CHEMICAL DEFENSE IN INVERTEBRATES

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Summary

Some animals can flee dangerous or unfavorable circumstances. Others can fight back with claws, teeth, or cunning, can endure an attempted attack by retreating into a shell, or can avoid attack by blending into their surroundings. Many organisms that do not possess mobility, weaponry, intelligence, structural defenses, or crypsis utilize chemical means of defense against predators, pathogens, and spatial competitors. The study of invertebrate animals and their interactions with predators, competitors, and parasites has led to the discovery of the greatest number of chemical defenses of any group of organisms. Chemical defenses can be unpalatable or they can injure, sicken, or kill enemies. The compounds that act as chemical defenses can be acids, cyanide, small organic molecules, or proteins. The structural classes of these compounds vary greatly: among the small organic molecules: the isoprenoids, polyketides, glycosides, peptides, and alkaloids are all well represented. Organisms benefit from the chemical reactivity of particular compounds by storing inactive forms, which are activated and released upon attack. Some have developed specialized glands and organs to release chemical defenses when in danger. Others release chemical defenses continually, to protect against constant threats like habitat encroachment. Overall, chemical defense seems to be a ubiquitous strategy that enhances the fitness of invertebrate animals.

1. Introduction

1.1. Why be Defended?

For a species to avoid extinction, its members must be defended against various threats that would otherwise prevent them from passing on their genes. These dangers come from other organisms (biotic threats) and from their environment (abiotic threats). Biotic threats include predation, microbial infection, and competition for space and resources from neighboring and settling organisms. Abiotic threats involve physical stresses such as ultraviolet light, wind, water (or lack thereof), and temperature conditions that limit organisms.

Many animals can flee dangerous or unfavorable circumstances. Others can fight back with claws, teeth, or cunning, can endure an attempted attack by retreating into a shell, or can avoid the probability of an attack by blending into their surroundings. Many organisms that do not possess mobility, weaponry, intelligence, structural defenses, or crypsis utilize chemical means of defense. It is difficult to assess whether chemical defense is an evolutionary primitive condition or an advanced one. Prokaryotes and eukaryotes alike utilize forms of chemical signaling, and some notoriously chemically defended organisms, such as skunks and snakes, are higher animals. It is now recognized that even humans possess chemical defenses against microbial pathogens, in the form of antibiotic proteins that function as innate immunity responses. However, a large proportion of animals known to be chemically defended are immobile or slow-moving, soft-bodied, and conspicuous to enemies, and their body parts would be nutritious to predators if it were not for their chemical defenses. Among these traits, invertebrate animals are highly represented. This chapter will use examples from the scientific literature, particularly from the last 10 years, to illustrate mechanisms and ecological consequences of chemical defenses in invertebrates.

1.2. Variations in Chemical Defense due to Selection Pressure

Like other heritable traits, chemical defenses would be lost through evolutionary time if the costs outweighed the benefits to the organisms that possess them. Thus, it is expected that chemical defenses would be more prevalent among organisms that face a greater intensity of threat. In order to test this hypothesis, the palatability of organisms or their extracts have been compared for different communities. Marine sponges in mangrove habitats where there are few large predatory fish were found to be more palatable than sponges growing on fish-occupied reefs, suggesting that chemical defenses are especially important where there is intense predation. In another study, a greater proportion of tropical sponge and sea cucumber species were found to have toxic extracts than temperate ones, correlating with the greater intensity of predation in tropical than in temperate habitats. The studies with marine invertebrates reported similar results to those testing plant–herbivore interactions. In those studies, a greater number of tropical seaweeds were found to be chemically defended than temperate seaweeds, and within the tropics, plants on herbivore-rich reef slopes were less palatable than plants on herbivore-poor reef flats and sand plains. However, Antarctic organisms appear to be highly chemically defended, refuting either the notion that warm habitats have greater predatory pressure than cold habitats or that chemical defenses are correlated with such pressures.

1.3. To Kill or to Deter?

When attacked, the preferred outcome for the victim is survival with minimal injury. Successful use of a chemical defense by the victim could leave the attacker dead from toxic exposure to the chemical defense, alive but physiologically injured or ill, or alive and physiologically unaffected but behaviorally deterred from persisting in the current attack. Otherwise stated, chemical defenses can span a range of useful properties from lethally toxic to merely distasteful. One might predict that lethal chemical defenses are more effective than merely distasteful ones because with a lethal defense the enemy is removed. Certainly, acutely toxic chemical defenses exist, for example cardenolides in monarch butterflies and tetrodotoxin in octopus and pufferfish. However, a larger number of non-lethal chemical defenses are known to cause non-lethal physiological distress to the attacker or behavioral avoidance due to negative taste or smell. Why only hurt or deter an enemy when you can kill one? One possible reason is that compounds that are acutely toxic to an enemy might also be toxic to their host, and therefore these compounds may require specialized storage and deployment structures or may require acquired resistance mechanisms such as toxin-insensitive ion channels.

There are consequences to community structure that may favor less drastic forms of chemical defense than lethal toxicity. Many animals can learn to avoid an unpleasant physiological or sensory experience, even after only one exposure early in life. Thus, a predator exposed to a chemical defense may never again attack the defended organism, or any that resemble it. For the victim, avoidance of future danger is less costly than enduring another attack. A population of enemies who have learned avoidance of defended organisms will be less of a future threat than a population of naïve individuals who constantly test the status of chemically defended individuals. If a chemical defense is sufficiently toxic to kill enemies after one encounter, then the remaining population will be entirely naïve. There is likely to be more selection pressure on the enemy population to overcome the lethal chemical defense (for example, through developing biochemical resistance pathways) than on an enemy population that can survive exposure to a non-lethal defense and then learn to choose other food. However, if food is limiting to the enemy, then resistance to all kinds of chemical defenses will be selected. Because most predator populations are not under constant food limitation, non-lethal defenses should be, and appear to be, more common.

At the other extreme, a feeding deterrent that is only unpalatable without exerting any physiological effect on consumers may be ineffective over evolutionary time if the enemy population is ever food-limited. In that situation, the enemy population will be under selection pressure to overcome chemical defenses in potential prey, beginning by ignoring or losing sensitivity to feeding deterrents that are simply distasteful. However, because many predator populations are themselves more often limited by predation rather than by food availability, feeding preferences may continue to be affected by unpalatable but physiologically inert chemical defenses.

Most chemical defenses appear to fall between the two extremes of lethal toxins and distasteful compounds. These compounds exert on potential predators some negative physiological effect that can be tasted and thus avoided, stopping attacks before critical injury to the victim and leading to learned aversion in the enemy. These chemical defenses present the most successful combination of behavioral deterrence and physiological punishment to potential enemies, lessening the immediate impact of an initial attack and preventing future attacks from that particular predator. Thus, the enemy is no longer a danger to the chemically defended individual, and may further help the latter by competing with individuals that are still enemies.

2. Mechanisms of Acquiring Chemical Defenses

Where do chemical defenses come from? Research aimed at identifying defensive compounds in various life stages of organisms, as well as manipulation of environmental and genetic factors, have revealed the biogeneses of some chemical defenses and led to hypotheses of their evolutionary origins. Generally speaking, defensive compounds are either endogenous (products of the metabolism of the defended organism) or exogenous (products of another organism). Some overlap of these categories exists: some organisms sequester compounds and then derivatize them to more or less toxic forms, and some invertebrate chemical defenses are the products of endosymbionts. Below, the exogenous and endogenous origins of chemical defenses are explored.

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Biographical Sketch

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