Predator Avoidance

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For prey species to be successful, they must balance the conflicting demands of obtaining the resources necessary for survival while avoiding being killed by predators. This has a hierarchy of approaches that begins with avoiding dangerous (=predators) times and locations, using dangerous locations but adopting behaviours and tactics that assist prey in detecting predators first. If a predator detects them they may also plan for this by staying in groups, thereby diluting the chance of being the individual that is killed or using coordinated group defence. Individuals may also employ toxins or specialized morphologies that deter a predator from attacking or assist in escape. Assuming individual behaviour is not affected by the presence of parasites, prey may also escape predators after capture using specialized morphologies, and even ejecting limbs. Ultimately captured prey may even try to attract other predators with the hope of escaping during the ensuing melee.

Advanced article

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At its simplest, animal survival hinges upon their ability to obtain food and convert this into offspring while simultaneously avoiding being killed by predators. Typically, strategies to minimize the chance of being killed by a predator are the antithesis of those required to obtain resources and bear offspring. Because it is both critical to avoid being eaten and obtain resources, their dynamic balance shapes animal behaviour and ultimately population dynamics (**Figure 1**). For prey to survive within an environment containing predators, they must avoid detection, capture and consumption.

Avoiding Detection

The simplest way to avoid detection is to occupy locations your predators cannot. And while it may seem like the prey should always use these locations, most refuges have a tradeoff associated with them. You might be safe from predators but have little or no access to mates, food, oxygen, etc. In these instances the use of refuges should occur at times when you are at most risk – when a stimulus suggests a predator is near or under conditions when predation is most likely (under certain light and weather conditions, or times of the year) or when you are most vulnerable and/or escape will be more difficult (e.g. animals that have recently moulted or females with dependent offspring).

In aquatic ecosystems the marine polychaete, *Serpula vermicularis*, retreats into its calcareous tube when disturbed. This behaviour provides safety from predators but restricts its ability to feed or respire (Dill and Fraser, 1997). The time spent within the safety of its tube versus exposed to predators to obtain resources represents a dynamic balance between these conflicting activities.

The use of burrows by terrestrial mammals is a similar system with different challenges. Unlike polychaetes, mammals can vary their behaviour in both time and space. If the burrow is located in dense vegetation it is possible for a predator to lie in wait undetected and capture the burrow's resident when it leaves. For this reason, burrows are located in habitats to provide a good opportunity of detecting predators that are in the vicinity (Lagos *et al*., 1995; Karels and Boonstra, 1999).

Prey can select habitats that do not provide absolute refuge, but do make their detection and capture very difficult (e.g. Manatunge *et al*., 2000). But such approaches have their effectiveness limited in the presence of multiple types of predators. For example, in the presence of terrestrial predators, but not avian predators, grasshoppers move to the highest points of vegetation. In the opposite scenario, they move to the lowest locations. When both avian and terrestrial predators are present, they occupy areas of vegetation of intermediate height but with an intermediate benefit (Pitt, 1999). Similarly, Johny darters (*Etheostoma nigrum*) can escape smallmouth bass (*Micropterus dolomieu*) predators by occupying small rocky crevices. But this location can make them more vulnerable to predation by crayfish

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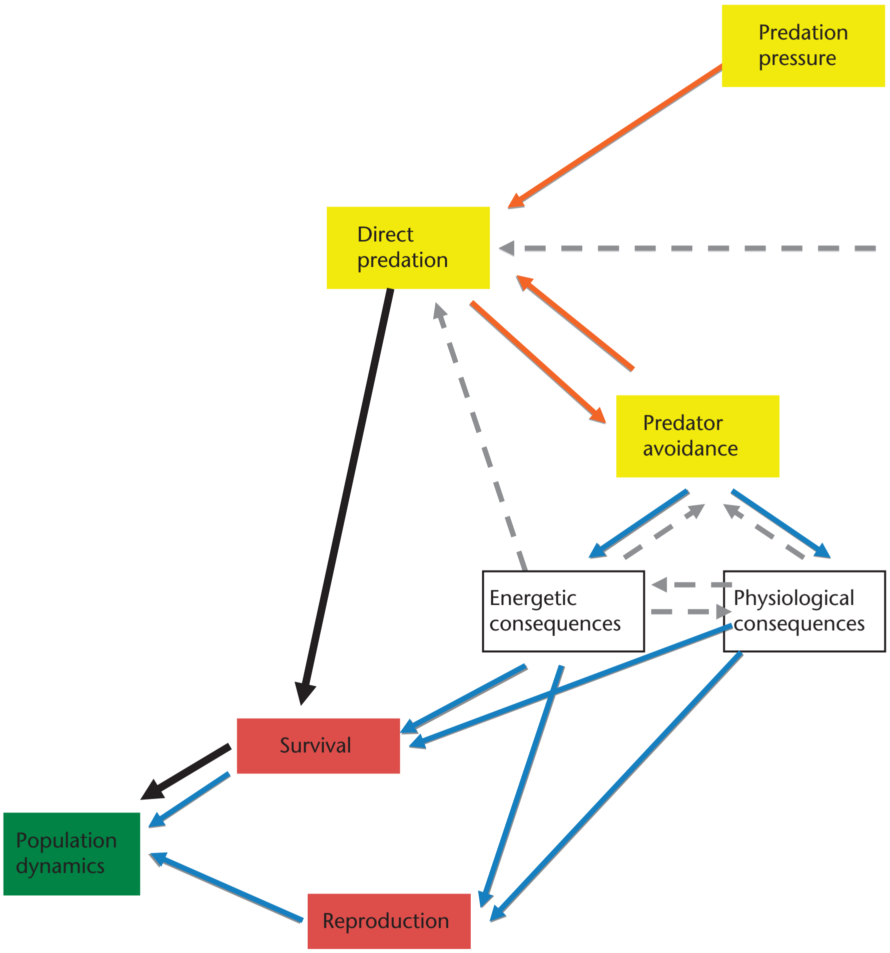

Figure 1 The pathways by which predation can affect the population dynamics of prey. The restricted view of predation as only affecting mortality is illustrated by two black arrows linking predation to prey dynamics by the way of survival. The consequences of predator avoidance are illustrated in the yellow boxes and orange arrows. These boxes demonstrate that predator avoidance by the prey can reduce mortality rate, but does so via energetic and physiological costs that will also impact prey population dynamics. The risk effects are illustrated by the blue arrows, with the likely feedbacks illustrated by grey arrows. Reprinted from Creel and Christianson (2008). Copyright (2008), with permission from Elsevier http://www.sciencedirect.com/science/journal/01695347.

(*Orconectes rusticus*). When both crayfish and smallmouth bass are present, avoiding smallmouth bass using crevices is no longer an option and the darters suffer increased predation rates (Rahel and Stein, 1988).

Spatial avoidance (vertical and horizontal migration)

In many lakes, both planktivorous fish and their piscivorous predators locate prey by sight. Although numerous hypotheses have been posed to explain this phenomenon, one is that prey take advantage of the impaired night time visual ability of their predators to feed at the surface (Clark and Levy, 1988). In the Antarctic, midwater fish select habitats based upon the diving limits of their predators (Robinson, 2003). During the night they move upwards in the water column but deep enough to avoid surface feeding seabirds (petrels) or seals (shallow divers 30–40 m). During the day, the primary predators are penguins which forage at depths greater than 250 m requiring the fish to move to greater depths.

Migrations can also be horizontal. These migrations are again hypothesized to be an attempt to avoid predators. Diel horizontal migrations of zooplankton are thought to be favoured when the littoral zone has an abundance of macrophytes and piscivores; the piscivores may restrict planktivores to open water habitats while the macrophytes provide cover to the zooplankton (Burks *et al.*, 2002). Fish may migrate offshore at dusk to forage on abundant resources present there and travel onshore at dawn as a potential predator avoidance mechanism. As larger fish generally remain in deeper waters and are largely visual foragers, planktivorous fish can avoid these predators by foraging in deeper waters at dusk. But these same locations are the most dangerous during daylight hours, reversing the migration.

Temporal avoidance (diel activity patterns)

For some fish such as juvenile Atlantic salmon (*Salmo salar*, Fraser *et al*., 1995) and the Eurasian minnow (*Phoxinus phoxinus*, Greenwood and Metcalfe, 1998) they become nocturnal at cold temperatures. Nocturnal activity reduces the overlap of the fish with their endothermic predators that are active during the day. These fish are less effective at feeding when it is dark, but the difference in motor abilities between ecothermic prey and endothermic predators trumps this reduction in foraging efficiency.

Accepting Detection but Detecting First

Although the ultimate goal of an individual is to avoid being detected by a predator, it is inevitable that most, if not all, individuals will be detected by a predator over the course of a lifetime. If prey can detect their predator first, then they will have some control over the chance that this encounter will be fatal.

Group vigilance

Group living animals have the opportunity to pool their sensory abilities to increase their probability of detecting a predator. When more eyes, ears or noses are available to scan the surroundings, individuals can decrease their own vigilance without experiencing an increase in predation risk (Pulliam, 1973). Groups can also offer other benefits to members – safety in numbers, dilution and confusion effects (see below). Furthermore, while increasing numbers within a group does increase sensory abilities, it also increases the probability that the group will be detected by a predator (Cresswell, 1994). For this reason, there are optimal group sizes when the goal is predator avoidance.

Alarm calls

When an individual lives within a group and detects a predator, one would assume that communicating this information to others would be the next logical step. To do so, this would normally be through some sort of alarm call, but providing this signal means that you may also identify your location to an approaching predator. Birds and mammals use vocal alarm calls to initiate a series of events that increase the probability of survival for the signaller (Bergstrom and Lachmann, 2001). These alarms need not merely signal the approach of a predator, but can also communicate the activity or intent of the predator, and the size, type and potential risk associated with the predator (Templeton *et al*., 2005). Depending on the predator, the signal may also be a call for mobbing or some other form of predator deterrence. Alarm calls are also believed to signal to the predators that they have been detected, and that initiating an attack would be futile.

Escaping Once Detected

Once detected, the probability of escape will depend on several factors including whether or not there are other potential prey in the near vicinity, the distance to cover and the ability of the prey to outrun the predator. How an individual is able to assess and react to the presence of a predator will determine the success of escape, as well as the efficiency, which it is done.

As a group

Individuals living in a group can benefit not only from increased vigilance in detecting a predator but, once detected, can also benefit from the reduced probability of being attacked. This form of passive defence can be influenced by the number of group members and the positioning of an individual within the group. In some cases, group members may even act together to aggressively fend off an advancing attack. Although there are obviously costs to living in a group (e.g. sharing everything), protection from predators is often cited as an important compensation indicating that there truly is safety in numbers.

Dilution effect

If you live in a group and you are attacked by a predator that can take only one individual, everything else being equal, the probability that it will be you is inversely related to group size – the dilution effect (Beauchamp, 2003). Evidence for the 'dilution effect' under natural conditions was first presented by Foster and Treherne (1981) who studied predation on the marine insect, ocean skater (*Halobates robustus*), by juvenile Pacific sardines (*Sardinops sagax*). Their research indicated a strong inverse relationship between the number of attacks on an individual insect per unit time and the size of the group to which the insect belonged. Turner and Pitcher (1986) argued that the dilution effect, in and of itself, was not sufficient to explain the benefits of grouping. As noted above, there are detection issues. However, the aggregation of prey into groups creates the 'avoidance effect' – this distribution of prey has a reduced encounter rate with predators (i.e. avoids predators) compared to the same number of solitary individuals.

Confusion effect

In their study on the predator–prey interactions between the Pacific sardine on ocean skaters, Foster and Treherne (1981) also discovered that the attack success by the sardine decreased as the insect group size increased. This latter finding was suggested to be due to the confusion imposed on the predator by the moving mass of insects. Such difficulty in pinpointing a prey item has been termed the 'confusion effect' (Miller, 1922; Neill and Cullen, 1974). Generally, predators target one individual prey item at a time (exceptions include animals such as humpback whales that feed on schools of krill, plankton and small fish) though it has been shown that a few predators may have more success swimming quickly into a group and grabbing any prey (Parrish, 1993). However, large groups of zigzagging or darting animals typically make targeting an individual difficult. For example, sticklebacks (*Gasterosteus aculeatus*) presented with 20 *Daphnia* prey items had a significantly greater targeting error (distance between a strike and the nearest prey individual) compared to when only 5 *Daphnia* were offered (Ioannou *et al.*, 2008). Even in groups of prey where neither escape nor quick movement was possible, both leopard geckos (*Eublepharis macularius*) and common marmosets (*Callithrix jacchus*) have been shown to take longer to catch one out of several prey when compared to capturing one prey when it occurs alone (Schradin, 2000). In this way, aggregations of prey individuals can take advantage of the neurological constraint of the predator, and attempts have been made to represent the visual processing of the predator on a prey item through neural network models (Krakauer, 1995; Tosh and Ruxton, 2006; Tosh *et al.*, 2006).

Domain of danger and the selfish herd

Simply joining a group may not give an individual all the potential benefits in avoiding predation. The position an individual holds within that group may mean the difference between being attacked and successfully avoiding it. If manoeuvring allows an individual to occupy the space in the centre of the group, that individual will decrease its domain of danger, or its surrounding area that is closest to the predator. Decreasing the domain of danger is a key component of the selfish herd theory. At the periphery of a group, an individual's domain of danger is large, whereas those occupying the centre of the group are surrounded by others that have a higher risk of predation (Hamilton, 1971). As the foraging predator will most often take the individual at the periphery of a group, potential prey should therefore minimize the space between it and its nearest neighbour with the best location being in the centre of the group. Spacing between redshanks (*Tringa tetanus*) proved vital in the risk of predation by sparrowhawks (*Accipiter nisus*), where targeted individuals were on average five body lengths further from their nearest nontargeted neighbour (Quinn and Cresswell, 2006). As not all individuals can move into the centre of the group, when one individual enters, it selfishly pushes another individual into an area of greater risk away from the centre. This behaviour has been documented in groups of fiddler crabs (*Uca pugilator*) under attack, where individuals ran towards the centre of the group rather than directly away from the predator (Viscido and Wethey, 2002). Attaining these central positions decreases an individual's probability of being the one attacked by the predator.

Mobbing

Typically discussions of antipredator behaviour focus on avoidance and escape; however, it is not unusual for individuals to approach and even directly harass a predator. Predator mobbing is a behaviour that has been widely reported among species of fish, birds, mammals and insects. There are some obvious costs to participants that engage in mobbing activities including the increased risk of injury or mortality, yet the behaviour persists suggesting an adaptive function. Several reasons have been presented to explain this behaviour which Ostreiher (2003) grouped into three main functional hypotheses: (1) an altruistic behaviour whereby participants put their own lives in danger for the sake of fellow group members (e.g. alerting others, chasing the predator away), (2) a parental response carried out for the benefit of the offspring (e.g. teaching the offspring to identify their predators) and (3) a selfish behaviour that benefits the performer alone (e.g. prey–predator communication, self advertisement). Interestingly, the latter hypothesis has received much support. For example, the Arabian babbler (*Turdoides squamiceps*), a species of songbird, was willing to mob a predator model in the absence of conspecifics, although it was noted that the intensity of a mobbing event increased when conducted in pairs (Ostreiher, 2003). Through aggressive behaviour towards a predator, mobbing may deter the predator from any further advance (the 'move on' hypothesis; Curio, 1978) and discourage the predator from attacking a difficult target (Dugatkin and Godin, 1992).

As an individual

Not all animals are social and hence for these individuals, there is no opportunity to employ the tactics or reap the benefits associated with group living. Under these circumstances, predator avoidance will be determined by the physical characteristics of the individual.

Aposematic colouration and their mimics

Some animals contain toxic substances that, if consumed by the predator, are either distasteful or make the predator ill. And if you contain such toxins, it is particularly useful to advertise this fact by having obvious markings that communicate this information (aposematic colouration). The expectation is that predators will attack or consume one individual and will carry forward their experience by avoiding all such individuals. The overall process can be enhanced when several species employ similar markings to warn of mutual toxicity (Mullerian mimicry). When the system is working, a predator encounter should not result in an attack, unless you are unfortunate enough to be the first (for an example see Kappan, 2001). Individuals that have similar colouration to their toxic counterparts, but contain no toxins, a phenomenon known as Batesian mimicry, can also parasitize this system (Pfennig *et al.*, 2001).

Acceleration

Owing to differences in morphology and design, there are differences in the acceleration abilities and sustained velocities of predators and their prey. For terrestrial mammals, the predator often has superior acceleration but the prey is able to sustain its maximum velocity for a longer period of time (Christiansen, 2002). These predators must get to within a critical distance of the prey in order to take advantage of these running speeds. As a consequence, these predators prefer habitats that afford some cover over those that contain prey in high density (Hopcraft *et al*., 2005).

Manoeuvrability

In many systems, predator and prey are distinguished by considerable variation in size. When this does occur, simple Newtonian Physics in the form of the law of conservation of angular momentum can promote a very effective escape strategy (Abrahams, 2005). Prey that are being pursued by a larger predator should make turns with the smallest possible radius. Because of its larger mass, the predator's turning radius will be larger than its prey resulting in a greater separation distance between predator and prey. Repeated appropriately, the prey may be able to create sufficient distance from the predator to make good their escape. This may also be enhanced by practicing their escape route, and building up motor memory to facilitate this process (Stamps, 1995).

The Mediating Role of Parasites

Despite the best efforts of the prey, and because of the best efforts of the predator, predator and prey are now united. Although we do not know any data that quantify the proportion of prey that will be ultimately consumed, in almost all instances this is a circumstance which prey would almost always prefer to avoid. One notable exception is when the behaviour of the prey has been altered by a parasite in order to allow that organism to transmit to a new host.

There are a variety of mechanisms that are used by parasites to increase encounter rates with predators. These may be as simple as imposing a significant energetic cost upon the host, forcing it to incur greater risk of predation while feeding. Some parasites in fish block the passage of light into the eye, resulting in the fish swimming closer to the surface and becoming more susceptible to fish-eating birds. Likewise, other parasites alter the swimming or buoyancy in fish, both of which make them much more likely to be the victim of a predator.

Parasites can also alter the physical characteristics of their hosts. For example, ectoparasites in fish schools result in the infected individual being obviously different than all others in the school. As defence within these schools relies upon all individuals being indistinguishable, providing a unique feature provides predators with a target they can follow and ultimately capture. More recently, Yanoviak *et al*. (2008) demonstrated that canopy dwelling ants in Panama *Cephalotes atratus* that are infected with a genus of tetradonematid nematode have their appearance dramatically altered. Normally, these ants are entirely black, but when infected their gaster becomes bright red, and resembles the red fruit that occurs within the canopy. To accentuate this, the infected ants also hold their gaster up, making it even more obvious to fructivorous birds, the ultimate host of this parasite.

Escape Once Captured

Excluding parasitized individuals, it is not an unreasonable assumption that prey would like to escape. Given that the prey is now physically connected to the predator, options still remain but their effectiveness hinges critically upon the characteristics of the prey, its predator and their relative size – the epitome of desperate times requiring desperate measures. To our knowledge, the last option for most animals is to give off a distress signal, either vocal (Conover, 1994) or chemical (Chivers *et al*., 1996), that is designed to attract more predators. The idea is that during the ensuing melee among predators, there will be some finite chance of escape. The odds of escape are likely to be very low, but given that this behaviour persists it must be better than zero.

The physical characteristics of the prey may generate one of four outcomes. Providing an armament so impenetrable that the predator is forced to give up either due to time constraints or because the exercise makes no energetic sense. The ability to eject the appendage that the predator has seized allowing the prey to escape. The release of noxious chemicals that forces the predator to release the prey. Or the possession of a unique morphology that makes it possible to pass through the predator's gut and emerge unscathed at the other end.

Armour

Many species have a morphology that strongly suggests it must provide some antipredator benefit. Examples include the quills of porcupines, the stinger of bees, the spines and urticating hairs of caterpillars and the spines and plates of fish, and the shells of virtually any animal possessing one.

As with other features below, one assumes that predators should be selected to be efficient in their foraging behaviour. In particular, they should seek efficiencies in their net rate of energy acquisition. Those species that pose a significant challenge to consumption after capture will make for a significantly less energetically profitable meal. Indeed, such selection should mean that these species may be less likely to be attacked by a predator, and may then exploit this advantage to use environments that are too risky for other species.

Betz and Kölschb (2004) review the use of adhesive chemicals in predator–prey interactions among arthropods. In this system the predator will attempt to physically 'glue' itself or some substance to its prey allowing capture. Such systems are then defeated by prey by quick and powerful physical movement that allows escape before there is a chemical bond. Prey may also coat themselves with substances of low surface energy thereby preventing the adhesive from spreading over the body and providing a stronger bond. Prey may also surrender a part of their body surface, forfeiting a part rather than the whole. This is achieved with a cover of hair or scales.

Prey can also make use of adhesives in their defence and include those that physically bind them to the substrate, preventing them from being consumed by a predator.

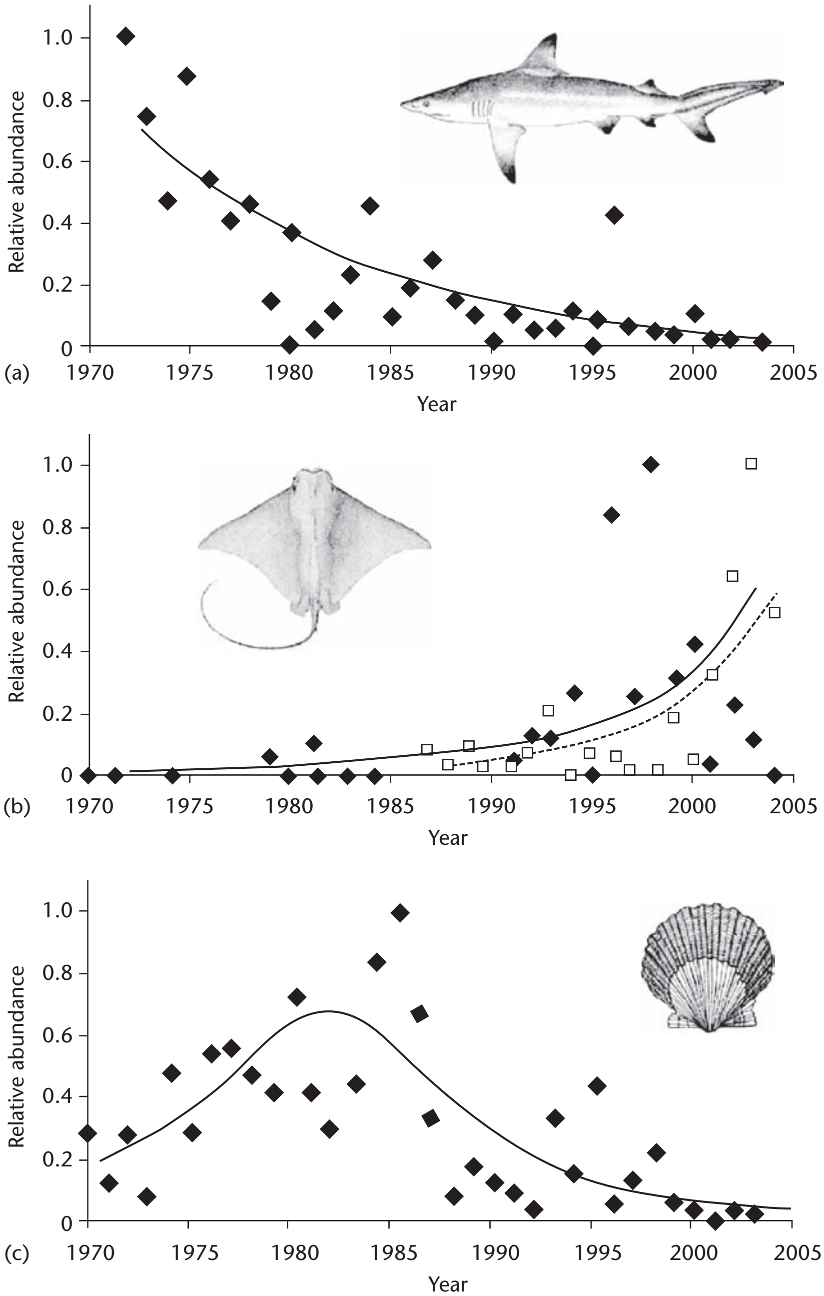

Figure 2 The cascading impact that the removal of predators has upon a marine ecosystem. As (a) catch rates of largest sharks declined, (b) the population of one of their prey, the cownose ray, increased resulting in (c) declines in the catches of North Carolina bay scallops, presumably due to increased predation from the larger population of rays. Reprinted from Heithaus *et al.* (2008). Copyright (2008), with permission from Elsevier http://www.sciencedirect.com/science/journal/01695347.

These adhesives can also be used proactively including a sticky chemical that is sprayed at a predator, gluing its mouth parts together.

Appendage ejection

If seized, some animals have the ability to eject the body part that has been captured by the predator. This process, known as autotomy, allows the animal to sacrifice a body part while retaining its life. The best known examples include the tails of lizards and the limbs of arthropods. However, while these body parts can ultimately be regenerated, it does come at a cost (Naya *et al.*, 2007).

Noxious chemicals

As noted in the section on aposematic colouration and Mullerian mimicry, some animals produce noxious chemicals that are toxic or distasteful to predators. Those that have such chemicals on their exterior (and one wonders why you would do otherwise) have a reasonable chance of being immediately rejected by the predator.

Surviving consumption

Some animals also have the ability to survive being consumed by a predator and pass unscathed out the other end. This ability is limited to very small species (e.g. bromeliad ostracods) and it is not clear from any known examples that their consumption was intentional (Lopez *et al*., 2002). Nevertheless, it does appear that those species that have a morphology that functions to provide resistance to extreme environmental conditions can reap the added benefit of surviving predation. In fact, such a feat can then provide the bonus of allowing these animals to use mobile predators as a mechanism for dispersing to other habitats (Lopez *et al*., 2002).

Revenge from Beyond

Once inside the body of the predator, it would normally be assumed that predator avoidance has been unsuccessful and in the overwhelming majority of cases this is a correct interpretation. However, there are some instances in which prey refuse to give up. Some species of dinoflagellate (a small single-celled aquatic organism approximately 40 μm in diameter) are capable of emitting light when they are mechanically disturbed. One common source of disturbance is when they are being preyed upon by predatory copepods, another small aquatic organism that is also transparent. Abrahams and Townsend (1993) created two groups of dinoflagellates, those that retained the ability to bioluminesce and those that did not. These two groups were then placed in the presence of copepod predators, and the predators of the copepod, a fish. The result was that the ability to bioluminesce increased the mortality rate of their copepod predators. The evolutionary explanation is that this species is clonal so that such mortality imposed upon their predators will ultimately benefit genetically identical kin. Human emotion suggests that under the circumstances, revenge is sweet indeed.

Summary and Future Directions

The simple reality that in almost all instances prey do not want to be killed by a predator has given rise to a range of new insights into ecological processes. Within ecosystems that have been stable for long periods of time, predators and their prey will be in a dynamic equilibrium. Prey species will select habitats, be active at certain times and cooperate (or not) with conspecifics to have some control over their risk of being killed. But this risk can never be zero. To do so would eliminate their ability to obtain resources that are critical for survival and reproduction. The importance of this observation is its application to conservation ecology and the ability to promote biodiversity and resuscitate endangered species. Perturbed ecosystems usually disrupt predators first, with cascading effects that impact many trophic levels (**Figure 2**). This situation is exacerbated as the behavioural traits described above will no longer provide their former benefits. Animals continue to pay the costs associated with these behaviours without reaping any rewards. This is a situation where an ecosystem may be primed for disturbance by an invasive species and once this occurs, it may be very difficult to restore it to its former state. If restoration is the goal, the solution will be more complicated than simply reintroducing the endangered species. Understanding the principles and processes that are important to avoiding predators is both important to the health of an individual and critical to maintaining ecosystems.

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