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Predator Defense

Bibiana Rojas and Emily Burdfield-Steel
Centre of Excellence in Biological Interactions, Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland

Synonyms

Antipredator strategies

Definition

A set of traits and mechanisms by which prey avoid being detected, recognized, subjugated, or ultimately consumed by their predators.

Introduction

Most organisms are at risk from predation. For this reason, many species have evolved certain traits or strategies that confer different degrees of protection. Such traits and strategies can be physical (morphological), chemical, or behavioral and can be exhibited by both individuals and groups. As a result, predator defenses are very diverse and are widespread across the animal kingdom. However, several key strategies have evolved separately in multiple groups of animals.

In order to classify and understand these defenses, we must first understand how animals fall prey to others. The process of predation can be thought of as a sequence, beginning with the detection of the prey by a potential predator, followed by its recognition as a suitable prey item, its subjugation and, finally, its consumption (Endler 1991). Animal defenses can intercept and disrupt this sequence at any stage, and many species possess defenses that act on several stages. From the prey's perspective, defenses that interrupt the process at the earliest stages, i.e., before the subjugation stage, may be particularly valuable as they reduce the opportunity for injury or energy loss from fighting or escaping.

Preventing Encounter and Detection: *Avoiding the Issue*

The first line of animal defenses includes those that prevent encounter or detection. Encounters can be avoided by prey being in low densities, so as to reduce the per capita probability of being found by a predator. Alternatively, prey may try to create spatiotemporal separation from predators, by either avoiding areas inhabited by potential predators or using those areas at different times than the predators. Prey can also use hiding shelters (Fig. 1a) at known locations within their home ranges and may remember and use set escape routes. One extreme example comes from the Chuckwalla (*Sauromalus obesus*), a lizard that

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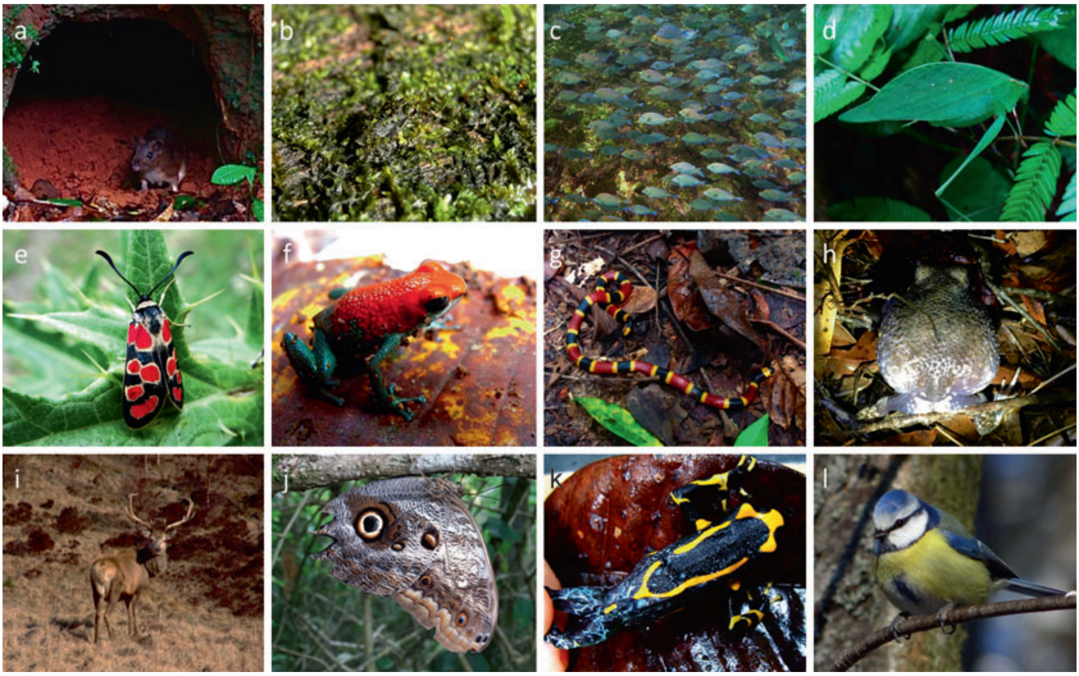

Predator Defense, Fig. 1 Examples of animal defenses against predators. (**a**) some animals use shelters or refuges within their home range; (**b**) many frog species avoid detection by displaying color patterns that match those of their background; (**c**) fish schools are an example of how some organisms move in groups to minimize the per capita risk of predation; (**d**) insects such as katydids avoid recognition by resembling inanimate objects, for example, leaves; (e-g), aposematic organisms display distinct color patterns that predators learn to associate with their unprofitability; (**e**) Burnet moths (family Zygaenidae) sequester cyanide compounds from their food plants, but are also capable to produce them de novo; (**f**) the granular poison frog (Oophaga granulifera) uses its vivid colors to warn predators about its possession of toxic skin secretions; (**g**) coral snakes (genus *Micrurus*) serve as models to some harmless colubrid snakes, which gain protection from predators by mimicking the coral snakes' color patterns; (**h**) body inflation helps animals appear larger than they actually are and discourage attacks from predators, or can make subjugation more difficult; (**i**) weapons such as deer antlers may be used for purposes other than protection from predators, for example, during male-male competition; (**j**) eyespots in the wings of butterflies are thought to mimic vertebrate eyes and thus can startle predators, making them hesitate to attack; (**k**) the defensive secretions of poison frogs contain mostly alkaloids that act as neurotoxins; (**l**) blue tits (*Cyanestes caeruleus*), among other species of Paridae, produce mobbing calls when predators are nearby (Photos taken by B. Rojas)

hides in rock crevices when threatened, and then inflates itself with air so it cannot be pulled out (Deban et al. 1994).

Once the prey encounters a predator, then there are behavioral and morphological mechanisms aimed to hinder detection. Rabbits can, for example, "freeze" in response to an unexpected noise. Immobility can also be employed by anuran larvae in the presence of a larger carnivore tadpole, such as an odonate naiad or a water bug. This strategy works because many predators are motion-oriented and, thus, fail to detect static, unmoving, prey. This behavior can be coupled to traits such as cryptic coloration (see below), which act in concert to make it harder for predators to detect prey. Prey can also aggregate, for example, through synchronized hatching (insects, amphibians, reptiles), or the formation of schools (fish; Fig. 1b) or flocks (birds) whereby the per capita risk of predation is very low; this phenomenon is known as the dilution effect. One famous example comes from periodical cicadas: these true bugs, from the genus *Magicicada*, have 13- or 17-year life cycles. They spend the majority of their life feeding underground as larvae, and once every 13 or 17 years emerge simultaneously as adults to mate and lay eggs. The sheer number of cicadas during this emergence means that predators quickly become satiated and cannot eat more than a small proportion of the population (Williams and Simon 1995).

Among the morphological mechanisms to thwart detection, those related to prey coloration are probably the most well known. Cryptic prey, for example, resemble the background on which they rest (Fig. 1c), or exhibit disruptive coloration, which breaks the prey's body outline (Stevens and Merilaita 2009). This can hide an animal's distinctive shape and make it harder to distinguish. Because in most cases predators form a search image to look for prey, research has shown that cryptic prey benefit from being polymorphic. That is, from exhibiting variable color patterns within a population to minimize per capita predation risk, as this makes more difficult for predators to create an efficient search image and stick to it. Other forms of color-mediated concealment are *transparency* and *countershading*, both of which are commonly seen in marine organisms. Transparency is widespread in pelagic (i.e., open water) species, in particular among small, free living organisms such as Ctenophora (or comb jellies), some Cnidaria (a group which includes jellyfish, sea pens, and hydra), and the larval stages of many crustaceans (Johnsen 2001). In countershading, animals have darker coloration on the top side of their bodies and lighter coloration underneath. As light usually hits objects from above, making them appear lighter on top and darker underneath, this form of coloration can mask this effect, making the animal's body appear less three dimensional, and therefore harder to spot. In particular, countershading has been suggested to function in marine animals such as whales, sharks, and fish, as when viewed from above the darker coloration on the dorsal (top) side of the both will blend into the darker-appearing waters below. In contrast, a lighter ventral (underneath) side will stand out less against the light filtering down through the water when viewed from below. While a great many species show this form of coloration, experimental evidence for its effectiveness against predators is limited, and it has been suggested that other factors, such as protection from harmful UV rays or thermoregulation, may also explain this pattern (Rowland 2009).

Preventing or Aiding Recognition: *It Is Not What You Think*

Once the prey has been detected, the predator needs to recognize it as an edible item worth attacking. At this stage, animals may benefit from imitating inanimate objects in their surroundings, a phenomenon termed *masquerade*. Stick insects, for instance, get their name from their extraordinary resemblance to sticks and twigs, praying mantises and some katydids also benefit from resembling green leaves (Fig. 1d), whereas some tropical toads look a lot like fallen leaves in the leaf litter, and the larvae of some lepidopterans look like bird droppings. Masquerade is often considered to fall between mimicry and crypsis, as it is often difficult to assess if a predator has truly misidentified the prey as an object or has simply failed to notice it. However, true masquerade should remain effective across many different backgrounds (Skelhorn et al. 2010). In nature it is likely that many species use a combination of the two, for example, by closely matching the most common items in their environment.

Aposematism is another strategy related to prey recognition but, in this case, prey recognition is enhanced rather than hindered. Aposematic animals (Fig. 1e, f, g, k) employ warning signals, often conspicuous color markings, to inform predators about the possession of secondary defenses (chemical, physical, or behavioral), which render the prey unprofitable (Poulton 1890). Predators have an unpleasant experience upon attack, which they will associate with the prey's appearance in future encounters. Thus, predators will learn that this particular type of prey should be avoided. While color polymorphism is favored in cryptic prey (see above), it is thought to be inconvenient for aposematic species. This is because variation in warning signals might make it more difficult for predators to learn their association with prey unprofitability.

Aposematic species may resemble each other, making it easier for predators to learn to avoid them. This is known as *Müllerian mimicry* and leads to so-called "mimicry rings," where multiple defended species in the same area possess similar colors and markings. One example is the prevalence of yellow and black stripes across many wasp and bee species. Such mimicry can also be exploited by prey species without secondary defenses. These undefended species can mimic the appearance of defended ones and take advantage of predators having learned to avoid them. This is known as *Batesian mimicry*. For example, humans, along with many other predators, now associate black and yellow stripes with the stings of wasps and bees, but many harmless hoverfly species also have black and yellow stripes. The hoverflies then benefit, as fewer predators are likely to risk attacking them, for fear of being stung. Likewise, some harmless colubrid snakes mimic the color patterns of the deadly coral snakes (Fig. 1g) obtaining protection from predators.

Animals can also deter predators through threat, or warning, displays. These can include both honest displays, such as those of tarantulas that draw attention to the animal's defenses (in this example fangs), and dishonest, or bluffing, displays, where an animal attempts to appear more dangerous than it truly is. Many mammal species, for example, erect their fur when threatened in order to appear larger. A similar tactic is used by some frogs, which inflate their bodies with air (Fig. 1h).

Aposematic animals can also make use of behavioral displays to advertise their defenses to would-be predators, and just as the physical marking of these species may be mimicked by other for protection, so too are these behavioral responses. Nonvenomous snakes in the family Colubridae will often perform similar body flattening or inflating displays as venomous ones when threatened. This similarity can be further enhanced by so-called head-triangulation, whereby snakes flatten their head in order to make it appear more triangular, like those of vipers (Valkonen et al. 2011).

Finally, animals may try and convince a predator that they will not make a suitable meal by pretending to be dead. Also known as thanatosis, this strategy relies on the fact that many predators only capture live prey and is found in a wide variety of taxa ranging from insects to frogs and mammals. Indeed, an alternative name for this behavior is "playing possum" after the common opossum (*Didelphis marsupialis*), which has been recorded to feign death for up to an hour following attacks by dogs (Francq 1969).

Preventing Subjugation: *Fight or Flight*

Before they can be eaten by predators, prey must be subjugated. Perhaps the best-known mechanisms for preventing this are fighting or fleeing. While many animals fight back by whatever means are available to them, for example, by biting or scratching, others have weapons, such as the antlers of deer or the claws of crabs, that can be used against would-be predators. Notably, most animal weapons are not solely for defense against predators, but often play an important role in feeding or sexual competition. Deer, for example, use their antlers (Fig. 1i) during male-male competition, while male fiddler crabs use their large claws to court females (Pope 2000). Thus the antipredator function of weapons may often be secondary. In contrast, other mechanisms for avoiding subjugation are highly specialized. Physical defenses such as spines can make it difficult for predators to approach or attack. Some of the best-known physical defenses are the quills of porcupines and the spines of hedgehogs. As well as physical, defenses can also be chemical. Bombardier beetles can spray would-be attackers with a mix of toxic chemicals. These beetles store hydroquinone and hydrogen peroxide in specialized glands. When threatened, the compounds are secreted into a chamber near the tip of the abdomen and their oxidation and decomposition creates a powerful chemical reaction which produces a hot jet of fluid. Ejecting noxious chemicals at predators is not only confined to beetles, indeed the most famous animal to use this kind of defense is a mammal, the skunk, which sprays its enemies with foul-smelling volatiles such as sulfides.

Another strategy to escape capture is to startle or scare the attacker. This can be done in a number of ways, from appearing to suddenly change size, to flashing bright colors or making a loud noise. These kinds of defenses differ from aposematism in that they do not rely on predator learning, but instead aim to elicit the predators fear or startle responses, or simply overwhelm their senses momentarily, giving the prey a chance to escape. One example is the mountain katydid (*Acripeza reticulata*), which is a type of bush cricket found in Australia. Mountain katydids appear dull brown until startled, when they lift their wings to flash their brightly colored abdomens (Umbers et al. 2017). Another example is the eyespots displayed by some butterflies (Fig. 1j). These are markings with circular shape that are thought to look like vertebrate eyes and are thus believed to intimidate or startle predators making them hesitate to attack.

Finally, many, if not all, strategies to avoid subjugation rely on fleeing. Once the predator is startled, injured, or simply distracted, prey must escape to safety. Escape may entail more than simply running away, however. Many lizard species possess tails that detach when pulled, other animals such as crayfish can detach legs, and this ability is widespread across arthropods. This is done through processes known as *autospasy* (when the body part is lost in response to an outside pressure, such as pulling) or *autotomy* (when the part can be detached by the animal itself), which allows animals to sacrifice body parts with minimal blood loss. This enables them to escape, leaving their attacker with only a leg or tail. Fish scale geckos can even shed their skin when grabbed (Scherz et al. 2017). Some lizards take this one step further and have bright markings on their tails to encourage would-be predators to strike there (Castilla et al. 1999). This sort of misdirection is also seen in insects, like the butterfly *Bicyclus anynana* which has conspicuous *eyespots* along the margins of its wings. These have been shown to draw the attention of attacking preying mantids, which are more likely to strike at the wings, rather than the head or body, of butterflies with these eyespots (Prudic et al. 2014).

Another strategy to avoid attack and subjugation is *motion dazzle*, whereby patterns with high contrast (i.e., stripes, bars, or zigzags) make it difficult for a predator to assess accurately the speed or direction of a moving prey (Thayer 1909). This is because such patterns may create a visual illusion of reduced speed or immobility. Previous correlational work with snakes (Jackson et al. 1976), poison frogs (Rojas et al. 2014), and lizards (Halperin et al. 2016) has suggested the matching between color patterns and movement, such that animals with striped or elongated patterns move linearly and/or at higher speeds, two movement characteristics that may accentuate the visual illusion.

However, animals are often most vulnerable to predators when they are unable to escape, for example, as eggs or during larval or early development stages. For this reason many species actively protect their young through mobbing or otherwise distracting predators that get too close to their offspring. Other species, such as the red-eyed tree frog (*Agalychnis callidryas*), have embryos that are capable of hatching prematurely when the egg masses are attacked by snakes (Warkentin 1995).

Preventing Consumption: *The Last Line*

Even once caught and subdued, animals have one last hope of escape if they can prevent their captor from actually consuming them. This can be achieved in one of several ways, by being toxic or poisonous, by tasting bad, or by simply being too difficult to swallow. Many animals use chemicals to render themselves toxic or unpalatable. These can be sequestered from their diet or created by the animals themselves. As they are unable to move away from predators, plants often use chemical defenses (also known as secondary metabolites or allochemicals) to deter herbivores. However, some herbivores have not only evolved strategies to deal with these chemicals, but can also store them in their own bodies for defense. This strategy is particularly widespread in insects and examples include monarch butterflies (*Danaus plexippus*), whose larvae sequester cardenolides from milkweed plants (Brower and Fink 1985), pine sawflies (*Neodiprion sertifer*, *Diprion pini*), who sequester resin acid from pine trees, and bella or rattle box moths (*Utetheisa ornatrix*), which sequester pyrrolizidine alkaloids from the seeds of their host plants (Conner 2009). Burnet moths (family Zygaenidae) (Fig. 1e), on the other hand, are also capable of sequestering cyanide compounds from their food plants and use them as a defense against predators across their different life stages. However, when this source is scarce, they are able to synthesize these compounds *de novo* (Zagrobelny et al. 2007). Many of these insect species are also aposematic, but predators may "taste-reject" them even if they are not deterred by their warning signals. But there are examples of toxicity among vertebrates too. Poison frogs, for instance, can sequester toxins from their diet, which consists mostly of ants and mites. These secretions (Fig. 1k) contain mostly alkaloids, several of which are neurotoxins (Saporito et al. 2012); one of them, batrachotoxin, which is also a cardiotoxin, is one of the most potent alkaloids known and the reason why the golden poison frog was given the name *Phyllobates terribilis*. Some species of harlequin toads, California newts (*Taricha torosa*), and puffer fish (family Tetraodontidae) are known to possess another potent neurotoxin called tetrodotoxin (see below). In most cases, its origin is uncertain but, at least in the case of the puffer fish, it has been shown to be produced by symbiotic bacteria (Magarlamov et al. 2017).

"Social" Defenses: *Safety in Numbers*

Many of the defenses described above work more effectively in groups. For example, aposematism has been shown to be more beneficial when animals aggregate (Riipi et al. 2001). However, there are also strategies that rely on social behavior. The first of these is group *vigilance* behavior, which is widely used in several bird and mammal species. Vigilance simply means that animals are aware of their surroundings in order to detect potential predators; however, remaining vigilant can interfere with other behaviors such as feeding. By foraging for food in groups, animals can reduce their own vigilance while relying on the combined senses of the group in order to remain safe. Some species, such a meerkats (*Suricata suricatta*), take this one step further by having "sentries," i.e., individuals who keep watch for predators while the rest of the group forages.

In addition, while many species rely simply on sensing their neighbors fleeing to communicate a threat, some also give specific *alarm signals*. Vervet monkeys (*Chlorocebus pygerythrus*) are famous for having three distinctive alarm calls, one for leopards (*Panthera pardus*), one for snakes, and one for eagles. Many small birds, including tits from the family Paridae (Fig. 1l) will produce so-called mobbing calls in response to nearby predators. These calls not only function as alarm signals, communicating the presence of the threat to others, but they also harass the predators and recruit other birds to join the mobbing. Mobbing birds will stay in the area of the predator, performing mobbing calls and displays. These calls can also vary depending on the type of predator and how dangerous it is. Mobbing may also include attacks on the predators, with the aim of preventing them from hunting or driving them out of an area. Notably, these mobbing calls can warn and recruit members of other species, and multispecies mobbing groups are often observed. Despite this, Paridae species vary considerably both in how much information their mobbing calls convey about the threat posed by predators and how this information is encoded in their calls (Carlson et al. 2017).

How Do Antipredator Strategies Evolve?: *An "Arms Race" Between Predators and Prey*

Predators need to feed, and prey must avoid being eaten. Thus, predators continuously evolve better tactics to ensure they can successfully find, subjugate, and consume prey, while prey improve their defenses to prevent predators from succeeding. This has been likened to an "arms race," in which an improvement in one side's abilities results in a corresponding improvement by the opposing side. For example, as predators improve their visual acuity in order to increase prey detection, prey might elaborate their camouflage strategies or adopt different spatial distributions that make it more difficult for predators to find them. Likewise, as prey evolve toxins to avoid been consumed, predators may develop detoxification abilities or toxin resistance mechanisms. Such is the case in garter snakes (*Thamnophis sirtalis*), which have evolved molecular mechanisms to avoid getting intoxicated by the powerful tetrodotoxin from rough-skinned newts. Tetrodotoxin (TTX) is a neurotoxin that blocks the sodium-potassium channels in nerve cells, leading to paralysis. Garter snakes are capable of avoiding this effect of TTX because they have evolved sodium channels with a different shape, impeding the TTX molecule from binding them. Furthermore, garter snakes from populations co-occurring with the newts have shown to be more resistant to TTX than those from populations without co-occurring newts (Brodie and Brodie 1999).

Conclusions

Predation is undoubtedly one of the greatest forces shaping evolution, and this is reflected in the huge diversity of defense strategies seen in nature. Animals use every possible tool they have available in order to survive. However, no defense is perfect as predators are also constantly adapting to overcome the barriers prey put up against them. As a result many species use multiple defense strategies and may switch between radically different strategies as the predation attempt progresses. Indeed, a single species of frog found in Malaysia has been found to respond to attacks by "fleeing, feigning death, crouching, hiding among leaf litter, diving underwater, inflating the body, body-raising, defensive call(s), and bladder discharge" (Shahrudin 2016). Furthermore, a single strategy can act across more than one stage. A frog that inflates itself may threaten and dissuade predators with its increased size, but if this fails the inflation may also serve to make it too large to swallow. Thus, species can alter their defensive behaviors based on the identity of their attacker, and if one strategy fails to deter them they simply switch to another.

Cross-References

- ► Alarm Calls
- ► Aposematism
- ► Arms Race
- ► Camouflage
- ► Dilution Effect
- ► Eyespots
- ► Fight or Flight Response
- ► Mimicry
- ► Predation Risk
- ► Predator Detection
- ► Primary Defenses
- ► Secondary Defenses
- ► Toxins
- ► Vigilance
- ► Warning Coloration

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