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Risk-Taking in Self-Defense

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Introduction

Animals go to great lengths to minimize their risk of death by predation, and these efforts run the gamut from varying pre-encounter activity rates relative to risk level to the struggle for freedom from the grasp of the predator. Throughout the entire attack sequence, animals typically try to avoid contact with predators and keep them at a great distance. Strategies for reducing risk in this way include limiting exposure to times and places where predators are not likely to occur, maintaining high levels of vigilance to detect predators from as great a distance as possible, and fleeing as rapidly as possible when the probability of attack reaches some threshold, to keep as much distance between themselves and the predator as possible. However, many species have adopted unique behavioral responses to predators that appear to increase predation risk during encounters with predators but are actually intended to reduce predation risk or increase fitness in some way.

This article focuses on these apparently risky behaviors by prey animals toward predators during encounters. The discussion of different types of risky behavior will follow the attack sequence from predetection risk-taking (e.g., formation of highly visible large groups, freezing behavior in an attempt to be cryptic) to preattack behaviors intended to warn conspecífics (e.g., alarm calls and fear screams) and/or deter further pursuit by the predator (e.g., communicative calls or displays of health, aposematism, predator inspection, defense calls), to postattack behaviors intended to physically accost the predator (e.g., mobbing) or defend oneself or one’s offspring (e.g., counterattack, nest defense). This article will also briefly address the issue of the difficulty of assigning functionality to antipredator signals: Are signals intended to warn conspecifics, deter predatory pursuit, or both? I will not include discussions of behaviors that increase predation risk but benefit the animal in a nonpredatory context (e.g., a peripheral position in a group enhances both predation risk and feeding efficiency) as they are covered in other articles; this article will only deal with apparently risky behaviors that are actually intended to reduce the risk of predation or increase inclusive fitness. As most research in this area has been conducted on vertebrates (especially birds and mammals), this article will focus on vertebrates; however, the basic principles apply to invertebrates as well, and invertebrate examples do exist.

Predetection Risk-Taking

When no predators are currently detectable, animals behave to maximize reproductive fitness in a variety of ways. Many of these fitness-enhancing tactics increase the risk of predation, but the benefit in a nonpredatory context outweighs the predatory cost. Many behaviors enhance visibility to predators (e.g., showy mating displays), make prey more localizable (e.g., territorial vocalizations or chemical signals), or increase vulnerability (e.g., moving into exposed areas to feed on high-quality forage). As these phenomena are covered in great detail in other articles, this section focuses on two types of predetection behaviors that have both costs and benefits in a predatory context: group formation and freezing behavior.

Large Group Formation

The antipredator benefits of group living have long been recognized and were, earlier in the history of the study of behavior, a major focus of studies of the evolution of social behavior. While these benefits are covered at length in another article, there are a few noteworthy highlights for this discussion. Jens Krause and Graeme Ruxton reviewed the costs and benefits (both antipredator and other types) of grouping in animals. In addition to benefits in mate choice, foraging, thermoregulation, and locomotion, antipredator benefits include many-eyes effects, dilution, predator confusion, predator swamping via reproductive synchrony, selfish herd effects, defense against parasites, communal defense, and enhancement of aposematism. Clearly, group living has antipredator benefits; however, relevant to this article are the predatory costs of group living—the ways in which large aggregations of animals increase the risk of predation.

The primary predatory cost of group living is that predators may more easily detect and preferentially target large groups of prey animals. While theory to support the association between detectability and group size is limited, three-spined sticklebacks detect and attack larger groups of Daphnia more rapidly than smaller groups (Figure 1). Given their greater nutritional potential, predatory cichlids preferentially attack larger guppy shoals; however, a general preference for larger prey groups is likely lost as the size differential between predator and prey is reduced, fewer prey being required to satiate a predator. There are other potential ways in which grouping increases predation risk: interference between fleeing prey increases the predator...
success rate as prey group size increases, and prey remaining motionless while grouped are more vulnerable to predators restricting their searches to small areas.

Freezing and Immobility

Crypsis is probably the most widespread antipredator strategy that prey employ to reduce predation risk, and morphological camouflage is covered in detail in another article. Clearly, animals with cryptic morphologies must also remain relatively motionless (e.g., stick insects) or hide in deep vegetation (e.g., neonate ungulates) in order for the coloration to be effective. In contrast, some noncryptically colored species freeze upon detection of a predator, and this phenomenon is often associated with habitats that provide natural camouflage (e.g., dense forests). Immobility or a reduction in movement reduces risk upon detection of the predator in many species because many predators are highly reliant upon motion cues to detect and/or track their prey. In fact, many species that normally flee may come in the form of simple, low-cost alert postures (e.g., gravid or autotomized lizards). When the probability of successful escape by fleeing is reduced, prey freezing allows the predator to approach to a shorter distance before the prey animal takes flight.

Preattack Risk Taking

Upon detection of a predator, an animal may emit a chemical, auditory, or visual warning signal that captures the attention of other animals (presumably the predator and/or conspecifics) in the vicinity. The majority of these signals are thought to have one or two functions: (1) to deter further approach/pursuit by the predator by signaling the prey’s ability to escape quickly, the prey’s ability to physically defend itself (e.g., weaponry or aposematic coloration with toxin), or the fruitlessness of attack when a predator’s stealthy approach has been detected; and/or (2) to warn nearby conspecifics of the presence of the predator, allowing them a better chance of successful escape. Signals falling into these categories are apparently costly in that they might increase the risk of the signaler, either by making the signaler more localizable by the predator or delaying flight and allowing the predator to approach more closely, relative to an animal that flees outright upon detection at long distances. Here, I will discuss each of these potential functions in detail and show how it is extraordinarily difficult to demonstrate antipredator signal function.

Pursuit Deterrence

Any behavior will certainly increase fitness if it reduces the probability that its performer will be attacked by a predator. Indeed, animals have evolved a wide array of signals that function to discourage the predator from pursuing them further. However, while all of these signals have the same desired outcome, they may signal one of a great many different reasons for the predator to cease its pursuit, and these behaviors come in a variety of different forms.

Advertisements of perception

First, many predators depend on stealthiness while hunting in order to approach very close before ambushing their prey from a close distance. Mountain lions must approach undetected to within only 5–10 m of a deer in order to have any chance of successfully capturing it. Clearly, if prey detects a predator at a greater distance, signaling the predator that it has been detected should reduce the likelihood that the predator will continue to waste energy on a fruitless approach; the predator will likely move on to another area to try again on less-informed quarry. These perception advertisement signals may come in the form of simple, low-cost alert postures or tail-flagging; however, some prey use a more obvious auditory signal of awareness (e.g., snorting in ungulates). Klaus Zuberbühler, Ronald Noë, and Robert Seyfarth found that leopards spent less time in hiding after being detected by vocalizing Diana monkeys, suggesting that the monkey vocalization informed the leopards that a stealthy approach was no longer possible and that the leopards gave up on their hunts upon being signaled.

Perception advertisement also may come in the form of high-cost behaviors like predator inspection, in which an animal, upon detecting a predator, repeatedly moves toward and dashes away from its foe. Anne Magurran
studied the inspection behavior of a live predatory pike by minnows; inspecting fish avoid entering the ‘attack cone’ around the predator’s mouth, thereby minimizing risk. She found that the attack rate of the pike was reduced when minnows performed inspection approaches (Figure 2). Therefore, although predator inspection may reduce predatory attacks, it does not prevent them entirely, and inspectors may incur a great deal of risk. In addition to advertising perception to the predator, inspection may also allow the inspector and other conspecifics to learn more about the predator and/or maintain visual contact with a dangerous stealthy predator.

Advertisements of quality
Second, individuals vary in their physical strength, agility, and ability to outrun or outmaneuver a predator during an attack. In fact, many predators preferentially single out and attack apparently lame or infirm individuals from a group, which improves the predator’s likelihood of success and decreases the chances of prolonged unsuccessful chases of healthy prey. Therefore, if able-bodied prey can signal their escape ability to a predator prior to attack or even during the early phases of a chase from a long distance, the predator may halt the attack to avoid wasting more energy or risking physical injury on a likely fruitless effort. Stotting or bounding is a common behavior performed by many groups of ungulates while fleeing from predators. During flight, the animal stretches all four limbs downward, keeping them stiff, and springs upward in a high leap; the legs are kept together as the animal returns from the leap. Stotting is a slower form of locomotion than outright sprinting and, therefore, increases risk and imposes costs on the performer. Tim Caro investigated 11 potential functions of stotting in Thomson’s gazelles and concluded that, although stotting is likely an advertisement of perception in response to cheetahs, which rely on stealth and tremendous bursts of speed, it is likely an advertisement of quality/body condition in response to wild dogs, which chase gazelles over a long distance but at a slower pace (wild dogs preferentially chased gazelles that stotted at lower rates). Caro also suggests that stotting by mothers whose neonates are being pursued may be a way to distract the predator’s attention away from her young. Many other examples of advertisement of quality exist, but it is usually quite difficult to tease apart the true function of these signals (see discussion in the following section).

Advertisements of defensive weaponry
Third, many animals have toxins or defensive weaponry that help protect them from predators. These animals often allow their predators to approach very close to them and advertise the presence of their arsenal with bright coloration or exaggerated behaviors. Aposematic coloration, bright contrasting color patterns advertising defensive toxins or weapons, and defensive chemicals are discussed in detail in other articles. In addition to these patterns, animals can behaviorally modulate their body or coloration to enhance its visibility and direct the predator’s attention to the presence of their defense. For example, tail piloerection and handstanding enhance the visibility of the contrasting black-and-white pelage of spotted skunks and draw attention to their anal region, the source of their noxious defensive spray. Skunks and other protected animals are often less wary than typical prey and allow potential predators to approach to within just a few meters before responding. Some bold or naïve predators attack anyway. Therefore, while toxins and weaponry go a long way toward reducing predation risk, their displays are not always effective, and these animals accept some risk by allowing the close approach of potential predators that may attack despite their coloration or behavior.

Defense calls
Many animals that lack defensive weaponry or toxins may also stand their ground when a predator approaches, and some will make an abrupt noise that can mimic a more threatening species. Some rabbits growl like large
carnivores; some birds hiss like snakes; and burrowing owls produce a rattling sound to mimic a rattlesnake. The callers incur greater risk by not fleeing at greater distances. However, most of these calls appear to startle the predator, causing it to delay its attack for a brief time, giving the caller a few extra seconds to escape. We know very little about the function and ubiquity of defense calls, and most information that is known is anecdotal in nature.

**Death feigning**

Finally, one behavior that involves considerable risk but may function to halt a predator's continued attack and consumption of a prey item is death feigning, the assumption of a false catatonic state in which the animal appears rigid and lifeless. While it takes place after attack and capture, death feigning, also known thanatosis, letisimulation, or death shamming, has been documented in many birds and mammals, most famously the opossum. While most knowledge of death feigning is anecdotal in nature, Alan Sargeant and Lester Eberhardt found that bouts of feigning in ducks lasted, on average, 4 min, and 29 out of 50 ducks that feigned death after being captured by foxes survived the incident. Foxes typically cached and abandoned immobile ducks rather than delivering a final death bite, which allowed the ducks time to regain consciousness and escape. Death feigning is probably most effective against predators that capture, move, and consume their prey at a later time.

**Warning conspecifics of danger**

Many species have evolved signals that are emitted when a predator is detected. These signals can function to warn nearby conspecifics of the presence of danger, and in some cases, the type of predator and its location. Earlier detection of threat allows animals to take flight earlier and increase their probability of surviving the attack. Callers may incur high survivorship costs in the form of increased predation risk. These warning signals come in many forms (acoustic, chemical, or visual), and some species even have individuals designated as sentinels to warn the rest of the group. This section will focus on the costs and benefits of these apparently risky alarm calls. Detailed discussions of structure and alarm call type can be found in other articles.

**Costs and benefits of warning conspecifics**

It seems intuitively likely that alarm callers increase predation risk and incur survivorship costs by drawing the predator's attention and making themselves more locatable, but there is some debate as to the actual level of these costs. Indeed some species may incur high survivorship costs for calling, while others may incur very little to none at all. For example, Paul Sherman measured capture rates of Belding's ground squirrel alarm callers and noncallers, and he found that although alarm callers had a higher probability of being captured by terrestrial predators than noncallers (i.e., high survivorship costs), alarm callers had a lower probability of being captured by aerial predators than noncallers (i.e., no survivorship costs and high survivorship benefits). Others suggest that the fact that prey in some species produce alarm calls only when they are a safe distance from the predator is evidence of high survivorship costs. On the other hand, many alarm calls are structured to make the caller less localizable or detectable, suggesting low survivorship costs. In sum, the risk incurred by alarm callers likely varies with the prey's level of exposure, and the predator type, speed, and distance from the prey.

There are three potential benefit structures of alarm calling. First, selfish alarm calls may benefit the caller but harm the receivers by inciting receivers into flight and distracting the predator's attention away from the caller. However, this proposed benefit has received theoretical attention but no real empirical support; most studies suggest that receivers always receive at least some benefit from alarm calls, and no study has ever shown a net cost to attending to alarm calls. Second, alarm calls may be mutually beneficial: both callers and receivers benefit and the predator's success rate is reduced by the altered behavior of the receivers. Receivers typically benefit by early detection, which leads to adaptive responses, and callers may benefit by a number of different mechanisms, including increased monitoring of the predator by all group members, initiation of coordinated group flight or defensive behaviors, initiation of a swarm of prey taking flight in different directions that may confuse the predator, or protection of a nearby mate. Third, alarm calls may be kin-selected and result in a net cost to the caller (i.e., reduced survivorship – see previous paragraph), but the recipients (kin with whom the caller shares genes) benefit by earlier detection of the predator and increased escape probability (i.e., nepotism). In nepotistic alarm calls, receivers again typically benefit by early detection, and callers benefit by increasing the probability that individuals with whom they share genes will survive the attack, thereby increasing their indirect fitness (n.b., the caller may receive no direct benefit from calling, but the indirect benefits due to relatedness with the receivers may exceed the potential survivorship costs of calling). Paul Sherman found that female Belding’s ground squirrels called more often than expected when closely related conspecifics were in the area (e.g., sisters and offspring), whereas males that had dispersed into the group and had no kin in the group called much less often than expected.

**Sentinels**

In most groups, individuals do not coordinate vigilance behavior, and animals alternate between foraging and being vigilant at some individual rate. However, in
some taxa, one or a few individuals take on a sentinel or guard role for the group, while the other members enjoy uninterrupted time to forage. Sentinels usually position themselves in exposed positions, are more likely to spot predators from afar, give alarm calls to alert conspecifics, and therefore, would seem to incur greater risk from predators. However, sentinels are the first individuals to detect threats and usually position themselves in locations that, while exposed with visibility to the surrounding area, are close to refuge. In fact, studies of meerkats show that guards were never attacked by predators, indicating few, if any, costs to sentinel behavior. Theoretical investigations have shown that when an individual has sufficient energy reserves, it pays to be a sentinel when no one else in the group is occupying that role, and it pays to continue foraging if a sentinel is already on duty. Therefore, sentinels likely incur very little, if any, risk and benefit from assuming the sentinel role by fleeing very early from predators, increasing foraging efficiency when they are not vigilant, and helping to protect conspecifics from predation (i.e., via kin selection or reciprocal altruism).

**Fear screams**

Individuals of some species, when captured by a predator, emit high-intensity, broadband vocalizations in addition to struggling physically to free themselves. These calls are called fear screams. Given that the individual has already been captured, using any remaining energy to intensify its physical struggle for freedom would seem to be the most adaptive strategy; however, Michael Conover has proposed five functions for fear screams: mobbing, startling the predator, warning kin of danger, calling for help from conspecifics, and attracting other nearby predators to distract the captor. While empirical evidence supports the idea that fear screams have several functions, the function with the most support is conspecific warning. Fear screams by some bird chicks at the nest induce flight behavior in their siblings; probability of fear scream behavior is positively correlated with flock size in some birds. Playbacks of fear screams are commonly used by wildlife managers to keep some bird species away from sensitive areas. While fear screamers may, indeed, improve their chances of escape via startling, distracting, or chasing the predator via mobbing, it is apparent that callers can also benefit by warning related kin during their final seconds of struggle, thereby increasing their indirect fitness.

**Teasing Apart Functionality**

From the foregoing discussion, it is clear that many different types of signals may reduce predation risk in a variety of ways. However, testing functionality empirically in a wild population of animals is usually quite difficult. Typically, a number of a priori functional hypotheses and their supportive predictions are stated, an experiment is conducted or a set of natural observations is recorded, and the data are compared with the predictions. This strategy works well when the trait has only one function, but when a trait is multifunctional and provides its bearer with multiple benefits, the predictions of one function may be at odds with the other and both may be disregarded erroneously. For instance, if a signal functioned to warn conspecifics, we might predict that the signal would not be given by solitary animals. However, if that signal also served to advertise perception, then we would expect solitary animals to give the signal. Therefore, if the signal served both functions, then, given the data, we might conclude that it did not warn conspecifics of danger because solitary animals also signal. Great care must be taken when selecting predictions and planning experiments in order to avoid this potential problem. One must find ways to test each hypothesis independently of the validity of other hypotheses. Due to conflict among predictions, many experiments provide only marginal confirmation of one hypothesis, lacking sufficient evidence to rule out the others (i.e., just because solitary animals signal, does not exclude use of the signal to warn conspecifics when they are present).

**Physical Attack and Engagement**

Some animals decline to flee from predators and actually approach and attack certain types of predators they encounter. Physical engagement takes many forms, including saving offspring from attack (e.g., nest defense), calling conspecifics to the cause and mobbing a predator, and even throwing substrate or other inanimate objects at the predator to drive them away. Alternatively, animals that, when attacked, simply defend themselves with chemical or morphological weapons typically do so after all attempts to discourage the predator to cease its attack (e.g., warning behaviors, contrasting coloration, escape attempts, etc.) have failed, and these weapons are covered in detail in other articles.

**Offspring Defense**

If a predator approaches into close proximity of a young animal, parents often defend their offspring at some cost to their own survival. This discussion will focus on nest defense in birds, but the same principles apply to parental defense in other taxa (e.g., Susan Lingle’s work on adult mule deer defending their fawns from attack by predators). Nest defense is a major part of parental investment that requires parents to weigh their own long-term survival against the survival of the current offspring. Although the benefits of nest defense are obvious
(increased survivorship of offspring resulting in increased direct fitness), this section will focus on the costs of nest defense in the form of increased risk to the parent.

Birds defend their broods in many ways: flushing explosively, feigning injury (e.g., broken wing) to entice the predator to attack the parent and not its young, alarm calling, and individually attacking the predator with dives and strikes. Distraction displays take many forms, and Michael Gochfeld groups a large number of nest protective behaviors into this category, including running behaviors, injury feigning, tail flagging, and erratic flight. Most distinctive behaviors make the performer appear to be easier to capture, and therefore an easier and more profitable meal than the parent’s offspring, whether they have been detected or not. There is great variation in the form of these behaviors, and the type and frequency of behaviors used vary from individual to individual.

Although the most apparent cost of nest defense is increased risk of injury or death to the parent, there is little empirical evidence to suggest that this cost exists, and anecdotal evidence suggests that death is only occasional. Parents likely defend young in a manner that minimizes risk to themselves and may take fewer risks when the risk of predation posed by a particular type of predator is high. Additionally, parental survivorship costs of nest defense may be overstated because many defensive behaviors are performed in response to predators that pose little risk to the parents and only really threaten the offspring. The likelihood of nest defense in relation to costs may also depend on the parent’s nesting potential (e.g., older parents, lower quality individuals, or parents nesting at the end of the breeding season when there is no chance of surviving the winter may take greater risks to protect their current offspring).

Mobbing

In many gregarious species, groups of animals sometimes advance toward a predator to inspect, follow, harass, or attack it until it leaves the area. Predators usually escape with just a few bites or pecks, but sometimes predators are captured or killed by mobbers. Mobbing is usually a group effort of offspring defense, varies considerably within and among prey species in form and intensity, and may take different forms specific to particular types of predators. Clear benefits of mobbing include reduced predation on gregarious species and increased reproductive success as a result of defending offspring. Eberhardt Curio outlined specific direct and indirect benefits of mobbing in birds: mobbing can harm or kill a predator (reducing risk), advertise detection of the predator and encourage a predator to leave an area sooner, dilute risk of any one individual attacker, attract larger predators that pose a risk to the attacker, alert other conspecifics to danger, or induce silence from offspring. Costs of mobbing, in addition to temporal and energetic costs, should include decreased survivorship via the increased risk of reducing the distance between the predator and prey. Although anecdotes suggest that prey are occasionally captured while mobbing predators, the best evidence of the costliness of mobbing is indirect and contextual. Riskiness of mobbing may be inferred from observations of mobbers being more cautious (1) with more dangerous predators, (2) when closer to a dangerous location, (3) when terrain makes it difficult to escape, (4) when fewer mobbers are available, and (5) when prey are less nimble. Mobbing may also attract additional predators to the area, and mobbing parents may inadvertently leave their offspring unprotected and more vulnerable to predation.

Individual Attack

Members of some species show a willingness to confront a predator on their own. While many of these species also mob predators in groups, individuals are often capable and eager to take on approaching predators without help from conspecifics. Ungulate mothers sometimes confront predators to defend their offspring, attacking with their hooves and head ornaments (e.g., horns or antlers). Donald Owings, Richard Coss, Ron Swaisgood, and Matthew Rowe, among others, have studied the preemptive individual attacks by California ground squirrels to rattlesnake predators for many years. Squirrels may approach, dart toward, and retreat from the snake, tail flag, or bite or throw substrate (dirt) at the snake. This snake harassment behavior is undoubtedly influenced by the squirrels’ resistance to rattlesnake venom and their interest in protecting more vulnerable offspring from predation: mothers are more likely than other squirrels to harass snakes.

Some prey launch counterattacks against predators that have attacked them. Species with noxious or toxic defenses are most famous for their counterattack strategies: skunks and striped polecats are exceptional in their ability to spray a target with anal gland secretion from several meters away. As these types of weapons are discussed in detail in another article, here I will focus on other forms of counterattack. Most nonnoxious prey that fight back against predators defend themselves with sharp teeth and claws. The small mustelid carnivores (e.g., weasels, martens, polecats) are excellent examples of small species with razor-sharp teeth that evolved to suit their voracious carnivorous appetite but that also are useful in defense. Many of these species can severely harm/maim an attacker in a cloud of dust and blood – the ratel (honey badger) is particularly well known for being fearless, pugnacious, and relentless in its response to harassment. Other animals may regurgitate oils onto their predators, which can lead to predatory birds becoming waterlogged and drowning and mammalian predators’ fur
becoming foul-smelling. Some vultures regurgitate food when frightened; the vomit is highly acidic and can drive away predators. Clearly, the likelihood of counterattack depends on the costs and benefits of attacking versus flight and is based on the size and dangerousness of the predator, the size of the prey, the escape options on hand, and other environmental factors (e.g., availability of cover or refuge).

Conclusion

Clearly, when confronted by a predator, animals often do not flee immediately and behave in apparently risky ways that would appear to increase survivorship costs. However, in nearly all cases, closer examinations of the behaviors suggest that these ‘risk-takers’ are actually either optimizing fitness, so that fitness benefits exceed fitness costs, or are not behaving in a risky way at all, or both. Prey behave in risky ways throughout the attack sequence, whether they are alarm calling while the predator is still far away or purposely drawing a predator’s attention away from a nest of defenseless offspring. While some animals that accept increased survivorship costs at one stage of the predation sequence often compensate at a later stage by playing it more safely, other animals accept more risk in all contexts (i.e., a behavioral syndrome). While it is difficult to empirically assign functionality to risky antipredator behaviors, carefully designed experiments and attention to environmental circumstances during the performance of the behavior can shed light on the benefits that performers might receive.

See also: Acoustic Signals; Alarm Calls in Birds and Mammals; Defensive Chemicals; Defensive Coloration; Defensive Morphology; Economic Escape; Group Living.

Further Reading


