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## Predator Detection



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chapter we will first elucidate the different mechanisms enabling animals to differentiate between non-dangerous animals and predators. We will then introduce the different cues animals use to detect the presence and motivational state of predators. Finally, we show how the presence of group members increases a prey's chance to detect predators and how such information about risk is transferred within the group.

## Introduction

The chance of prey to escape predation strongly depends on its ability to detect the predator before getting attacked. In order to avoid potential lethal attacks, prey species need to be constantly vigilant. At the same time, they need to engage in other activities such as feeding and mating. This creates trade-offs between the time invested in antipredator vigilance and all other activities. Optimizing the outcome of such trade-offs requires a precise knowledge of the predator appearance in order to minimize false alarms and at the same time maximize correct identification. Predator recognition can be either inherited or learned, for instance, based on own or public information. To recognize the presence of a predator, prey animals may employ various cues, often involving different modalities such as olfactory, visual, or acoustic information. Moreover, the chances to detect a predator will further increase when several individuals are vigilant. In this

## How to Recognize a Predator?

Many animals, including humans, show inborn fear reactions toward other potentially dangerous animals (Davey 1995). These prey species do not need to learn respective predator cues but intrinsically react with appropriate behaviors after detecting the predator. In contrast, others need to learn about the potential danger of unknown animals, often through repeated experiences with predators, either by direct contact or by observing others (Brown et al. 2011). Additionally, inborn predator recognition might be fine-tuned by further learning particular predator phenotypes. Whether innate recognition or learning is involved in predator detection often depends on the ecology of the respective species (Brown et al. 2011). Learning to detect predators is more beneficial when the risk of encountering a given predator is variable on a spatial and temporal scale (Brown et al. 2011). On the contrary, genetically determined predator detection is beneficial in

species that face always the same predators (Brown et al. 2011). Interestingly, many prey animals are able to generalize learned predator recognition to other predatory species, which are similar in appearance and smell. This enables prey to reduce the costs of learning to detect new predators because potentially dangerous encounters can be reduced (Brown et al. 2011).

### Genetically Determined Recognition

Many animals own an inherent, genetically fixed concept of the phenotypic appearance of a predator. Such concept can be very coarse, following simple rules of thumb (e.g., *avoid all animals that are bigger than you are*). However, such coarse recognition templates will readily lead to false alarms, which might prevent individuals from foraging or mating and which will lead to constantly having acute stress responses. It is thus not surprising that in many cases, more fine-tuned inherent recognition templates have evolved. The cichlid fish *Neolamprologus pulcher*, for example, is able to spontaneously differentiate between predatory and herbivorous cichlids that are of similar size (Fischer et al. 2014). It, thus, does not follow the rule “*all large fish are dangerous*” but rather uses more subtle differences in the respective fish’s appearance. Importantly, these behaviors were observed in laboratory-reared fish that had never experienced heterospecifics before, indicating that the fine-tuned recognition template is inherent and not learned (Fischer et al. 2014).

### Nongenetically Determined Recognition

Information about the predatory environment can also be nongenetically transmitted between generations from parents to offspring. Mothers are the key interface between the current environment and future generations. So-called non-genetic maternal effects are common in many species and lead to responses in offspring, which might not necessarily be adaptive. When offspring responses are adaptive, mothers use cues from the current environment to prepare their offspring for the potential future environment. For example, in yellow-legged gulls (*Larus michahellis*), offspring from mothers that were exposed to

predators show an increased antipredator response compared to offspring from mothers that were not exposed to predators (Morales et al. 2018). Adaptive responses are particularly beneficial when environmental conditions of mothers match the environmental conditions experienced by their offspring. However, maternal exposure to predators can also have detrimental effects on offspring behaviors and survival. For example, in three-spined stickleback (*Gasterosteus aculeatus*), offspring from mothers exposed to predators show less efficient antipredator behaviors compared to offspring from mothers that did not experience predators (McGhee et al. 2012). In such cases mothers may experience acute stress while exposed to predators and consequently lay eggs of lower quality, resulting in less developed and less adapted offspring.

### Learned Recognition

Some prey species either don’t possess a genetically determined template to recognize predators or do not show appropriate responses. In the first case, animals need to learn to detect predators in order to assess potential danger. For these animals it is crucial to gather information about the identity of potential predators either through personal or social experiences. Gathering personal information can be very costly as animals that misjudge the prevailing danger have the considerable risk of getting injured or killed while learning. Here, employing the knowledge of other, more experienced individuals can be beneficial. Social information about predators are transmitted from one individual to another, for example, through alarm calls, chemical warning substances, or sentinel behavior. Observing experienced individuals interacting with predators is also an effective way to gain information about successfully interacting or evading predators. For example, juvenile Siberian jays (*Perisoreus infaustus*) start mobbing predators only after observing a knowledgeable individual mobbing the same predator species. This information is crucial for juveniles as it improves the survival during the first winter, when they interact the first time with predators (Griesser and Suzuki 2017).

## Sensory Ecology of Predator Detection

Prey animals use a broad range of different cues to detect predators. The used sensory modality strongly depends on the species ecology. For example, visual cues play an important role in terrestrial, diurnal animals. However, when vision is hampered, for example, in nocturnal or aquatic species, other modalities become more important. Finally, cues from different modalities are usually not used in isolation. Instead, prey animals gather multimodal information to optimize their chances to detect a predator as early as possible. In the following we introduce how animals use different modalities to detect predators.

### Visual Detection

Vision is an accurate and reliable sensory modality to detect predators. Visual cues are transmitted fast and can be perceived over long distances. Accordingly, many diurnal animals rely on visual cues when prospecting potential danger. Here, a large field of view without head movements is beneficial. Therefore, the eyes of most mammal prey species, like antelopes, mice, and rabbits, are located far apart from each other on opposite sides of the head. This increases the field of view and allows them to scan a huge space range on both sides of their body. Similar adaptations occur in many fishes or birds. Woodcocks (*Scolopax rusticola*), for example, have a nearly panoramic view of 359° in the horizontal plane (Cronin 2005). However, this increase comes at the cost of reduced perception of depth and a hampered ability to see in 3D.

As an adaptation to the good eyesight of many prey species, some predators have evolved cryptic coloration, making it difficult for prey to spot them. Many sharks, for example, show different color patterns on their dorsal and ventral body side. While the dorsal part is dark, the ventral part is often lighter. Seen from above, the dark color camouflages the shark against the dark deeper water below, while from below the pale color conceals the shark against the lighter water surface (*Countershading*, Marshall and Johnsen 2011).

Despite the benefits of vision to transfer information fast and over a long distance, vision is not

always the best modality for predator detection, as the transmission of visual cues is easily hampered. For example, visual cues are blocked in highly structured habitats like forests. Furthermore, visual perception is limited during the night. Finally, vision is strongly reduced in aquatic systems due to high turbidity or the lack of light in deeper water bodies. Under such conditions other modalities gain importance.

### Chemical Detection

Prey animals use a variety of chemical cues to detect predators. Such chemical cues can be produced by predators, conspecifics, or other prey animals (Hettyey et al. 2015). Predator-derived cues are mostly released unintentionally. As they reveal the predator's presence to the prey, they are indeed disadvantageous for the producer, though they might have functions, for example, in intraspecific communication. Furthermore, smell might arise from the integument of the predator or from its digestive tract. Finally, feces or urine might contain parts of the predators' gut flora, as well as metabolites of digested prey items (Hettyey et al. 2015). Prey animals readily use such olfactory information to detect the presence of a predator and adjust their behavior accordingly. For example, small freshwater crustaceans (*Gammarus pulex*) avoid the smell of predatory fishes and form social aggregation, even if the predators were not fed on gammarids before (Baldauf et al. 2007; Kullmann et al. 2008). Similarly, many snake species show characteristic defensive behaviors to the odors of snake-eating snakes, and rats respond with characteristic defense and fear responses toward cat odors (Dielenberg and McGregor 2001). Other predator defense responses might be long-lasting or even irreversible, such as morphological adaptations. For example, many tadpoles develop stronger tails in the presence of a predator's olfactory cues, allowing them to escape faster (Hettyey et al. 2015).

Chemical information about the risk of predation can also be prey-borne and produced when animals are stressed, attacked, captured, or digested (Hettyey et al. 2015). Such chemical cues might be passively released from injured prey tissue and serve others as information. This

phenomenon has been already described by Karl von Frisch (1942), one of the founders of modern ethology. He found that European minnows (*Phoxinus phoxinus*) show an intense fear response when exposed to conspecific skin extract imitating a predation event and coined the term *Schreckstoff* for such damage-release cues. While some of these damage-released cues are passive by-products of the predatory act itself, others have evolved to act as active signals for warning other individuals. These signals are costly to produce, and do not directly benefit the sender, which is why they are a puzzle in the evolution of the communication of risk. One solution is that damage-release signals might have evolved mainly in species that live together with close kin. Warning relatives may hence lead to indirect fitness benefits for the sender. For example, sea anemones (*Anthopleura elegantissima*) live in colonies of genetically identical individuals. Injured individuals release a pheromone that induces a typical self-defense response in neighboring individuals, which retract and protect their tentacles (Howe and Sheik 1975). Similarly, honeybee workers (*Apis mellifera*) attack predators threatening their colony by stinging. Stinging is a suicidal act because the sting together with the whole abdomen stays attached to the intruder. At the same time, the sting continues to simultaneously release venom inside the victim and a pheromone to the outside to attract more worker bees (Breed et al. 2004).

### Acoustic Detection

Acoustic cues are important means to detect predators, especially in habitats with low visibility (Hettena et al. 2014). To discover a predator by acoustic cues, many animals have evolved distinguished hearing abilities to accurately locate sounds. Many herbivore mammals like antelopes, deer, horses, and rabbits are able to move their ears in almost 180°, increasing their acoustic perception and allowing them to accurately locate the origin of sound. Detecting acoustic predatory cues becomes especially important, when predators themselves employ sound waves to find their prey. This is the case in many bats that use echolocation to spot and catch prey insects. These

nocturnal hunters emit high-frequency calls and listen to the echoes to determine the size and location of their target (Jones et al. 2016). As a counter adaptation, however, many moths and other nocturnal insects can detect the echolocation calls of bats, allowing them to initiate evasive flight maneuvers. A peculiar defense behavior is shown by dogbane tiger moths, *Cycnia tenera*, which produce high-frequency clicks that disturb the echolocation function of the approaching bat (Jones et al. 2016). Finally, acoustic cues also serve as signals that transfer information about an approaching predator from one prey individual to another. Prominent examples are warning calls in many bird species but also in alpine marmots or cooperatively breeding meerkats (Caro 2005).

### Mechanical Detection

Some animals are able to detect approaching predators using mechanical cues. For example, tree-living insects use leaf vibrations to detect the presence of predators (Yack 2016). Thereby, many insects make use of specialized cells arranged in body parts close to the substrate such as legs or antenna (Yack 2016). Furthermore, vibrational signals actively emitted by prey after detecting a predator also act as an antipredator response to deter the attacker and warn conspecifics.

Fishes, as well as some amphibians and cephalopods, possess a special organ that consists of neuromasts located around the head and along the lateral part of the body. In fishes, these neuromasts are arranged in a long line along the flank, which gives the organ the name *lateral line* (Janssen 2004). The neuromasts are sensitive to pressure changes and hence enable the animal to detect fluctuations in water pressure caused by the movement of con- or heterospecifics. As such, they enable the animal to detect the swimming activity of predators. The lateral line system further plays a crucial role in orientation and shoaling behavior, which is the most common antipredator behavior in fishes and tadpoles (Janssen 2004).

### Multimodal Predator Detection

Each of the previously described sensory systems has its own set of benefits and limitations. For

example, chemical cues are particularly useful for gaining information about a predator's presence but are not as reliable for gaining information about the exact location of the predator. Here, visual cues can be more reliable. Still, visual cues have their limits when predators are camouflaged or when light conditions are bad. Acoustic cues might easily be overheard because of other background noises. Thus, in order to gain optimal information about the potential presence of a predator, animals commonly use multiple sensory modalities at the same time (Munoz and Blumstein 2012). For example, mosquitofish (*Gambusia affinis*) uses visual and chemical cues to avoid predators, while each cue in isolation would be sufficient to induce the correct anti-predator response. Nevertheless, if both types of cues are available at the same time, these fish show an increased antipredator response where individuals almost double their distance from the predator (Smith and Belk 2001). Cues perceived in different sensory modalities can further transfer different information (Partan and Marler 2005). For example, animals might detect the general presence of a predator by recognizing its smell. Still, they would lack information about the acute risk, which might be provided by additional visual information about the approaching speed. Thus in this case, olfactory information might lead to an increased level of vigilance, while the visual cue will induce a fast flight response.

The use of multimodal cues in predator detection is not only important to increase detection accuracy but also allows to detect predators under fluctuating environmental conditions. For example, changing weather conditions limits the relative importance of single cues (Caro 2005; Saunders et al. 2013). The need to base decisions on multiple cues is not restricted to terrestrial environments but also of importance to aquatic animals. For example, seasonal rainfall will lead to a temporal reduction in visibility in the African Rift Valley Lake Tanganyika, caused by algae blooms and floating sediment. In this environment, the highly social cichlid fish *N. pulcher* uses olfactory and visual cues to detect predators, and both cues lead to comparable antipredator responses (Fischer et al. 2017).

In recent years, most natural habitats faced drastic human-induced changes, including altered visibility due to algal blooms caused by eutrophication and soil import, increased noise levels, changes in water chemistry, and chemical pollution (Hildebrand 2009; Barber et al. 2010). These changes have strong impacts on predator detection abilities in many species. For example, traffic noise impacts the production and perception of alarm calls in great tits (Templeton et al. 2016) and impacts the use of alarm calls in dwarf mongooses (Morris-Drake et al. 2017). Using different modalities might allow animals to increase their success in predator detection in such modified environments. Still, the relative importance of different sensory modalities governing predator-prey interactions in changing environments is mostly unknown (Hale et al. 2017). Human-induced perturbations might not only influence predator detection in one modality but might influence other sensory systems as well. For example, traffic noise on land and underwater hampers the recognition of chemical cues associated with predation risk in fish and mammals (Morris-Drake et al. 2016; Ferrari et al. 2018).

### **Predator Detection as a Driving Force in Social Evolution**

Perfect protection from predators requires constant vigilance. However, animals also need to invest time in feeding or mating, and these activities are reduced while being vigilant. Solving the problem of allocating time between being vigilant and other activities is challenging, and diverse strategies exist, which are dependent on the social organization. Most solitary animals increase vigilance only during dangerous situations and decrease vigilance in safe situations. This requires individuals to constantly assess the local predation risk, which has been termed the threat-sensitive assessment of risk (Brown et al. 2011; Fischer et al. 2017) and is an important way to reduce costs of antipredator behaviors. However, this requires animals to possess a reliable estimate of the local predation risk, which might not always be possible. Other animals live in groups,

where vigilance can, for instance, be split among group members.

### Predator Detection and Sociality

The risk of predation is probably the strongest force leading to group living in animals. One benefit of living in groups is that the chances of at least one individual detecting the predator and alarm the rest of the group increases with increasing group size (Pulliam 1973). This *many eyes effect* exists in many animal species (Davies et al. 2012). Such detection benefits do not necessarily require more *eyes* as it is nicely illustrated by a colonial social spider (*Metepeira incrassata*). Here individuals join together and build large communal webs. Individuals within these colonies gain antipredator benefits by detecting mechanical vibrations transmitted through the communal web when other colony members are under risk (Uetz et al. 2002).

An individual in a group might not only benefit from an earlier predator detection but might further share the costs of being vigilant by alternating scanning behaviors between group members. As a consequence, the vigilance of the whole group will be increased, while each individual has to be less vigilant compared to solitary conspecifics (Beauchamp 2015). Such beneficial effects of group vigilance can be further enhanced, if group members actively warn others, for instance, by alarm calls. The information content of such alarm calls can be highly fine-tuned. For example, meerkats (*Suricata suricatta*) emit different alarm calls depending on whether the predator is a bird of prey or a snake (Manser 2001). Furthermore, the calls might indicate different grades of urgency. This enables other group members to show the respective adequate antipredator behaviors.

While alarm calls are beneficial for recipients, producing such calls is costly in terms of time and energy spent. Furthermore, the caller might increase its risk of being spotted and attacked. Still, emitting alarm calls might lead to direct and indirect benefits for the producer as well as for the receivers within the group, which is why alarm calls are widespread (Caro 2005). For example, alarm calls in the common redshank

(*Tringa totanus*) cause the entire flock to fly off together, which might confuse the predator (Will Cresswell 1994), and directly increase the survival chances of the caller. Furthermore, the caller will gain indirect fitness benefits when warning relatives, which therefore are more likely to produce offspring sharing genes with the caller. Belding's ground squirrels (*Urocitellus beldingi*), for example, emit alarm calls more readily when accompanied by relatives (Jill 2010). The most pronounced forms of shared vigilance can be found in highly social species, such as cooperatively breeding meerkats. Here, the sharing of vigilance between group members has evolved into a sentinel system where some individuals entirely stop foraging for a specific period and watch out for predators to alarm the rest of the group. Here, the individual nutritional state is a major predictor of sentinel activity with hungry individuals resuming to forage and saturated individuals acting as sentinels (Clutton-Brock et al. 1999).

Finally, alarm calls are not restricted to within-species communication. Indeed, many birds and mammals react to alarm calls of other species, especially when both species share the same predators (Meise et al. 2018). For example, dwarf mongooses (*Helogale parvula*) respond to alarm calls of tree squirrels, with which they share predators, but not to alarm calls of baboons, which are vulnerable to different predators (Morris-Drake et al. 2017).

### Reliability and Cheating

In contrast to using own information, obtaining information about predation risk from others poses the risk of being unreliable and inaccurate. This is, for example, the case when predators differ in threat depending on species, size, sex, or age of the prey individual. Consequently, animals that have the choice between different sources of information shall incorporate the reliability of the respective sources in their antipredator response. For example, zenaida doves (*Zenaida aurita*) show a higher level of vigilance during playback experiments using calls from red-tailed hawk (*Buteo jamaicensis*) compared to playbacks of conspecifics' wing whistles, which

serve as alarm cue (Barrera et al. 2011). The reliability of social information is also dependent on the identity of the sender. For example, dwarf mongooses reduce their vigilance more strongly following warnings of experienced dominant individuals compared to subordinate and more inexperienced individuals (Kern et al. 2016).

A further source of unreliability is the probability of deceptive attempts by the caller. Fork-tailed drongos (*Dicrurus adsimilis*), for example, mimic alarm calls of other species when they handle food. Target species like meerkats and pied babblers (*Turdoides bicolor*) readily react with a fleeing response, abandoning their food, which is then taken by the drongo (Flower 2011).

## Conclusion

To survive in risky environments, prey animals need to detect predators before being attacked. Some prey species have a genetic predisposition to detect and recognize predators, whereas others need to learn appropriate responses by direct or indirect experiences. Visual, olfactory, chemical, acoustic, and mechanical cues are used in isolation or in combination to detect predators and to communicate predation risk to others. Finally, the benefits of increased predator detection and defense are probably one of the main driving forces in the evolution of animal sociality.

## Cross-References

- ▶ [Aposematism](#)
- ▶ [Benefits of Group Living](#)
- ▶ [Cryptic Coloration](#)
- ▶ [Escape Response](#)
- ▶ [Mullerian Mimicry](#)
- ▶ [Predation Risk](#)
- ▶ [Vigilance](#)

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