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THE CHEMICAL ECOLOGY OF DEFENSE IN ARTHROPODS

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Introduction

Trophic webs are influenced strongly by chemical signals [semiochemicals (105) or ecomones, sensu Pasteels (139, 140)], among which defensive substances play a prominent role. Since the publication twenty years ago of the first review on chemical defense in arthropods (164), a considerable amount of work has been devoted to the identification of new defensive compounds. We will not attempt an exhaustive review of this large body of literature. The excellent and recent books of Bettini (10) and Blum (19) fill this need. The aim of this review is to disclose patterns allowing reasonable predictions as to which arthropods will be chemically defended, against whom, when, where, and how. Defensive compounds also frequently function as intraspecific signals and are discussed in this context.

Some obvious exceptions to patterns of chemical defense are due to mimicry, but space limitations exclude an exhaustive review of this topic. Batesian mimicry is omitted completely, but Müllerian mimicry is examined briefly as a factor that may influence the diversity of defensive secretions. Mimicry in arthropods has been reviewed elsewhere (e.g. 58, 160).

Defense is only one aspect of the chemical interactions existing between arthropods and their enemies. Host- or prey-searching behavior is also mediated by chemical clues, and some predators emit very specific allomones to capture or kill their prey. This aspect is covered in several reviews (e.g. 133, 201).

Chemical interactions between plants and herbivores are already illuminated by theories that permit predictions (78, 79, 111, 161). In this paper the theory of plant chemical defense is used as an analogy.

The number of possibly significant ecological parameters is obviously high, and their interactions are complex. Their relative importance is mostly unknown, and some are still unrecognized. The existing data are therefore complemented by some speculation, and in many cases questions are raised rather than answered.

The Patchy Distribution of Chemical Defense Within the Arthropods

Only a small fraction of arthropods have been examined for their ability to secrete defensive compounds, and some groups have been studied more intensively than others. Our present view of the distribution of chemical defense in the phylum is therefore undoubtedly distorted. Nevertheless, it is clear that chemical defense is very unevenly distributed. For example, the defensive metathoracic glands of the Heteroptera are so commonly present that they are considered characteristic of the taxon (35). On the other hand, chemical defense seems to be absent or rare in the Ephemeroptera or Diptera. Within the Coleoptera, some families are regularly chemically defended, e.g. Carabidae (123) or Tenebrionidae (195, 196), whereas in some other families, e.g. Elateridae, Curculionidae, chemical defense has to our knowledge never been reported. Further, the distribution of chemical defense is often patchy within a given family, e.g. among the Coccinellidae (144), Chrysomelidae (47), Staphylinidae (3, 138), or Tenthredinidae (6, 139) in which chemical defense has evolved several times, and has been lost secondarily in some taxa. Clearly, phylogeny alone does not determine the distribution of chemical defense.

Ecological conditions may be a more important factor. Chemical defense should be positively correlated with the probability of discovery by predators [apparency, sensu Feeny (78)] and negatively with the existence of alternative defense mechanisms. Thus, within the Chrysomelidae, the flea beetles (Alticinae), which possess a quick escape jump, have reduced or even lost the defensive glands that are conspicuous in their slow-moving relatives, the Chrysomelinae. The Hispinae, also Chrysomelidae, have strong cuticular spines covering their dorsum but lack defensive glands (47). Chemical defense, conspicuous in many termite species (149), is absent in the alates; the strategy adopted by swarming alate termites is escape in time (46). In many species, swarming is strictly seasonal and restricted to particular hours of the day or night (134). During swarming the capacity of the predators may also be saturated by the sudden appearance of thousands of insects. On a longer time scale, escape in time and predator saturation are common strategies employed by otherwise relatively undefended organisms, including insects (e.g. 17-year cicada) and plants (e.g. mast fruiting in Dipterocarps). Social insects actively protect their symbionts, so that myrmecophily and termitophily can occur as an alternative to chemical defense in both insects and plants. The tergal defense glands of aleocharine Staphylinidae are strongly reduced and sometimes lost in highly specialized termitophilous species (137). The cornicles are often short or rudimentary in myrmecophilous aphids (209). Ant-acacias have lost the chemical defense of nonmyrmecophyte species (155).

The apparency of a potential prey is determined in part by the nature of the predator. For example, aposematic insects living on herbs are apparent to birds, but nonaposematic insects living on the soil surface are probably more apparent than the former to predaceous ants as they explore the ground in search of food. Several factors influence the apparency of prey: longevity, size, spatial distribution, habitat, and feeding habits, and we shall assess their effect on the distribution of defensive allomones.

Longevity increases apparency and therefore favors defense. Indeed, short-lived insects, e.g. adult Ephemeroptera, are usually not chemically defended. Within the butterflies, the danaids, heliconiids, ithomiines, and acraeids are known to be chemically protected, and at least the first three are unusually long-lived for their group (57, 61). Blest (12) suggested that postreproductive longevity in such unpalatable aposematic insects might be adaptive because it could improve the individual's fitness by educating predators as to the color appearance of its kin; this has not, to our knowledge, been substantiated. On the contrary, longevity is associated with continued oviposition in *Heliconius,* whose pollen-feeding habits provide them with a continuous source of dietary nitrogen, usually thought to limit reproduction and longevity in Lepidoptera (57).

Most known chemically defended insects are large or medium sized. This might be taken to indicate a reduced predation pressure, or selection pressure in a different direction, on small insects. Small arthropods often behave as *r*-strategists, relying upon high reproductive rates and using spatial or temporal refuges (189). They offer little food reward to vertebrate predators; further, they can easily hide and are often cryptic. They are however subject to heavy predation by other arthropods. For example, Collembola are the favorite prey of several species of ants (33). The biological control literature abounds with examples of such predations, e.g. upon aphids and mites by coccinellids, syrphids, hemipterans, or chrysopids. Moreover, chemical defense has in fact been reported in Collembola (200), aphids (60, 171), thrips (109), and in 3 mm-long staphylinids (103). The fact that most identified secretions are from large- or medium-sized insects may principally reflect the attraction that their copious secretions have for chemists.

Chemical defenses are very likely to occur in aggregated arthropods for at least two reasons. First, birds, as well as some arthropod predators, tend to explore longer the surroundings of places where they have already found food (42). Second, gregarious insects frequently come from the same batch of eggs and are thus closely related. The mechanism for the evolution of aposematism may require kin selection favoring signals potentially detrimental to the individual but beneficial to the kin (87). Warning signals associated with toxicity could therefore evolve easily in clumped insects. Gregariousness in aposematic insects also increases the effectiveness of warning signals. Aposematic beetles (69) and Heteroptera (1) emit aggregation pheromones; *Phymateus* grasshoppers are visually attracted to each other (175).

Habitats and feeding habits influence the distribution of arthropods and consequently their apparency and defensive strategy. This is best seen by comparing aposematic and cryptic species of insects. Predators are usually more mobile and dispersed than, say, specialist herbivores. More aposematic species are therefore to be expected among the latter. Some apparent exceptions can be explained on other grounds. For example, some predaceous European ladybugs are commonly found grouped on plants in summer; this aggregation is, however, secondary to that of their aphid prey whose colonies sometimes aggregate on plants of patchy distribution.

At least in the temperate regions, aposematic insects seem to be found more often on herbs or shrubs in open habitats than on forest trees; for example, chemically defended chrysomelids feed primarily on herbs (141) and are aposematic. Bright colors in the Heteroptera are reported to correlate with herbaceous habitats (178). Looper caterpillars (Geometridae) feeding on trees in deciduous temperate forest are cryptic insects par excellence, resembling twigs; but an obvious exception is the aposematic looper caterpillar of the magpie moth *Abraxas grossulariata* feeding on currants, gooseberry bushes, and Ericaceae. Among predaceous insects, the seven-spot ladybug beetle *Coccinella 7-punctata,* preeminently aposematic among the European ladybugs, is commonly found on herbs; species such as *Aphidecta obliterata, Calvia 14-guttata,* or *Myrrha 18-guttata,* which hunt aphids on trees, are far more cryptic.

Among phytophagous insects, aposematism seems to be associated with monophagy or oligophagy. Aposematic chrysomelids are less polyphagous than cryptic species (47). Many aposematic caterpillars are specialists, e.g. *Tyria jacobea, Papilio machaon, Pieris brassicae,* and many other aposematic insects are specialists on toxic plants. Since local food plant preference can be narrower than the total spectrum of plants eaten over the whole distribution area of the species, this trend is difficult to assess from published information. Wiklund (213) made a detailed field census of the host plants of three oligophagous caterpillars in Sweden, *Papilio machaon, Anthocaris cardamines,* and *Leptidea sinapis.* Interestingly, the only aposematic species (*P. machaon*) was also the only one that behaved as a monophage, although nine of its potential host plants were present in the area studied. Such behavior appears to be characteristic of *P. machaon;* 19 different host Umbelliferae are listed as occurring in Fennoscandinavia, but populations of *P. machaon* specialize on different plant species in this family at different localities. An apparent exception to this association between aposematism and monophagy is found in the wide-range feeding romaleid grasshoppers that are known to sequester plant toxins (18, 67) and are aposematic. This may, however, be considered as oligophagy on toxic plants, rather than true polyphagy (C. H. Rowell, in preparation).

Several factors appear to be involved in these trends. Visual aposematism could be more effective in open habitats, and there are probably more hiding places in forests or on the ground than on herbaceous foliage. The association between aposematism and herbs may exist because, according to plant defense theory, less apparent herbs are usually more toxic than perennial trees (78). Herbivore insects can find in those plants toxins that they can sequester and use for their own defense (52, 166); the close association between aposematic insects and toxic plants is amply documented (32, 166). The availability of plant toxins, although favoring the evolution of aposematism, is however not in itself sufficient to explain it. Several aposematic species, both predators and herbivores, manufacture their own toxins, e.g. meloids (188), coccinellids (199), chrysomelids (142), and the staphylinid *Paederus* (36). Insects that store plant toxins may additionally produce their own toxins (168). The cyanogenic glucosides linamarin and lotaustralin found in the Zygaenidae and in *Acraea* and *Heliconius* butterflies are manufactured by the insects themselves, although they often feed on cyanogenic plants (44, 45, 126). The ability to synthesize cyanogenic compounds, and to be immune to them, may have preadapted these insects to cyanogenic plants (166). A similar mechanism is also suggested for arctiid moths (168).

Oligophagy increases the probability of an aggregative distribution for the insects, even more when the food plant is an ephemeral herb and has a patchy distribution. An additional clue is available to predators of oligophages if they are able to recognize specific plants. Some parasitoids use clues derived from the food plant of their host (202). If oligophagy renders insects more predictable to predators as compared to polyphagy, it calls for reinforced defense. Predatory ladybugs feeding on seasonal, aggregated, and food specialist aphids are also themselves highly predictable (see above), and their own chemical defenses may in part be an adaptation to this characteristic.

There are numerous exceptions to the above generalizations about the habitats and feeding habits of chemically defended insects. The black and red staphylinids *Paederus* spp. as well as the black and orange glomerid *Glomeris hexasticcha* live on the ground surface. Several of the aposematic caterpillars listed by Marsh & Rothschild (112) are forest tree feeders, sometimes little specialized in their host plants. A better knowledge of the ecology of toxic aposematic species and of their predators is needed to understand their evolution and distribution. For example, in the forest sawflies *Diprion* and *Neodiprion* feeding on conifers, gregariousness increases the survival of young larvae by facilitating the first attack on tough needles (81). Efficient chemical defense is provided by tree terpenes sequestrated in special foregut diverticula (68). Gregarious life associated with aposematism and chemical defense is thus a more efficient strategy for these forest insects than crypsis and aleatory distribution.

Target Specificity of Defensive Allomones

Most defensive allomones appear to be effective against a large array of potential enemies. For example, the whipscorpion *Mastigoproctus giganteus* repels predators as diverse as ants, solpugids, birds, lizards, and mammals by ejecting a mixture of acetic and caprylic acids (73). Salicylaldehyde secreted by some chrysomelid larvae (141) is both toxic to insects and bacteriostatic (145). The defensive secretion of the fossorial cydnid *Scaptocoris divergens,* a mixture of aldehydes, furans, and quinones, repels ants and is fungistatic (163). Many other antipredator compounds have antibiotic activity (51). Host terpenes regurgitated by sawfly larvae are effective against parasitoids and birds (153) as well as against ants and spiders (68). The sequestration of plant toxins by herbivores is well known as a defense against birds (31, 166) but can also have deleterious effects on the herbivore's parasitoids (52). The lack of specificity of defensive allomones may be selected for by the diversity of predators. Large-scale comparative studies on the activity of defensive compounds on diverse terrestrial predators are urgently required. It remains difficult to assess the specific action of defensive compounds on predators.

Some defensive allomones appear to be directed at specific predators. A few studies suggest that the compounds used for chemical defense in aquatic insects were selected for their efficacy against fish, which are thought to be the main predators in fresh water environments. Miller & Mumma (119) compared the toxicity and anesthetic activity of a large variety of steroids, including those secreted by dytiscids, to the fish *Pimephales promelas.* The most widely occurring components of the dytiscid secretions 4-pregnen-3-ones and related derivatives were among the compounds most active in bioassays. The authors concluded that "the defensive arsenal of dytiscids has been so selected to include only those steroids highly anesthetic and toxic to fish." Hepburn et al (88) tested 25 known arthropod defensive secretions belonging to various chemical classes (acids, esters, carbonyl, or phenolic compounds) on the omnivorous fish *Tilapia sparmanni.* As a rule, defensive secretions produced by aquatic arthropods were more repellent to the fish than those of either cryptozoic or terrestrial arthropods.

Some cases of narrow specificity of defensive allomones are found in arthropod venoms. The venoms of buthinine scorpions contain selective mammal toxins that are inactive on their arthropod prey (219–221). The venom of the harvester ant *Pogonomyrmex badius* is more toxic to mammals than any other known insect venom, and it appears to have evolved as a deterrent for vertebrate predators (184). Although it is a potent neurotoxin for mammals, it is only moderately toxic for insects and is devoid of specific neural toxicity (185). Moreover, indirect arguments are available for suggesting possible patterns of specificity.

Defensive secretions can be roughly classified in three categories according to their mode of action. First, sticky, slimy, or entangling secretions, acting mechanically rather than chemically (19, 64), impair the movement of enemies or glue their mouthparts or sense organs. Like plant gums, resins, or mucilages, they are chemically diverse: proteinaceous as in the millipede *Glomeris marginata* (63, 182) and probably in syrphid larvae (19); terpene resins as in nasute termite soldiers (70, 148); mixtures of C_{22}–C_{27} hydrocarbons and mucopolysaccharides as in the latex of *Coptotermes* soldiers (121); or waxes in various Homoptera, e.g. aphids (60).

Second, nonspecific irritants acting as repellents exert their action via the "common chemical sense" (63, 65). They include quinones, aromatic compounds, small aliphatic aldehydes, ketones, acids, or monoterpenes and are usually quite volatile and rather reactive compounds. Eisner (63) and Happ (85) observed that the acids and aldehydes denature proteins, as do histological fixatives, and are therefore nonspecific. Several authors suggested that they could also act on chemoreceptors by inactivating or overstimulating the receptors (16, 17, 20, 51, 85).

The third category includes true poisons acting at specific sites or interfering with specific physiological processes. Their effect is often delayed, e.g. emesis or vesication (63); but they can also have more immediate effects because of the "bad taste" often associated with poisons. They are usually heavier compounds than nonspecific irritants and are equivalent and sometimes identical to the compounds classified as qualitative defenses in plants (78, 161). Examples of such toxins are the cardenolides found in various insects (31, 143, 167, 187), bufadienolides produced by fireflies (75), cantharidin characteristic of meloids (41, 91), quinazolinone alkaloids secreted by some glomerid millipedes (63, 182), and in all probability many of the various alkaloids sequestered or produced by arthropods (reviewed in 198). The pharmacological properties of most of them are unfortunately still unknown.

These categories are not necessarily exclusive. Hydrogen cyanide is a well-known toxin but probably acts also as an efficient olfactory repellent and interferes with the functioning of the chemoreceptors (107). Cantharidin is a potent feeding deterrent to insects, with possible irritant properties (37).

These different functional categories of defensive compounds can be directed primarily at specific groups of predators, their apparent broad spectrum of action notwithstanding. Entangling secretions are mainly efficient against arthropod predators (19, 63), and sometimes against parasitoids (60). Vertebrates are probably not very affected by these secretions unless they are enriched with more toxic compounds (63). This type of defensive compound seems to have evolved most frequently in slow-moving arthropods, unable to escape quickly after having released their secretion and highly exposed to ant predation, e.g. soil arthropods such as onychophorans (59, 63), glomerid millipedes (63, 182), geophilomorph and lithobiomorph centipedes (120), and isopods (C. De Vroey, unpublished observations). Viscous secretions are also well known in other terrestrial or soil animals, e.g. earthworms and snails (63, 64). Aphid-eating syrphid larvae or ladybugs have a high probability of encountering ants and they too sometimes adopt this mode of defense (64). In coccinellids reflex bleeding deters ants, even in those species that do not secret alkaloids, e.g. *Aphidecta obliterata* or *Rhizobius litura* (J. M. Pasteels and C. De Vroey, unpublished observations). The blood is very viscous in these beetles and clotting is quick. The efficiency of this mechanical defense against ants has been described in detail for the secondarily phytophagous coccinellid *Epilachna varivestis* (86). Termites are handicapped in their fights against ants, which are probably their main enemies (46), by the relative clumsiness of their movements and the slowness of their reactions (70). It is therefore not surprising that besides the emission of volatile irritants like monoterpenes, ketones, or quinones (46, 149), sticky secretions impairing the movement of ants have evolved at least six different times. *Nasutitermes, Trinervitermes,* and related genera (Termitidae, Nasutitermitinae) forcibly eject from their frontal gland a viscous solution of diterpenes in monoterpenes, forming a sticky resin (148). *Coptotermes* (Rinotermitidae) produces in homologous glands a mixture of mucopolysaccharides and hydrocarbons (121). Soldiers of *Odontotermes badius* (Termitidae, Macrotermitinae) use their saliva for defense and secrete a mixture of proteins and quinones, which, when drying, rapidly becomes sticky and rubbery (217). A somewhat similar defense mechanism has evolved independently in the primitive termite *Mastotermes* *darwiniensis* (Mastotermitidae) (121). The soldiers of *Globitermes sulphureus* (Termitinae) burst open when molested, releasing copious, sticky salivary secretions from the ruptured abdominal wall (132). Rupture of the abdomen is also observed in the workers of some soldierless termites (Termitidae, Apicotermitinae) that release viscous fecal material accumulated in large pouches of the hindgut (177). Sticky secretions are sometimes used by ants against larger ants (114).

Volatile, nonspecific irritants appear to be aimed mainly at arthropods, and possibly at mammalian predators, and seem to be less of a deterrent to birds. There are many reports of ants being repelled by these compounds (13, 21, 56, 207, 212). Several things suggest that nonspecific volatiles are aimed particularly at ants or other arthropods. First, because of their small size the ants cannot avoid having their antenna bathed in noxious vapor when they are close to defended arthropods. Volatile deterrents are ideally suited to keep small but numerous predators at a distance. Second, the nonspecific irritants are often produced in admixture with more lipophilic compounds, such as fatty acids, esters, or hydrocarbons, which considerably enhance both penetration through and spreading over the cuticle of the predator (see below). Third, Blum (18) pointed out the similarity between defensive volatiles and the alarm pheromones of ants. He suggested that some compounds could mimic the alarm pheromones, allowing the prey to escape while causing panic in the ants. As with entangling secretions, nonspecific irritants are important defensive compounds of ground arthropods, e.g. ground beetles, tenebrionids, and staphylinids (with the exception of *Paederus* spp.) (reviewed in 211). The stink glands of Heteroptera also secrete volatile irritants (reviewed in 210), especially in species living on the soil surface (178). Other arthropods living on the ground, e.g. millipedes and centipedes, secrete nonspecific irritants, including hydrogen cyanide which can also be a potent but nonspecific toxin (53, 65, 116). Ants themselves are major producers of this class of compounds (reviewed in 22, 23). Maschwitz (114) commented that these chemical weapons supplement the sting apparatus and are more efficient against other ants, their major enemies.

Birds are sometimes deterred by volatile irritants when they are produced in large amounts or when they are sprayed and reach the bird's eyes (62, 73, 74). In many instances, however, the irritants are not sprayed and their effectiveness may be far less. The volatiles produced by many Heteroptera do not repel insectivorous birds (reviewed in 190). Sawfly larvae with well-developed scent glands, like *Nematus* spp., probably produce benzaldehyde (139) but can be heavily preyed upon by birds (6). The notodontid caterpillar *Dicranura* (= *Cerura*) *vinula* secretes a 30% solution of formic acid (183) but is readily eaten by the blackbird *Turdus merula.* The secretion appears, however, to deter parasitoid insects (186). The acid secretion of the ground beetle *Cychrus caraboides* repels small mammals but not the common jay *Garrulus glandarius* (39); however, the bird was never hit near the eyes. It seems that most of the volatiles are lost before reaching any sensitive tissue when the birds manipulate their prey. Subsequent poisoning after ingestion is unlikely because the reactive molecules would be quickly altered in the gut, as suggested for benzoquinones (65).

Specific toxins appear to be much more effective than nonspecific irritants against birds and probably other vertebrate predators. Indeed, vertebrates are more sensitive than insects to toxins such as alkaloids, cardenolides, or hydrogen cyanide (8), although millipedes producing phenols and hydrogen cyanide are preferentially eaten by barbets (Piciformes) and quails are highly insensitive to cardenolides (169). At least in Lepidoptera, aposematism is strongly correlated with toxicity (112). Most of the insect compounds acting as potent poisons when ingested have been isolated from aposematic species: e.g. cardenolides in the monarch butterfly (156, 157), the pyrgomorphid grasshopper *Poekilocerus bufonius* (203), *Aphis nerii* (171), lygaeids (187, 205), the ctenuchid moth *Syntomeida epilais* (173), cerambycids (54), and chrysomelid beetles (43); bufadienolides in fireflies (75); aristolochic acids in some swallowtail butterflies (172, 204), pyrrolizidine alkaloids in arctiid moths (168) and the grasshopper *Zonocerus variegatus* (9); still other alkaloids in coccinellids (144), some soldier beetles (124), and the staphylinid *Paederus fuscipes* (146); cyanogenic glycosides in zygaenids (45, 99), *Acraea* and *Heliconius* butterflies (126), and the rhopalid bug *Leptocoris isolata* (J. C. Braekman et al, submitted); and cantharidin in meloid beetles (49). These toxins are often sequestered from plants, but some are manufactured by the insects themselves (see above). We are not aware of cases of nonaposematic insects storing significant amounts of plant toxins for self-defense, except possibly against parasitoid larvae (34). The production of toxins is probably a prerequisite for the evolution of aposematism (166). Warning signals, which can be learned, are likely to be particularly effective against predators like vertebrates, since the conditioning of predators is rewarding only when the predators are few, long-lived, and frequently encounter prey. Aposematic coloration is recognized as efficient against birds, and other warning signals such as sounds (39, 117), odors (165), or taste (29) have been reported. Poisoning associated with warning signals such as colors, taste, or odors is very effective for the learning of food avoidance by predators (80, 136, 215). Color is a better conditioning stimulus than taste is for birds, but the reverse is true for mammals (214), monkeys being a possible exception (98). At least in rats, odor aversions can be induced if odor is first associated with taste (136). Aversive conditioning occurs often after a single trial, even when there is a considerable delay between ingestion and punishment (80).

The loose target specificity of defensive allomones could help to explain apparent redundancies in some defensive mechanisms of arthropods. For example, *Oncopeltus fasciatus* and possibly other lygaeids secrete both volatile defensive aldehydes (191) and cardenolides (55). All ladybugs emit sticky blood droplets, but only aposematic species contain alkaloids (144). The prothoracic glands of dytiscids produce steroids that are active against fish and amphibian predators (119, 180); their pygidial glands secrete hydroxybenzaldehyde and benzoic acid and various derivatives that are believed to be directed mainly against microorganisms (179). Benzoic acid is, however, an efficient fish repellent (88), and these compounds have not been tested on aquatic insect predators. Specialization in response to different predation pressures could also explain some of the differences in the defensive secretions of different instars of the same species (see below).

Biological Significance of Mixtures

With very few exceptions, defensive secretions appear to be remarkably complex mixtures. This is even more evident when minor constituents are searched for systematically. The defensive secretion of the staphylinid *Drusilla canaliculata* contains no less than 14 compounds: 4 aldehydes, 5 hydroquinones, 1 quinone, and 4 hydrocarbons (28). Gilby & Waterhouse (83) identified 18 components in the secretion of the stink bug *Nezara viridula,* and Tschinkel (197) identified 13 compounds in the defensive secretion of the tenebrionid *Eleodes beameri* and listed 10 additional unidentified constituents.

This complexity is poorly understood. Synergism between constituents has been demonstrated; many volatile irritants are polar, and their effectiveness is greatly enhanced by more lipophilic constituents, which facilitate the spreading of the compounds on the cuticle of arthropod predators and their penetration through it (72, 73, 158). The *n*-nonyl acetate present in admixture with formic acid in the defensive spray of the carabid genus *Helluomorphoides* greatly increases the sensation of burning pain because it enhances the penetration of formic acid through human skin, suggesting a synergistic effect on vertebrates as well (72). Some constituents could also delay evaporation of more volatile ones, prolonging the activity of the secretion (see 25). It is thought that the main function of only slightly toxic compounds such as hydrocarbons, which are commonly found in defensive secretions, is to act as surfactants, penetrators, or evaporatory retardants, but some authors have suggested that these compounds could have a less obvious but important defensive role by interfering with chemoreception (16, 20, 51).

Defensive compounds are often poisons for living tissues, including those that secrete them. Consequently, the final steps of biosynthesis are often performed in extracellular spaces or reservoirs (66, 84, 181). Some of the constituents of the defensive secretions may be precursors or byproducts of these final reactions. An obvious example, glucose may occur when the precursors of the active compounds of the secretion are glucosides (26, 94). The enzymes catalyzing these last steps are themselves sometimes detected in the secretion, and it has been suggested that this could be reason for the presence of the protein fractions detected in otherwise nonproteinaceous secretions (2).

In many cases, the diversity of defensive constituents within the same secretion remains unexplained and appears unnecessarily redundant. Tschinkel (196) suggested that "within limits, the chemical nature of the compounds is of not great importance as long as the secretion meets certain physical requirements (lipophilicity, volatility, melting point, irritant value)." This could allow much diversity that is not necessarily of adaptive significance. The complexity of defensive blends could also be a way to avoid counteradaptation by predators, but there is no evidence to support this hypothesis.

Intraspecific Variability in Defensive Secretions

Individuals of the same instar and sex may produce secretions differing in quantity and quality [reference in (19)]. Some variation only reflects stages in biosynthesis (19, 191, 194) or regeneration after depletion (208). Seasonal variation is described in water beetles and can be at least partly related to age differences and to the frequency of utilization (118, 128, 129).

Genetic polymorphism in defensive chemistry is poorly documented, but mutants differ in their biosynthesis of defensive compounds and in their sequestering of plant toxins (76, 168), and considerable variation can occur between various morphs of *Danaus chrysippus* from the same locality (174). Intraspecific variation in chemical defense could reduce counteradaptation (see below), as in plants (4, 50).

Interpopulation variation probably reflects genetic differences. The defensive secretions of different populations of tenebrionids (196), chrysomelid adults (43) and larvae (141), ants (27), and termites (150) differ qualitatively and quantitatively. The storage of cardenolides also appears to be different in various populations of the butterfly *Danaus chrysippus* even when reared on the same food plant (174). In the chrysomelid beetle *Chrysolina polita,* populations differ in the TLC patterns of cardenolides; the differences remain constant in successive laboratory generations reared on various species of mint (43). No satisfactory adaptative explanation has been proposed for such genetic differences. They may be due to a lack of specific selective pressure, perhaps exemplified by the different proportions of diterpene found in *Trinervitermes bettonianus* (150). The diterpenes form a sticky resin when dissolved in monoterpenes (70), and Prestwich (148) suggested that "a higher overall concentration of glue molecules can be obtained if there is a mixture of structural type." A mixture is selected for, rather than any one precise combination.

Sexual Differences in Chemical Defense

Female aposematic Lepidoptera have been reported to be more toxic or emetic than males (30, 112). These sexual differences may merely reflect the fact that a large amount of toxins is incorporated within the eggs, e.g. in *Arctia caja* (170) and *Zygaena filipendulae* (44). Until this hypothesis is disproven, more complex evolutionary explanations seem unnecessary.

In several instances, the ability of males to synthesize noxious compounds seems to be greater than in females. For example, in the adult spanish fly *Lytta vesicatoria* only the males are able to manufacture cantharidin, which is stored in the accessory glands of the male sexual organs and injected into the female during copulation (188). The metathoracic repugnatorial gland is better developed in some male Heteroptera than in females (reviewed in 190), but the reason remains unclear. Strongly odorous substances are transferred by males to females during mating in the butterfly *Heliconius erato* and probably act as antiaphrodisiac pheromones (82). It has also been suggested that the odor could have a more general defensive function (40). So-called aphrodisiac pheromones in Lepidoptera are often identical to well-known insect defensive compounds. Their role in courtship has been established in only a few instances (5) and they could well have a defensive function (11). The production of defensive compounds by males and their transfer to females could spare the female the cost of their synthesis and may represent male investment in the brood. Moreover, their release during mating could protect insects in copula.

Differences in Chemical Defense Between Instars and Castes

In the chrysomelid tribe Phaedonini, larvae secrete from segmental abdominal glands autogenous volatile cyclic monoterpenes or salicylaldehyde derived from the food plant (141, 176). In contrast, the adults secrete isoxazolin-5-one glucosides and corresponding nitropropionate derivatives (141). Both the larvae and the adults eat the same plant. Larvae are less conspicuous than the aposematic adults. These differences in defensive chemistry may reflect a difference in the nature of the main predator (see above). The composition of the osmeterial secretion of some swallowtail caterpillars changes at the fourth ecdysis (93) from a complex mixture of mono- and sesquiterpenoids into various carboxylic acids and related esters. These chemical changes are synchronous with a complete change in appearance. Young larvae are cryptic; the last instar is aposematic. The role of carboxylic acids and esters is obscure. They are effective against ants (71) but, at least in *Papilio machaon,* they are not necessary to induce rejection of the caterpillars by birds; larvae deprived of their osmeterium are also rejected (97). The odor of the osmeterial secretion is more intense in the last instar (93). It may act as an additional warning signal for vertebrate predators; this remains pure speculation, however.

More difficult to interpret are the differences observed between the volatiles produced by larval and adult Heteroptera [reference in (190)]. For example, in *Corixa dentipes, trans*-4-oxo-oct-2-enal constitutes ca 92% of the larval secretion, but *trans*-4-oxohex-2-enal accounts for 95% of the secretion of adults (192). No ecological interpretation has been given for such a small but striking difference.

The defensive devices of insect eggs have been reviewed by Hinton (90). Toxins present in the females may be transferred to the eggs, sometimes during oviposition. They appear to be long-lasting feeding deterrents or contact repellents on the surface of the eggs. The female meloid beetle covers the eggs with cantharidin received during copulation from the male (38). Similarly, *Culex* and *Culesita* mosquitoes deposit defensive fluid on each egg (89, 90).

Remarkable differences are sometimes observed in the composition of the defensive secretions of different castes of the same colony of social insects. Thus in the termite *Ancistrotermes cavithorax* the labial gland secretion of the small soldiers differs from that of the large soldiers. The minor soldiers produce the sesquiterpene ancistrodial, the major soldiers secrete the isomeric ancistrofuran in admixture with a bicyclic unsaturated dialdehyde, small amounts of toluene, and α- and β-cyclogeraniolenes (77). These subcastes most probably originate from different female instars during postembryonic development (131). Small soldiers usually accompany the foraging parties while the major soldiers stay in the nest (100), but this polyethism has not yet been related to the chemical composition of the defensive secretion.

Convergence or Divergence of Chemical Defense in Sympatric Species

Defensive allomones are usually considered at the species level, and comparisons are made on a taxonomic basis. They have rarely been considered at the community level; this is necessary, however, if one is to understand their function and evolution.

Rothschild (165) suggested that the strong odor characterizing many aposematic insects could act as an additional warning signal for predators and that Müllerian mimicry of odors could be frequent. This would predict a convergence of defensive odors in sympatric species. The odors of different aposematic beetles, e.g. lycids, cerambycids, and coccinellids, are chemically identical (125). We suggest that convergence of odors would be favored when the odor is distinct from the main toxin, as is apparently true in many aposematic species (125, 165).

Parallel evolution of identical defensive allomones has been observed in completely unrelated species (reference in 19). Convergence, however, does not appear to occur between nonaposematic species. For example, the defensive secretions of closely related chrysomelid larvae show distinctly different mixtures of monoterpenes (141). These differences are of the same order of magnitude for both sympatric and allopatric species. Chemical diversity within a community could limit the ability of predators to overcome defensive allomones. Habituation of fish predators to a given chemical has been reported, and this should favor divergence of secretion among sympatric species (88). Moreover, the predaceous sawfly *Tenthredo olivacea* can be conditioned to select as prey sympatric chrysomelid larvae, differing principally in their defensive secretions but not in physical appearance (J. M. Pasteels and J. C. Grégoire, unpublished results).

Pheromonal Functions of Defensive Secretions

Defensive allomones can easily turn into alarm pheromones in social or gregarious insects. In several gregarious Heteroptera (95, 108, 115), but not in others (1), the alarm pheromones that cause the dispersion of the insects when attacked are the major defensive allomones. In various termites, the alarm pheromones are defensive monoterpenes (122, 206). In several aphids, the waxy secretion from the cornicle contains alarm pheromones, either trans-β-farnesene or germacrene A (127, 130). Alarm pheromones in social Hymenoptera are usually produced in defensive glands, often in close connection with the main weapons, the mandibles and the sting (15, 113).

Wilson & Bossert (216) speculated that alarm is best accomplished by rather simple volatile compounds, even at the expense of specificity, which is of little importance in this context. As seen above, the emission of volatiles is also an effective chemical defense against arthropod predators and is frequently encountered in arthropods. Thus both alarm and defense have similar physicochemical requirements.

In higher Hymenoptera, defensive allomones often alert recruits and are emitted in other contexts than the defensive. Formic acid recruits ants in several formicines, not only during defense but also during predation (113). It is the "leading pheromone" emitted by recruiters of *Camponotus socius* to guide nestmates towards food (92). In several meliponine stingless bees, the mandibular secretion is used to build aerial recruitment trails leading to food (102). The terpenic mandibular secretion of the meliponine bee

Lestrimellita limao is an intraspecific attractant, but it is used as an offensive deterrent during raids against *Trigona* bees (14). Ants similarly utilize defensive secretions from the Dufour or poison glands while sacking other ant nests (24, 154).

Bergström & Löfqvist (7) suggested that ants could specifically label foreigners or intruders with their defensive secretions. This could partly explain the complexity of some secretions, like those of the Dufour glands in which specific minor compounds are often observed (19). This attractive hypothesis remains to be tested.

Defensive secretions are also reported to act as assembling scents in gregarious insects. The secretion from the pygidial gland of the tenebrionid *Blaps mucronata* acts as an alarm pheromone when produced in large quantity, turning into an aggregative pheromone after 14 to 48 hr (193). In the stinkbug *Eurydema rugosa trans*-2-hexenal is an alarm pheromone but acts as an aggregation pheromone for the first instar when emitted gradually in very small quantities (96). The dorsal abdominal glands of *Dysdercus intermedius* produce a secretion that is suspected to influence aggregation (218). However, evidence for the participation of defensive substances in the aggregation of Heteroptera has been questioned (190). The source and nature of the assembling scents remain unknown in *Cimex lectularius* (106) and in aposematic coreids (1). In the acanthominid bug *Elasmucha grisea* the cohesion of larvae and mother is assured by a trail pheromone released by the larvae (115).

To our knowledge, in only two cases were defensive secretions reported to repel individuals of the same species, favoring dispersions. The flour beetle *Tribolium castaneum* utilizes its defensive quinones to repel conspecific adults (110). Adult leafbeetles *Gastrophysa viridula* are repelled by the defensive secretions of the larvae. This avoids overcrowding of insects on single plants and could be highly adaptative in specialist herbivores (159). Many epideictic pheromones are continuously deposited by herbivores while feeding (reference in 152) or by some parasitoids during exploration (e.g. 151). Communication by pheromones requires only minute amounts of the compounds. In contast, high concentration of chemicals are discharged suddenly in defense. This could limit the overlap between epideictic and defensive functions.

Arthropods Versus Plant Chemical Defense

Arthropods and plants often use the same chemical weapons for defense (162). The biological status of plants and that of arthropods are so distinct, however, that divergences must be expected, at least in the relative frequency of occurrence of particular modes of protection or in the ways both groups use chemicals for defense. Plants can regenerate and survive even after large parts have been bitten off. A single wound can be fatal for arthropods, but they are usually able to flee and to control the emission of their defensive secretions. Selective pressure is much stronger in arthropods for the development of a chemical defense effective at the earliest instant after an encounter with a predator or, even better, before. Repellent secretions (best served by volatiles) and warning signals dominate arthropod defensive strategies, whereas feeding deterrents [sensu Dethier et al (48)] and antibiotics are more frequent in plants. Arthropod defensive chemistry is dominated by small molecules stored as highly concentrated mixtures in external reservoirs invaginated in the body. Of the 304 terrestrial Coleoptera listed by Weatherston & Percy (211), 283 produce compounds with a molecular weight less than 150.

Some remarkable adaptations have been observed in arthropods that allow the predator to reject toxic insects by taste only. In the monarch butterflies, cardenolides are more concentrated in the wings, which are the part first bitten by birds (30). Most of the cardenolides present in chrysomelid beetles are concentrated in the secretion that covers the pronotum and elytra as soon as they are attacked. The concentration of cardenolides in the secretion has been estimated to be as high as O.2 M for *Chrysolina herbacea* (143). The bug *Oncopeltus fasciatus* emits dorsal droplets of fluid in which the cardenolides are concentrated at the level of more than 150 μg/μl (55). The rejection of unharmed aposematic insects by birds is very common and it has been postulated that individual selection alone may be sufficient to explain the evolution of aposematic coloration (97, 214).

Arthropods, with the possible exception of some social insects, are a far less predictable source of food than apparent plants. Quantitative defenses similar to those of trees are only expected in some social insects, e.g. perennial termite and ant societies living in densely distributed, apparent nests. In termites like *Nasutitermes* or *Trinervitermes,* chemical defense is ensured by sterile soldiers. Defense is their sole function; they are even unable to feed themselves. Their proportion varies from 10 to 30% of the active population of the society (46). About 15% of the annual production of *Trinervitermes geminatus* is devoted to the production of soldiers (101). The soldiers produce a mixture of di- and monoterpenes, a chemical defense quite similar to that of coniferous trees (148). Each major soldier of *Trinervitermes gratiosus* contains about 315 μg of terpenes, i.e. 8% of the fresh weight (147); this would represent 45% of the energy equivalent (in joules) of the soldiers as estimated by Josens for a very similar species (101). This quantitative defense is effective against vertebrate predators. The earth wolf *Proteles cristatus* is specialized for feeding on *Trinervitermes bettonianus,* which forage in the open in South Africa (104). This entomophagous hyaenid is only able to capture small numbers of termites at the start of its attack, when the workers still largely outnumber the soldiers. The workers quickly withdraw, but soldiers are recruited to the place of disturbance. The earth wolf seems unable to feed on soldiers only, and is apparently repelled by the strong concentration of terpenes.

Quantitative chemical defense is also spectacular in some ant species. Workers in the subfamily Formicinae are well known for the large amount of formic acid they store in the reservoir of their poison gland. In European *Formica* spp. the concentration of formic acid in the venom reaches 61 to 65% (135). According to the figures of Osman & Brander [Table 1 in (135)], the amount of venom per worker of *Formica polyctena* varies from 0.7 to 1.4 mg, which represents from 9.5 to 13% of their fresh weight. Unfortunately, precise data that would allow a comparison of investments in chemical defense in social and nonsocial insects are lacking.

Chemical defense has been secondarily lost in many termitids, perhaps because it is so costly. Defense is then transferred to intricate nest structures from which the inhabitants are very difficult to disentangle (J. Deligne and J. M. Pasteels, in preparation). Perhaps the nest material in these species is another analogy to the quantitative defenses of apparent trees.

Conclusion

Blum (19) lists 316 empirical formulae of compounds used by arthropods for defense. The total number of known allomones is even greater because of the existence of isomers. Among the small molecular weight compounds, these allomones range from chemicals as simple as hydrogen cyanide or formic acid to cardiac glycosides or alkaloids as complex as pederin.

In this review, we suggest that, despite their great diversity, patterns of occurrence of defensive compounds can be recognized. The distribution of chemical defense depends on the "apparency" sensu Feeny (78) of the prey to their major predators. Monophagous or oligophagous herbivores may be more predictable for predators if the latter use plant clues in their search. Insects feeding on herbs may sequester toxins from their food plants, and clumped distribution resulting from the patchiness of the herbs increases their apparency and favors the evolution of aposematism by kin selection.

Notwithstanding their apparent broad spectrum of action, defensive compounds are not equally effective against the various types of predators. Entangling secretions are effective against small arthropod predators. Volatile nonspecific irritants are effective against arthropod predators, and maybe against mammals, but less so against birds. Entangling secretions are expected in slow-moving animals and volatile irritants in faster ones. Specific toxins are probably the most effective chemical defense against vertebrates, which can additionally be conditioned by warning signals. Apparent redundancy in chemical defense or differences between instars may be partly explained by this target specificity.

Complexity of defensive mixtures is partly accounted for by the need for synergism between compounds and partly by the presence of biosynthetical byproducts or precursors. In some instances a mixture of compounds with certain physicochemical properties is selected for; this allows a great variability in the precise composition of the defensive secretions. Sexual differences in chemical defense can be interpreted in part as different degrees of reproduction investment between the sexes.

Convergence in the warning signals of sympatric species can occur, but convergence in the toxins themselves is improbable. Divergence of defensive secretions, impairing possible adaptation by predators, could partly explain the complexity of some secretions and their interspecific variation in sympatric species.

Some defensive compounds have additional biological meanings, e.g. as pheromones. These functions must also be considered when evaluating the ecological significance of chemical defense.

Quantitative defenses analogous to those found in perennial trees are found in some social insects in which the investment in nonspecific toxins is considerable. While comparing the chemical defense of plants and arthropods, we suggest that the emphasis on instantaneous defense is much greater for the latter. This explains why volatile irritants and warning signals, associated with toxins, dominate the chemical defense of arthropods.

The generalizations proposed in this review are sometimes based on indirect or scarce information. They should be considered as heuristic predictions needing confirmation or amendment. A better knowledge of the precise mode of action of defensive compounds is urgently needed, preferably within an etho-ecological framework in which parameters such as the apparency and predictability of prey species under natural conditions play an important role.

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