021).

Predator recognition

Features

All of the above mentioned strategies presume that the predator is correctly recognised. Ignoring a threatening species may be lethal, while mobbing a harmless species is a waste of time and energy (Caro 2005). Distinguishing a predatory and nonpredatory species is usually quite easy task for most birds (see Fuchs et al. 2019 for review). The reason is simple, predators usually possess some characteristic features used for processing the prey (curved beaks, talons, teeth, claws), which can be used for recognition by the prey at the same time. There is rich experimental evidence that these features are essential for appropriate recognition of raptors and owls. Curio (1975) showed lower antipredator responses of flycatchers (*Ficedula hypoleuca*) toward pygmy owl (*Glaucidium passerinum*) with prolonged beak, and barn swallows did not attack the mount of the great horned owl (*Bubo virginianus)* with beak artificially removed (Smith and Graves 1978). Similarly, our experiments with red-backed shrikes defending their nest showed that commonly attacked kestrel is not recognised as a threat once its beak is altered with those of a feral pigeon (*Columba livia* f.*domestica*, Němec et al. 2021; Chapter 7; Figure 6) despite all other features such as body size and colouration remain unchanged. Somewhat contradictory results are provided by Beránková et al. (2014) showing that, the presence of the pigeon's beak in the Eurasian sparrowhawk body did not decrease the fear of the sparrowhawk, but the presence of the sparrowhawk's beak in the body of the pigeon increased the fear of the pigeon. It is obvious that the potential to study the importance of particular features on predator recognition is biased by the experimental setup, focal bird motivation, and availability of other features usable for recognition (Fuchs et al. 2019).

Some other features can even be used to recognise particular predators. There is a precondition that the two predators represent different threat for the focal bird, and that the bird performs different antipredator behaviour in the presence of them. For example, conspicuous yellow eyes of Eurasian sparrowhawk very likely identify this particular species (Beránková et al. 2014). It is a specialised small passerine hunter and thus an eminent threat for great tits used in this study. Once its eyes were red colour (pigeon eyes) it elicited only few fear responses. Similarly, conspicuous yellow eyes in common cuckoo are also essential for its appropriate recognition by great reed warblers (Trnka et al. 2012) threatened by this brood parasite.

Anyway, eyes are a very important part of the bird body, and a lot of attention is paid to them. Many birds show the ability to ascertain the threat posed by the predator based on the following of its gaze (Watve et al.2002; Carter et al. 2008). Once the predator is not watching, the prey shows less stress behaviour. Therefore, there is broad evidence that predators are not recognized once their eyes are missing (Nice and Ter Pelkwyk 1941; Scaife 1976; Smith and Graves 1978) and sometimes even only one eye missing suggests that the predator is not threatening (Curio 1975).

The process of recognition is quite complex, and our understanding of all effects that affect it is still quite poor. There are many studies describing the process of object recognition based on the operant conditioning experimental paradigm. These studies show that the capacity of bird brain enables forming well defined categories, of not only relevant object like mates or predators (Patton 2006), but also abstract categories like chairs (e.g., Lazareva et al.2004) or impressionism (Watanabe et al. 1995). The question remains how these mental processes are used in real life in the wild, when you only have a split second to react.

We decided to transfer the task introduced to trained pigeons by Cerella (1986) into the wild. Cerella showed that pigeons can recognize a cartoon figure of Charlie Brown (series Peanuts) based only on the presence of a zig-zag pattern on its shirt. No matter how the body of Charlie was built, as long as the pattern was present, the pigeons treated the stimulus as Charlie. This process is in concordance to the classical ethological understanding of the use of specific features in the recognition of relevant objects in birds. Lack (1939) showed that robins (*Erithacus rubecula*) attack not only robin mounts but also just a bunch of orange breast feathers, suggesting that the breast colouration is the key feature in a rival recognition (called releaser in ethological terminology). Similarly, the red dot on the lower jaw of a gull (*Larus argentatus*) parent triggers begging in the chicks (Tinbergen 1948) and specific raptor flying silhouette triggers hiding in poultry (Lorenz 1939). The simple presence of a characteristic and specific feature obviously suffices to trigger the appropriate behaviour. We tested whether specific features of the raptor features like conspicuous eye, curved beak, or talons with claws can act as such releasers following Cerella's Particulate features theory.

We presented a sparrowhawk that preserved all features but with mixed body parts at a winter feeder and observed the willingness of birds to attend such feeder (Nováková et al. 2017; Chapter 9). We showed that body mutilations did not decrease the threat represented by the unmodified sparrowhawk, and birds hesitated to attend the feeder in the presence of such dummies. This result suggests that the presence of the raptor characteristics is essential and sufficient to recognise a sparrowhawk. In our follow-up study with red-backed shrikes defending their nests (Nováková et al. 2020; Chapter 10), we obtained completely opposite results. Shrikes did not attack a kestrel with a changed body arrangement despite that all kestrel-specific features were still present. This significant discrepancy in results can be explained by the different motivation of the tested birds. Tits visiting a feeder are rather cautious in the presence of these weird dummies, whereas shrikes do not want to risk attacking them. We can conclude that in both studies, the birds were unable to recognize the original raptor and treated the stimuli as something weird, which resulted in cautious behaviour. The sole importance of raptorial features as releasers is therefore unlikely.

Colour

The process of predator recognition may be more detailed, once different predators differ in the threat they possess. A good example is the nest defence situation, where some predators threaten the nest content (eggs or chicks), while others may prey upon the parents (Fuchs et al. 2019). Strnad et al. (2012) showed that red-backed shrikes vigorously attack the common kestrel (*Falco tinnunculus*) moult, while they hesitate to attack the Eurasian sparrowhawk. The reason lies in the diet of these two raptors, kestrel is specialized in eating small rodents (Kečkéšová and Noga 2008), while sparrowhawk is a specialized bird-hunter (Zawadzka and Zawadzki 2001; Bujoczek and Cziach 2009). The shrike parents thus dare to chase the kestrel away from their nest as it may represent some threat to the chicks or fledglings, but has quite low capacity of capturing an adult shrike. Attacking a sparrowhawk is riskier, and the shrikes prefer guarding it. The difference in the behavioural response to these two raptors presumes that the shrikes are capable of distinguishing them. For this purpose, they cannot use specific raptor features as described in the previous chapter, as they both possess it. The Kestrel can be differentiated from the sparrowhawk in terms of quite fine details in their colouration. Sparrowhawk female used in the Strnad's experiment possesses fine dark undulating on the belly, while the female kestrel possesses dark streaks. The general hue of colouration is rustier in kestrel and greyish in sparrowhawk. Nevertheless, for most untrained people, these two raptors are unidentifiable. Shrikes can obviously pay attention to very fine details in colouration, as long as it is crucial for their survival.

In a follow-up study, we focused on the importance of kestrel colouration in its appropriate recognition by red-backed shrikes (Němec et al. 2021; Chapter 7). Using textile dummies, we altered the kestrel colouration in two ways. Once we removed the dark streaking on the belly of female kestrel the intensity of shrike attacks decreased, making the response significantly nondifferent from the response to baseline stimulus (pigeon moult). A similar and even stronger effect could be seen when we exchanged the overall kestrel colouration with a colouration of an unfamiliar south Asian raptor, the black baza (*Aviceda leuphotes*). We were thus able to show that the dark streaking pattern on the kestrel belly may act as the feature essential for its appropriate recognition (releaser sensu Tinbergen).

We also tested the importance of the colouration of a sparrowhawk in its recognition by passerines visiting a winter feeder (Antonová et al. 2022; Chapter 8). The sparrowhawk textile dummy placed at the feeding place significantly decreased the number of arrivals by all observed bird species. This was not true for sparrowhawk dummies with colouration of two harmless species, pigeon and great tit. Birds did not hesitate to visit feeders associated with these two dummies, despite both possessed hawk beak, conspicuous yellow eye, and talons with claws. This was also true for an artificially coloured sparrowhawk (violet-white chequer pattern) used in another study using very similar methods (Veselý et al. 2016). It is obvious that the raptor-specific features do not suffice for a proper sparrowhawk recognition, once its colouration is completely different. However, Veselý et al. (2016) showed that a sparrowhawk with a plain light belly without a typical dark undulating pattern is still perceived as a threat. Similarly, a sparrowhawk coloured as a European robin is perceived as a threat, very likely due to the orange colouration of the breast, typical for male sparrowhawk (Veselý et al. 2016; Antonová et al. 2022; Chapter 8; Figure 6).

These results were confirmed in a study that observed details of the behaviour of great tits in captivity (Beránková et al. 2015). Tits in cage were confronted with the very same textile dummies as presented at the feeders in the above-mentioned studies. The unchanged sparrowhawk elicited a fear response (knee bending, rising feather on the head and alarm calling); while in the presence of the baseline pigeon stimulus, the tits ate the seed and searched the cage bedding. Sparrowhawk coloured as a great tit elicited a similar result as a baseline stimulus, sparrowhawk coloured as a pigeon elicited rather interest (approaching the dummy), while sparrowhawk with robin colouration elicited fear.

Together, these experiments suggest that the colour difference must be significant to prevent proper sparrowhawk recognition, which is in contrast to previously mentioned experiments with shrikes defending their nest (Němec et al. 2021; Chapter 7). The reason for this discrepancy in result lies again, very likely in the motivation of birds visiting the feeder and defending their nest.

Size

Another very important feature of a potentially dangerous species is its size. It may generally be assumed that greater objects represent larger threat. This was shown in shrikes defending their nest against particular species of corvids (Němec and Fuchs 2014). Shrikes vigorously attacked smaller jays and nutckrackers (*Nucifraga caryocatactes*), while hesitated to attack large ravens, crows, and rooks (*Corvus frugilegus*). The authors suggest that the shrikes presume that they will not succeed in chasing the larger species away from the nest. Nevertheless, there is evidence from several bird species attacking much larger object than themselves (e.g., kestrel vs. human – Carrillo and Aparicio 2001; Arctic tern vs. polar bear – Stempniewicz et al. 2014).

In case of raptors, the smaller species tend to prey on birds rather than on mammals, as they usually have to show more acrobatic flying skills (Christie and Ferguson-Lees 2010). Their avian prey subsequently shows more pronounced antipredator behaviour towards smaller species.

Courter and Ritchison (2010) showed that tufted titmice engages in mobbing longer, to include more 'dee' notes in their alarms, and to resume feeding chicks later when confronted with Eastern screech owl (*Megascops asio*) and sharp-shinned hawk (*Accipiter striatus*) rather than Cooper's hawk (*Accipiter cooperi*) and red-tailed hawk (*Buteo jamaicensis*). Screech owl and sharp-shinned hawk weight 100 to 200 grammes, while coopers hawk and red-tailed hawk weigh 300-700 grams and 700-1500 grams respectively. Both small raptors are specialised to small passerines hunting, while the coopers hawk hunts larger birds and the red-tailed hawk prefers mammals. Titmice were obviously able to use the body size as a cue of a potential threat the particular species represented.

The importance of body size in predator recognition can also be seen in studies creating unnaturally sized predators, while keeping all other features (e.g., colouration) unchanged. Beránková et al. (2015) showed that tits in cage show high fear even in the presence of a sparrowhawk that is significantly reduced in size. This result is in concordance with the previous study suggesting that even a smaller predator may represent a threat as long as it is equipped with the claws and curved beak. Antonová et al. (2022; Chapter 8) showed that only the change of body size together with the total change of colouration prevents successful recognition of a sparrowhawk despite the permanent presence of curved beak and claw-shaped talons.

In summary, the recognition process depends strongly on the motivation of the bird and, perhaps more importantly, on the cue provided by the predator. The predator feature, which is most different from the original, is usually used as the main cue for recognition.

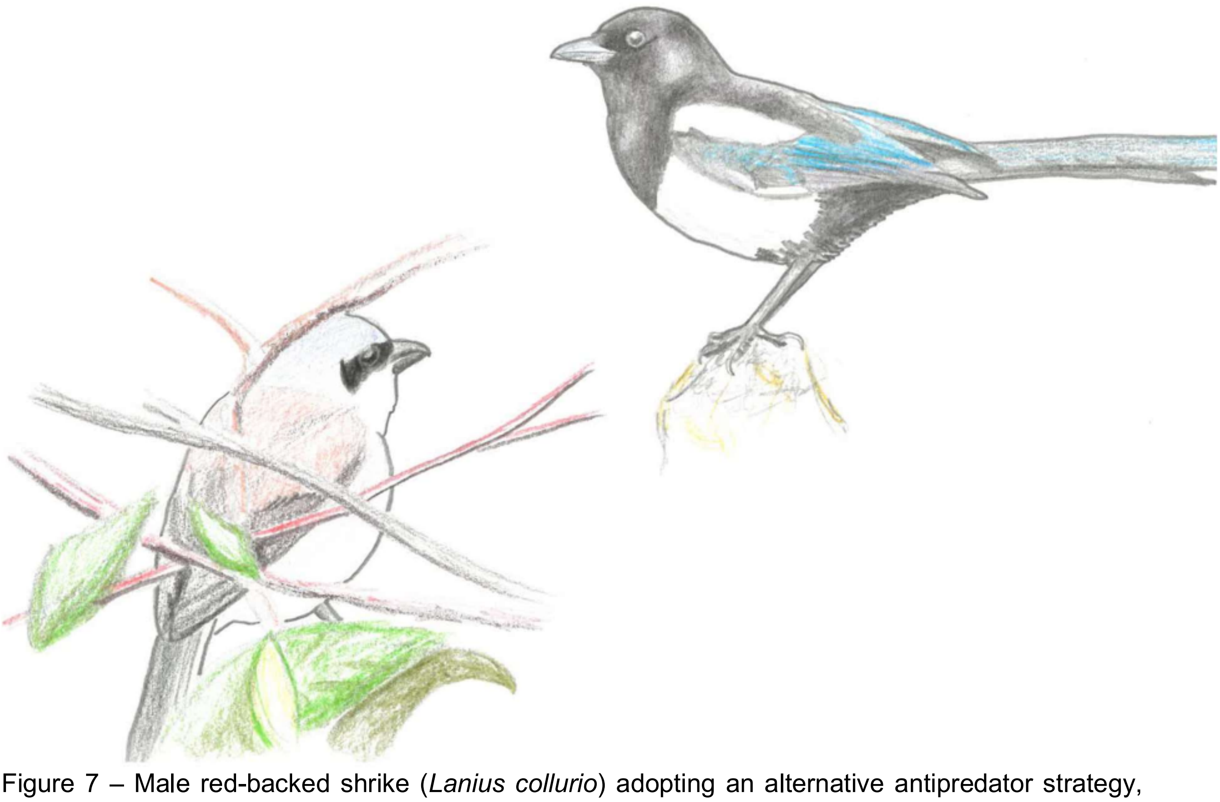

Figure 7 – Male red-backed shrike (*Lanius collurio*) adopting an alternative antipredator strategy, when Eurasian magpie (*Pica pica*) approaches its nest. He stays hidden in the shrub hoping that the magpie won't reveal the nest presence (Strnad et al. 2013).

Alternative strategies

As mentioned at the beginning of this text, there are several possible strategies that may be utilized in purpose of survival in face of the threat of predation. One individual may decide which of them to use according to the actual situation (Lingle and Pellis 2002). The decision process is affected by the individual condition (hunger, health), by the predator condition (threatening the individual or its offspring), and the circumstances (food-predation conflict, nest defence).

The chapter on predator recognition described the ability to respond differently to very similar predators, as long as they differ in the threat level they pose. Birds can switch between active and passive defence depending on the perceived threat for themselves. Our research on red-backed shrikes defending their nests brought more interesting results. Strnad et al. (2013) showed that shrikes vigorously attack Eurasian jay, while they hesitate to attack Eurasian magpie (*Pica pica*). This is particularly strange, since both these corvid species are common nest plunderers (Holyoak 1968). When a magpie appears in the shrikes' nest, the parents stay hidden in the shrubs and even do not produce alarm calls (Figure 7). We tested the hypothesis that shrikes adopt an alternative strategy towards magpies, as they don't feel capable of chasing it away from the nest. This was previously shown, for example, in blackcaps (*Sylvia atricapilla*), which did not want to draw the predator attention to the nest and hoped it would not find it (Leniowski and Węgrzyn 2018).

In a follow-up study (Syrová et al. 2016), we presented a mounted kestrel at shrike nest expecting vigorous attacks. Additionally, there was another mount placed 10 meters from the nest observing the shrikes behaviour. When this bystander was a jay, shrikes vigorously attacked the kestrel. However, when the bystander was a magpie, the attacks towards kestrel diminished. This suggests that shrikes generally hesitate to show active nest defence when magpies are around, likely to avoid drawing attention to the nest.

To be sure of the shrike strategy towards magpies, we set another experiment in which the mount was associated with a playback (Veselý et al. 2022; Chapter 11). Once the mounted magpie was associated with the shrike alarm playback, the shrikes crawled out of their cover in shrubs, started calling, and some even started attacking the magpie. The presence of the nest has already been uncovered, so there was a time for active defence. These experiments confirm that shrikes rely on the nest crypsis as long as possible, even when a threatening predator (kestrel) appears at it, stay hidden and calm, and only when another shrike starts calling and reveals the nest presence, they use active nest defence.

The only unanswered question remains, why do shrikes show this alternative strategy towards magpies and not towards jays. Shrikes respond differently to different corvid species, and Němec and Fuchs (2014) suggest that the main reason resides in the body size of corvid (see above). However, magpie and jay are almost of the same body size. Their diet is very similar, though little carnivore-biased in magpies (Krištín 1988). Both jays and magpies are ecological generalists with highly developed cognitive and mental skills including spatial memory and object permanence, enhancing the searching for hidden bird nests (Clayton and Krebs 1995; Pollok et al. 2000; Zucca et al. 2007; Zinkivskay et al. 2009). The only outstanding difference that possibly affects the shrikes nest defence behaviour is the social system of jays and magpies. Magpies more than other central European corvids tend to form long-lasting families. The magpie fledglings may stay with their parents for several years until their independence (Ekman and Ericson 2006). This is not a cooperative breeding strategy as seen, e.g., in azure magpies (C*yanopica cooki* – Valencia et al. 2003) as the offspring do not participate on breeding, but the magpie families may become large and highly social. In contrast, jay fledglings stay with their parents only until the next breeding season, when they start their own reproduction. Subsequently, a flock (family) of jays can be encountered from summer until winter, while magpies form family flocks throughout the year and even during the breeding season. Such families are highly cooperative, and once one member of the family is chased away from a nest by defending parents, it may return with comrades and search the area until they find the nest. In such a situation, avoiding drawing attention to the nest by active mobbing is an evolutionary stable strategy. In contrast, when one jay is chased away from the nest, it is unlikely that it will return.

These results suggest that birds usually dispose of a set of antipredator strategies and that they pick one according to a very complex decision process that involves multiple factors. Furthermore, choosing various strategies prevents predators from being counter-adapted to preys’ antipredator behaviour, resulting in arms racing and fluctuating balance that is notoriously known in predator-prey interactions (Abrams 2000).

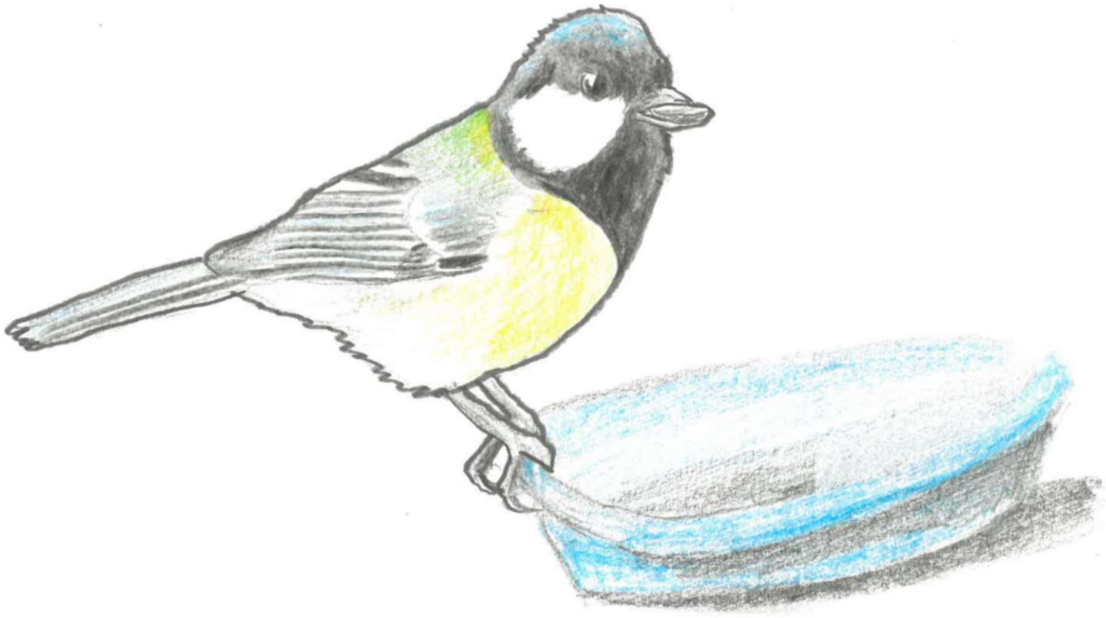

Figure 8 – Great tit (*Parus major*) tested in novel object experiment, presenting it a blue-painted dish with food (Nácarová et al. 2018b).

Personality

In all previous chapters, conclusions of the studies on antipredator behaviour were based on generalised behaviours of multiple individuals. Ecological studies need to show mean or median values in case there is a variability among individual observations. The variability is very likely under natural conditions, though. Every form of animal behaviour is affected by many features of the individual performing the particular behaviour (see, e.g. Pettorelli et al. 2011). This phenomenon is labelled personality (Gosling 2008), behavioural syndrome (Dingemanse et al. 2012), or coping styles (Coppens et al. 2010) and describes behavioural plasticity pronounced in various situations (food searching, predator avoiding, social interactions). Study of this variability is recently very developing and our knowledge of involved evolutionary and ecological processes, as well as utilisation of methods studying this phenomenon and terminology, has been very dynamic recently. Here, I will briefly describe how animal personality affects the antipredator behaviour of birds.

Koolhaas et al. (2010) suggested that individual variability can be described in a very complex way, with multiple dimensions of the individual relating to various situations. One of these situations is confrontation with the risk of predation, and one of the methods how to describe the animal personality is the observation of antipredator behaviour. This is quite surprising at first sight, because the response to a predation threat should be very strict, as any hesitation or incorrect response may be fatal. However, as mentioned previously, there are several alternative strategies that may be utilized in response to the threat of predation. The strategy is used by particular individual may be affected by its general attitude to solving natural problems. In birds, the complex personal multidimensional space is very often simplified into a single axis names shy-bold (Carere and Van Oers 2004), or slow-fast continuum (Verbeek et al., 1994). It always differentiates individuals which quickly and superficially explore new space and objects, and tend to face novel challenges in general from those staying hidden in cover, showing neophobia and fearful responses to novel and threatening stimuli but exploring stimuli in detail. This definition is based on the test used for description of these particular behaviours, but can also be identified in multidimensional approaches using a questionnaire approach to describe natural behaviour (Gartner 2023).

In reference to predators, the bold individuals should be more willing to perform active mobbing, while shy individuals opt often for escape or staying hidden (Carere and Van Oers 2004; López et al. 2005; Azevedo and Young 2006a; Cole and Quinn 2014). In birds, the most common subject of personality-study studies are great tits. Quinn et al. (2012) showed that great tits exploring novel spaces quickly are more willing to visit a winter feeder with a high risk of predation than the birds exploring the space slowly. Similarly, Vrublevska et al. (2015) showed that breeding pairs of great tits showing low level of neophobia toward novel object at their nesting box exhibited stronger antipredator mobbing responses than more neophobic pairs. However, the evidence of this simple correlation is still very poor in birds.

With respect to predator recognition, the predictions are not as simple. Bold (fast) individuals are supposed to be more willing to show active antipredator behaviour; nevertheless, they are also less sensitive to details and their exploring is usually superficial. This might prevent proper predator recognition, and as a result, their antipredator behaviour may be inadequate or ineffective. In contrast, shy and slow individuals are not willing to face the predator, but if they observe it, they are supposed to assess the threat they represent correctly (Sih and Del Giudice 2012).

In our study **Nácarová et al. (2018b; Chapter 12)**, we tested if there is any correlation between exploratory behaviour of great tits and their ability to recognise predator and non-predator dummies with mismatched features. First, the tits underwent four tests used to assess the exploratory syndrome of particular individuals. The novel environment test (Verbeek et al. 1994) introduced the bird in an aviary, the novel food and the novel feeder test tested the bird’s relationship to food and foraging (Verbeek et al. 1994; Figure 8) and the startle test (Van Oers et al. 2004) showed the emotional stability of the individual. Subsequently, the bird was confronted with either a wooden dummy of a sparrowhawk, pigeon, a pigeon with sparrowhawk head and a pigeon with sparrowhawk beak. The dummies were prepared with the purpose of testing the effect of the specific characteristics of the raptor head (conspicuous yellow eyes, curved beak) on the threat assessment by the prey. We were not able to show a strict difference in behaviour of fast and slow explorers to presented dummies. Nevertheless, we were able to show much pronounced behaviour towards particular dummies in slow explorer tits. Fast explorers tended to respond similarly to all presented stimuli, while slow explorers showed more pronounced fear responses toward sparrowhawk than towards any other dummy. These results suggest that slow explorers paid more attention to details in the mismatched dummies and were not confused in the same way as the fast explorers.

To conclude, we have evidence that personality of birds affects not only the choice of antipredator strategy when facing a threatening situation, but also the ability to assess correctly the level of threat represented by the stimulus. As a result, fast as well as slow strategies are present in the population as each provides a fitness advantage. Fast explorers have the ability to defend themselves against predators, while slow explorers avoid themselves to the danger so frivolously.

Figure 9 – Hand-raised young rheas (*Rhea americana*) are introduced a scary person to learn antipredator behaviour before they are released into the wild (Azevedo and Young 2006b).

Learning and forgetting about predators

Despite the rich evidence of predator-prey interactions in birds, very little is known about the process of learning about predators. Generally, the process of learning is quite difficult to imagine, as the individual experience with predator may be fatal. Evidence from fish and amphibians suggests that some part of their antipredator behaviour is innate, though social learning may be involved to improve the ability to respond to predators appropriately (Ferrari et al. 2008; Chivers and Ferrari 2013; Kelley and Magurran 2003; Kelley et al. 2003). In birds, there are only a handful of studies experimentally describing the learning process (see Griffin 2004 for review).

As birds are mainly vocal, their social learning usually works through alarm calling of associated individuals (Vieth et al. 1980). Nevertheless, Conover and Perito (1981) showed that visual cues suffice to teach other birds about the threat. Starlings (*Sturnus vulgaris*) in this study showed more vigilant behaviour once they experienced an eagle owl (*Bubo bubo*) holding a dead starling in their talons. Keen et al. (2020) showed that blue tits were able to learn the association between the demonstration of predator moults and alarm call of an unfamiliar individual. Moreover, they showed that even the most intelligent tis can learn this association from blue tits, even when they do not have personal experience with the predator. Curio et al. (1978) further showed that the acquired responses of blackbirds to predator presentation tended to diminish in time, suggesting that at least in some cases the learning has to be repeated to be reinforced. Dutour et al. (2019b) experimentally showed that learning to fear is easier when the conspecific alarm is presented, compared to the artificial trumpet voice. Nevertheless, the presence of the real threat (owl mount) was not necessary to learn.

The application of understanding the process of learning can be found in endangered species that are reintroduced in the nature. It is notoriously known that isolated bird populations tend to become defenceless, species lose their ability to fly, and sometimes only run (kakapo parrot, *Strigops habroptila*, dodo bird, *Raphus cucullatus*). This usually makes them vulnerable to changes in their environment, especially when invasive species are introduced at their islands (Milberg and Tyrberg 1993). There is evidence that training hand-raised endangered bird species for predator recognition before their release into the wild importantly increases their survival (Maloney and McLean 1995; McLean et al. 1999; van Heezik et al. 1999; Azevedo and Young 2006b; Greggor et al. 2019; Figure 9). The methods of teaching usually do not include any social context, suggesting that birds are able to learn the predator only from the individual experience (being chased by the predator). This is also confirmed by an experimental study on great tits (Kullberg and Lind 2002), suggesting that there is spontaneous maturation of the antipredator behaviour. Even chicks without any social or individual experience with the predatory event were able to show antipredator behaviour once they were old enough.

Generally speaking, it is hard to imagine how birds can forget their antipredator behaviour. Blumstein (2006) assumes that antipredator behaviour and predator recognition must be strongly genetically coded in a similar way to homeobox genes are. The possibility of losing this behaviour is thus very low. If the prey is freed from the pressure by one predator while others remain, the prey will not lose the ability of predator recognition and the defence even against the one predator, which is lost, unless retaining this ability is very costly and fitness decreasing. Carthey and Blumstein (2018) suggest that if the once-lost predator returns, the ability of the prey to defend itself depends on the presence of other predators. In other words, if the prey is used to co-existence with other predators, introducing a novel one is less threatening, and the prey should be able to recognise it and defend itself appropriately. If the population is completely freed from predator pressure, the ability of the prey to defend itself depends on the time (number of generations) since the last encounter with the predator. After a defined number of generations, the ability to respond correctly to predators would probably have diminished (Carthey and Blumstein 2018).

Isolated islands provide an optimal natural laboratory, where the process of forgetting and learning can be seen. Our recent project studies the responses of the Arctic tern population of the Svalbard archipelago to potential threats. The Svalbard population is specific in respect to the array of threats birds encounter, as the archipelago is extremely remote and only a handful of species (including predatory ones) inhabit it. Our already published paper observes the responses of terns to humans (Syrová et al. 2020; Chapter 2), suggesting that the individual experience plays a very important role. People are an uncommon and relatively new threat for most Svalbard terns, so we decided to do a follow-up research testing the antipredator behaviour towards natural predators. Preliminary results (Špička et al. in prep) suggest that terns vigorously attack only the common and familiar threatening species (gull – *Larus marinus*), while equally dangerous common raven is tolerated at their nest, as this species does not occur in Svalbard and therefore is unfamiliar to them. There are no analyses on the timing of isolation of the Svalbard tern population, but as there was still an ice shield some ten thousand years ago and the terns could not breed here, we can presume that the loss of antipredator behaviour can be quite fast. More research is needed to better understand this process.

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Conclusions

Antipredator behaviour is without any doubt one of the main types of behaviours securing higher survival probability and thus higher fitness. Birds are group of animals that performs an outstanding and marvelous array of behavioural strategies that prevent from predation of themselves, their offspring or allies. The essentiality of these strategies enables us to study this highly interesting part of bird live strategies and even in recent times to uncover new, and sometimes quite surprising manifestations of behaviour and their evolutionary importance, limits and conditioning.

The presented habilitation thesis summarizes research of our research group using experimental approach to observe multiple aspects of antipredator behaviour of birds. The most common experimental approach is the confrontation of the tested animal with a stimulus designed to elicit a specific behaviour. The main advantage of this approach is the certainty of collecting interesting data, under the condition the stimulus is properly designed and relevant to tested species.

The tested species we focus on stretch over multiple bird taxa, but especially those species that perform a concise and easy to read response to tested stimuli bring us reasonable results. The red-backed shrike, a passerine species, vigorously defends its territory and especially its nest, which we welcome, as we are easily able to distinguish the motivation and intention of the parents when confronted with predator-derived stimuli. Those stimuli recognized by shrikes as threat to their chicks in the nest are attacked, those stimuli threatening both chicks and parents are guarded (associated with vocalization) and those stimuli evaluated as harmless are ignored (the parents provision their chicks with food).

At the first sight, the raven might not seem like an ideal species to pick for testing antipredator behaviour as it is one of the largest passerine species and has only few natural predators. However, we chose this species for research of responses to alarm calls, as we seized the opportunity to establish a cooperation with a research group under the leadership by Thomas Bugnyar and Kurt Kotrschal. Within their research in Grünau in northern Alpes, they established an easily approachable population of free ranging ravens at the feeding spots within ZOO enclosures. This is a rare setup, which allowed us to observe raven flock responses to threatening stimuli.

Great tit is the third emblematic species of our research, whose higher adaptability to changing conditions allows us to observe its behaviour even in captivity. This gives us the most detailed view in antipredator behaviour, studying such details as effect of individuals features on their ability to recognize a predator. The study of great tits is very promising for the future, and we would like to have a look at the neuro-physiological fundaments of the antipredator behaviour.

It is not surprising that the species we test belong to the most cognitively developed species within the birds. Besides their cognitive performance, they also show high adaptability to the experiments. Choosing multiple species (preferably closely related) allows us to get the first insight into the comparative cognition research, a rapidly developing branch of behavioural research (see e.g. ManyBirds projects - https://themanybirds.com/studies/study-1-neophobia-in-birds).

Even when you choose a well cooperating species, you need to force it to respond to your stimuli. As mentioned in the Introduction part, the most common response to predators is fleeing, which brings you quite few information on the intention, and cognitive process of the observed bird. We complicated the situation of the tested bird by arranging two conflicting motivations – predator risk vs. foraging or nesting. Magpies, terns and shrikes in our studies had to decide if to perform breeding behaviour or deal with the predator. Ravens, tits, sparrows and finches had to decide if to feed on a feeder of flee from the predator present in its proximity. This conflict may result in various behaviours, where the ambivalent behaviours are the most interesting. A shrike hiding in the shrub from a magpie at its nest may be totally confused because it cannot win the fight with the magpie, or on the contrary very astute, aware of its inability to win the fight.

I personally am the most astonished by the fact that within a study of bird antipredator behaviour, such unexpected results like this alternative defence strategy of shrikes against magpies randomly appear. The most important scientific discoveries were often achieved when studying something different, and this gives me a new drive in seldom times when I doubt the importance of my research.

At the very end of this habilitation thesis, I would like to express my gratitude to all factors that did, do and will affect my research. These factors have prepared me moments of surprise, despair, satisfaction, disbelief and joy, and forcing me to keep on running in the race of science.

In České Budějovice on 24th January 2025

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RNDr. Petr Veselý, Ph.D.