

Chapter 6

Evolutionary Physiology of Personal Defence

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6.1 INTRODUCTION

In general, allocation of resources among defence, repair, storage and growth is moulded by natural selection to maximize the organism's genetic representation in future generations through the medium of sexual reproduction. Here, I emphasize the use of resources for personal defence against predators and parasites. Defence against 'the elements' and against competitors are not directly discussed.

At the outset it must be stated that a predator is a consumer that kills its prey for immediate consumption and that a parasite is a consumer that removes so little of the host's tissue or resource that the host is not directly killed by this act. A predator may therefore be a cobra swallowing a viper, a mouse gnawing up an acorn, a pitcher plant drowning a beetle, or Dutch elm disease killing an elm. A parasite is a mosquito on the back of your hand, a moose browsing a large willow, a black bread mold growing on a mouse's grain cache, or a mycorrhizal fungus on an oak seedling's roots at a time of year when the seedling does not have carbohydrates to spare. Clearly there is a broad grey zone between these two categories, a grey zone that has generated words such as parasitoid (exemplified by an ichneumon wasp larva that takes two months to kill its caterpillar host), hemi-parasite (exemplified by snapdragons that are both tapped into other plants' roots and harvesting their own ions) and mutualism (reciprocal parasitization where for both members the loss is less than the gain and exemplified by bees and flowers).

The array of defence traits is more diverse than is any other array of traits. Mating and sexual isolation traits are of course diverse, but in general each beast or plant is dealing with one acceptable type of organism and *all* the rest are unequivocally unacceptable (except in cases where interspecific introgression is of value to the introgressed). One or a few exclusion rules or traits keep out the unwanted visitors; there isn't much demand for interspecific

rape. Not so with the beasts that eat your body and suck your blood. Every species of organism is confronted with easily enough different kinds of predators and parasites to require a multitude of different defences. For example, a seed, hardly more than an embryo with a packed lunch, has at least the following defence traits: synchronous maturation with its sibs and conspecifics; maternal protection through green (immature) fruit hardness and secondary compounds; maternal protection through mature (ripe) fruit; attractiveness to the right animals and unattractiveness to the wrong animals; cryptic colouration of the seed coat; seed-coat hardness and secondary compounds; seed shape and specific gravity that determine its passage rate through a digestive soup; and numerous secondary compounds in the endosperm, cotyledons and embryo (e.g. indigestible starch and other polysaccharides, toxic proteins such as lectins and protease inhibitors, alkaloids and uncommon amino acids, cyanogenic glycosides or cyanolipids, digestion-inhibiting polyphenols and saponins, etc.). A list could be made of several hundred organisms which would eat any given seed if they could get by one or more of the seed's defences; each attacking organism carries a repertoire of largely unique tools for disarming its prey or host, in addition to its more generalized tools.

There are two quite different ways to organize a discussion of defences. I could catalogue known defences and reference examples of each. However, in keeping with the attitude in this book, an attitude usually missing in discussions of defence traits, I will attempt to generalize about the processes in common among personal defence systems, and leave it to the reader to decide if it applies to the particular system he or she is intimately familiar with. As is usual in ecology, the subjects of this essay do not fall in a neat linear hierarchy and no order of importance or 'key position' is intended by my order of discussion. Many of the references cited contain detailed discussions of the mechanics of defences. The interested reader is particularly referred to reviews in Robinson (1969), Harborne (1972, 1978 a and b), van Emden (1973), Zlotkin (1973), Gilbert & Raven (1975), Levin (1976a), Atsatt & O'Dowd (1976), Rugieri (1976), Wallace & Mansell (1976) and Rosenthal & Janzen (1979).

6.2 MULTIPLE USE

Actual defence structures or traits—a spine, fang, raphide, alkaloid, antibody, jump, bite—are very likely to be programmed by more than one gene and to be of several quite different uses to the organism. In like manner, the actual costs and fitness gains attributable to the structure will be intricately apportioned among

the different uses. Did snake fangs appear as a response to the value of immobilizing the snake's prey (protection against your prey and enhanced prey-capture ability) or as defence against predators, or both? If we elect the former role, which seems most reasonable, it is still clear that in at least one case, the spitting cobra, one aspect of fang use has been subsequently modified to a purely defensive role (Janzen, 1976c). The cyanogenic glycoside linamarin, which probably protects wild lima bean seeds from a variety of potential predators, is moved by the new seedling into vegetative tissues where it probably serves the same protective role as in the seed but against quite different organisms (Clegg, Conn & Janzen, 1979). However, another seed defence, canavanine, appears to be degraded in part by the seedling as a source of nitrogen in the first several weeks after germination (Rosenthal, 1977). Cellulose, long viewed solely as the master construction material of plants, was probably evolutionarily chosen for the same reason that we construct houses of concrete in areas of high termite activity. There are many structural polysaccharides. It is extremely unlikely that natural selection produced cellulose-rich plants for any other reason than that virtually no higher organism can digest it unaided. Needless to say, the plant 'pays' an enormous cost for this defensive indigestibility; it deprives itself of many repair options and cannot recover the primary carbohydrate from leaves and other plant parts to be shed. However, it is equally striking that plants apparently can enzymatically degrade their own cellulose when producing lateral roots (M. McCully, personal communication) and therefore it appears they can overcome their own defences when the return is high enough. The ultimate outcome of the multiple-use aspect of defence traits is a strong heterogeneity in the world's defence contour. A large viper very rarely uses its fangs for defence and they probably would never have evolved solely for this purpose. However, once evolved for prey capture, viper fangs are present as a horribly intense defence against a rare threat to one of these large reptiles.

6.3 UNTRIED DEFENCE

The function of each defence trait has an active and a passive component. The vast majority of the tannin molecules in oak leaves never see the inside of a herbivore. It is a classic error in herbivory studies to measure herbivore impact only by the amount of materials they eat or by the reduction in fitness caused by herbivory. I suspect that for most plants the biggest cost of herbivory is the cost of the defence chemicals, morphologies and phenologies that keep the bulk of the herbivores away. In other words, to determine the 'size' of the

herbivore trophic level, one has to measure not only its biomass and turnover, but also how much resource its presence causes the plants to put into defence, resources that cannot then be used, either directly or indirectly, for reproduction. This principle applies to all trophic levels.

Are untried defences recyclable? The cyanogenic glucosides in a surviving seed are translocated to the new seedling, presumably as part of its defence. The cellulose in a leaf is discarded in the autumn. Snake fangs are used for prey capture between defence bouts. The quills of a porcupine are shed as they age; they are dead tissue from the time they are fully formed on the animal. As a general rule, defence recyclability seems to fall into three categories: structures that are largely for defence and are often made of dead tissue or tissue that is non-degradable to prey and predator alike; structures of living tissues that are usually recyclable and of multiple use; and facultative defences that appear only at the time of the challenge.

Behavioural and physiological traits that appear at the time of the challenge (adrenalin, fever, skunk spray, running, threats, motionlessness, increased liver and kidney metabolism, antibodies, etc.) are well known to zoologists. Analogous traits have been well known in plants since the turn of the century, with respect to phenolics and other defence compounds and chemicals elaborated at the site in response to fungal and microbial attack. Likewise, African observers have often noted that the branches of arid-land *Acacia* respond to browsing by the production of longer thorns, smaller leaves and shorter internodes. However, it was only in the late 1960's that Ryan and his co-workers began to explore the production of protease inhibitors in leaves in response to leaf chewing by insects (Ryan, 1978).

6.4 HOW LARGE IS A DEFENCE?

There is a strong temptation to measure the intensity or size of a defence by its impact on the human that encounters it; it is hard to think of a more irrelevant measure. If a human consumes the products of three ground coffee seeds and gets a mild caffeine kick, coffee is labelled as non-toxic. However, a mouse that tries to eat a coffee seed may be making its entire meal of this alkaloid-rich food and the effect may be as though a human ate a kilogram of ground coffee in one meal. Although consumption of more than 30% rhododendron leaves in the diet causes rickets in deer, rhododendron leaves have been labelled 'non-toxic'; ever see a deer with rickets try to outrun a mountain lion? You may find that you can acclimatize to stinging nettles and acacia-ants; try eating them. A medium-sized parrot can draw blood and sometimes hurt a human slightly;

there is an instance where a parrot broke both wings of an attacking hawk with its bill.

The same caution applies to analyses of why certain parts seem to be defended differently to others. Why should some species of seed be so well defended when the plant makes so many? After all, it only takes one to replace the parent, or so the folklore goes. One of the many answers to that question is that the seed is well defended for the same reason that a young man protested at being sent to Vietnam. The tiny amount of material lost when a shoot apex is eaten is nothing compared to the loss of competitive height status in the time it takes for the plant to replace its shoot tip with an axillary bud. A mutant cedar tree with bubbles of a few milligrams of resin in its seed coats may have a much greater fitness than a mutant that puts massive amounts of resin in its cambial region. The human vascular system can withstand the loss of 100 mosquito stomachfuls of blood in one night, but such an event may give severe anaemia to a mouse. Your defence may be to swat the mosquito or ignore it; a mouse may spend many hours building a mosquito-proof nest or burrow.

6.5 WHY STENOPHAGY?

There seem to be three sorts of phytophagous insects: extreme polyphages which really can feed on many species of plants, host-specific polyphages that have a list of 2–15 or so species of plants (out of hundreds available in their habitat), and monophagous stenophages that feed on only one species of plant (in a habitat rich in plant species) (Janzen, 1980a). There are two puzzles about this defence–parasite interaction.

- 1 Why are those species that are capable of eating the foliage (or seeds) of many species not capable of feeding on all of them? The dogma is that those which they cannot eat contain some collection of defences which is simply insurmountable to that particular polyphage. However, since each polyphage has a different list of plant species that it can feed on in the *same* habitat (e.g. Rockwood & Glander, 1979) why isn't there one species of herbivore that has the combined defence capabilities of all of them (a sort of mega-army worm; Brattsten *et al.*, 1977)? Part of the answer may lie in a falsehood in the above background. It may well be that the most highly polyphagous species of insects are in fact largely stenophagous or even monophagous as individuals, and therefore the question and its answer move on to the next paragraph (see below). In this view, then, a large herbivore (cow, elephant) that unambiguously eats many species of plants

can be viewed as many herbivores as represented by the various strains of microbes that its gut contains. The large vertebrate herbivore is also, I should add, acting like a human drinking a cup of coffee; it is digesting at a level of toxin dilution at which the damage is less than the gain.

- 2 If one insect can be stenophagous on one species of presumably well-defended plant, and another species of insect can do the same on another species of plant, why can't there be a third species that possesses both of these quite separate defence degrading systems so that the same individual can feed on either plant species at any time? Furthermore, why can't an insect carry even more quite separate detoxification systems? The answer is not that there is so much resource that there is no selection pressure for such an event to occur. The answer is probably similar to the answer to why a soldier cannot be a warrior, a tank gunner, a radio communications specialist and a demolition expert simultaneously in the same war. Or the answer to why there can be no parrot-like hawk that preys on both mice and large hard tropical seeds.

6.6 ANACHRONISMS AND MISSING ATTACKERS

The study of defences has one particularly difficult aspect. You cannot study the defences of mice against owls in the daytime. Likewise, even if canavanine can be eaten in bulk by an English mouse, it may nevertheless be an effective defence of a Costa Rican canavanine-rich *Canavalia* seed against both the insects and the mice in its native habitat. If a *Cecropia* tree leaves its ants behind when it migrates to an island (Janzen, 1973a), and the *Cecropia* tree does well on the island (or in your garden), we cannot conclude that the *Cecropia* tree was not protected by its ant colony in its original mainland Central American habitats. Experimental demonstration of defence biology requires not only the prey but the predator to be present. This statement applies to both temporal and spatial heterogeneity.

In short, the individual organism cannot know when an attack is going to come, or even if there are any attackers out there. It can only genetically 'know' that there is some probability that an attack will come. In a certain sense, DNA programming may even be viewed as a defence against the costs of being inexperienced and learning by trial and error (W. Hallwachs, personal communication). The problem of missing challengers becomes even more *intractable when the defence trait is something also functional in some other context* (e.g. wasp stings as nest defence and wasp stings as subduers of prey). Some defences do not get used very often even as the normal state of affairs.

Then there is the complication of the missing evolutionary partner. There may well have been a time when wasps did not protect their nests well, and a number of vertebrates made much of their living preying on the nests. As stinging defences became more sophisticated, these vertebrates evolved other modes of prey capture. The same defences have then also prevented the evolution of new specialists in later millenia because the intermediate stage, as a moderately incompetent wasp nest predator, was too inhospitable. The thick hard nuts of palm fruits may well have evolved in response to mastodon or ground sloth molars 10 000 years ago (Janzen & Martin, 1981), and the contemporary interaction of the nut with nut-crushing peccaries (Kiltie, 1980) and nut-gnawing agoutis (Bradford & Smith, 1977) is pure serendipity.

The opportunity for evolutionary cycles, for anachronisms, for phylogenetic inertia and for uninterpretable natural histories is very great when such a scenario is replicated over millions of animals and plants and their personal defences. I suspect that tropical forests are living museums full of anachronisms left behind by the extinction of one member of a co-evolved pair of species. Even worse for the evolutionary biologist, we are not only dropped into the system knowing nothing of past trends, but nowadays we are often allowed to study only one or two of the members of complexes of defender and attackers. How can one hope to understand the extreme aggressiveness of the African honey bee (Fletcher, 1978) in contemporary habitats with most of the potential honey bee nest predators locally extinct or substantially reduced in density, nest sites greatly reduced in quality and quantity and the genome contaminated by introgression from docile European yard bees.

6.7 CO-EVOLUTION?

The fashion of the day is co-evolution. Every pair of mutualists, parasites and hosts, and predators and prey gets slapped with this label. This is one of those crazy cases where the general theory is probably fine yet often does not apply at all to many of the specific cases. Of course a pair of complex congruent interactants may be co-evolved, but they also very well may not be (Janzen, 1980b). Let me illustrate with a hypothetical example. A hypothetical weevil, *Immunotoxis cyanivorus*, is a euryphagous leaf-eater of the cyanogenic strains of trefoil (*Lotus cyanoambiguous*) in Europe. It has evolved the ability to metabolize cyanogenic glucosides and even use the by-products for normal anabolism. The trefoil has responded evolutionarily by extra-rapid toughening of its new leaves to a hardness the weevil can no longer chew. The weevil exists as a low-density population of individuals constantly searching for

tender new trefoil shoot tips, which are widely scattered in time and space. We know they are strongly co-evolved because we watched it happen between 1983 and 2076, following the introduction of the weevil from Australia in 1982 to control trefoil in European pastures. However, in 2041, a tourist from Hamburg carried the weevil to Costa Rica as cocoons in a floral display. Upon emerging, they wandered about in the vicinity of Liberia, Guanacaste Province, trying many of the 900 species of broad-leaved plants native to that region. Not surprisingly, one of them was a legume whose major defence against folivores was cyanogenic glucosides. *Phaseolus lunatus* also bears new leaves for only a short time of each year and the ability of *I. cyanivorus* to search them out allowed it to maintain a breeding population. No subsequent evolution of either weevil or plant occurred with respect to the traits that are directly related to their interaction.

In the current climate of calling everything co-evolution, the Costa Rican entomologist now finding *I. cyanivorus* and describing its interaction with *P. lunatus* would label the system co-evolved, as would a native person watching an introduced hummingbird working African sunbird flowers, watching neotropical syrphid flies that mimic honey bees, or watching an introduced agouti burying palm nuts in Africa. It is a fair guess that most organisms we see today are not being studied in the particular habitat where they evolved the traits they display (hardly surprising when it is clear that most organisms are a collection of traits acquired during evolutionary bouts in a variety of habitats). This means that a great number of congruences are unlikely to be co-evolved. The general process should be that when a species invades a new habitat or geographic region (where the habitat may be the same, but the participants different), it will quickly adjust its foraging and defence to be most congruent with the resources and challenges present. If the fit is good, as it will often be, subsequent evolutionary changes may be at best minor and the apparently highly co-evolved system may have come about through little or no evolutionary change in either partner. When the barn owl, well co-evolved with the mice it hunts, first moved into Australia and started hunting small marsupials, it may not have changed in an evolutionary sense at all. Even if the small prey evolved defences in response to barn-owl hunting pressure, that certainly is not co-evolution. When the first mastodon walked into a neotropical forest, it was instantaneously a pseudo-co-evolved disperser of many species of plants. The elephant that munches spiny acacias for lunch may well have evolved no special traits for this interaction, though the acacia has long been evolving an ever more wicked thorniness.

6.8 COST OF SAFETY CATCHES

Defences add two classes of cost to the resource budget. In addition to the cost of defence production and maintenance are costs of keeping the possessor from being injured. The safety catch of a rifle may be only a small part of the cost of a rifle, but it is largely indispensable. The cost of safety catches is of two sorts. The first is that a defence (or many defences) may be incompatible with another function for a tissue or structure. Secondary compounds, such as lectins, alkaloids, terpenes etc., lacking their individual safety catches (a glucose molecule tacked onto them), are very good defences against organisms that bore in plant tissue, but they cannot be sequestered in bulk in living cells. We, therefore, find the dead heartwood of a tree to be rich in the non-glucoside forms of such compounds but the living sapwood to be very poorly protected. While we cannot prove it, the generally high edibility of animal eggs is probably due to the difficulty of sequestering a really toxic material—and very toxic it would have to be to protect such a nutrient-rich structure—in a liquid medium adjacent to a rapidly developing organism; seeds, on the other hand, which are both not liquid and dormant, can sequester very potent toxins and digestion inhibitors in vacuoles (Orians & Janzen, 1974). Shoot tips of plants (more specifically apical meristems), are generally poor in good chemical defences (though they acquire them quickly after mitosis has ceased). They are thus more like eggs (probably for the same reasons).

The second type is the actual cost of protecting the organism from its own defences. Vacuoles filled with L-dopa cost at least the price of the vacuole itself, the space it occupies in the cell minus the volume of the defensive compounds, and the machinery for transporting the compounds into and out of the vacuoles. The sugar molecule(s) tacked on to inactivate cyanogenic glucosides, alkaloids, cardiac glycosides, lectins, etc. have a cost that may be energetically low in general, but then again at the time of compound construction might be high. They may even have a volume cost at times; seeds, where weight and space are costly commodities, are the only known source of cyanolipids, compounds that are functionally the same as cyanogenic glucosides except when the seedling decides to degrade them for its own energetic uses. A cubic millimetre of lipid will yield much more than a cubic millimetre of sugar. Snakes undoubtedly carry antibodies against their own venom, scabards are as old as knives, and some animals carry such potent chemicals that they mix them up at the time of use, as anyone who aspirates up a bombardier beetle (Carabidae) (Eisner & Dean, 1976) will learn to his chagrin.

Where defence involves a castle, the owner bears a cost of impeded knowledge of the environment and therefore may in fact have to maintain a higher average level of defence intensity than if the owner could facultatively adjust the castle's defences to the challenges as they come along. The seed dispersed via the gut of a large mammal has this problem. It has a hard, thick and liquid-impervious seed coat or nut wall that defends it against molars and digestive fluids during the voyage. However, if it falls below the parent tree without making this voyage, it is sealed in its castle and cannot know the season to germinate. In many species, such seeds do not germinate until a cue reaches them, for example the castle wall becomes scarified and moisture can enter. However, this can be any time during the growing season and the two-week-old seedling may find itself confronted with a northern winter or a tropical dry season. If it is scarified in its voyage through the animal, as its DNA is programmed for it to be, it is in fine shape upon emergence. However, if the mammal is unable to break down its defences, again it sits in its sealed time capsule, and then the accidental scarification that is bound to occur sometime may or may not occur at a good time of year for a seedling to make its start. Once a clam, armadillo, pangolin, or tiger beetle larva has retreated into its armour, it has staked its life on the chance that the attacker cannot broach the walls; there is no opportunity to iteratively tailor a flexible defence to an ever more accurate assessment of the attacker's strength. To make matters worse, the thus-defended animal is deprived of foraging time as well.

6.9 MAMA VERSUS THE KIDS

The parent-offspring conflict is an untouched area of evolutionary physiology, probably because adult humans largely control the worlds of their offspring in such a manner as to raise the fitness or the inclusive fitness of the adult; public study would undermine that control. The offspring is clearly a parasite in any system with parental care, and seed-bearing plants without exception display extensive parental care. Plant zygotes not only grow within the defences of parental tissues (the secondary compounds and physical protection of green fruits) but derive all of their nutrient resources from the parent until weaned at the moment of fruit ripening. Every botany textbook tells us there is a layer of polyploid tissue ($3N$ or better), between the angiosperm zygote and the $2N$ maternal tissues; it is called endosperm and made up of one paternal DNA set and two or more maternal DNA sets. These books offer not a sentence as to the adaptive significance of endosperm. I hypothesise that it is a mediator and controller of physiological squabbles between the parent and the zygote.

Squabbles there should be, and in abundance, as each zygote is in competition with its litter-mates for resources from the parent and somewhere during their development well over half of the zygotes will be rejected (aborted) by the parent in most species of higher plants. The endosperm thus becomes a defensive (and offensive) tissue for both the parent and the offspring. In many plants it atrophies to nothing but cell debris when the final seed crop size has been determined, but in others it goes on to become the site of resource storage in the full-sized seed.

It is not hard to find an analogy in the mammal placenta, though this tissue is purely maternal in origin. Nevertheless it is the first line of defence in both directions. In social animals, numerous social conventions serve the same defensive role; the most familiar are courts, schools, the military, adult chauvinism, marriage codes, wills, etc.

The expenditure of offspring as a type of defence that raises the inclusive fitness of the parent is hardly a new idea or practice; it is not the old or the females that are sent to war in our social systems. Figs pay 50 % or more of their zygotes for pollination services (Janzen, 1979a), allelopathic plants commonly kill their own offspring as well as those of conspecifics and allospecifics, in order to pre-empt the resources in their immediate vicinity, and perennial plants regularly abort large numbers of offspring that they deem unfit or too great a resource drain. What we have failed to explore are the offspring's defences against its parents. In humans, mimicry, addiction to subsidy types, fratricide and sororicide, sexual displays, imprinting, brute force and verbal deception are all behaviours used by offspring to maintain their place in the subsidy line. Surely the same events occur with solitary animals and plants. However, the highly adaptive taboos against exploring such a phenomenon in our own society have not been conducive to their examination.

6.10 WHO ARE THE UNDEFENDED?

As I suspect our ancestors have known for the past five million years, truly hard biotic containers often contain undefended objects. About the only seeds that can be eaten with relative impunity in a tropical rainforest are those that are encased in thick hard fruit (nut) walls, such as many species of palm (coconuts, etc.), *Coula edulis*, *Lithofagus*, Brazil nuts, *Dipteryx panamensis*, *Hippomane mancinella*, etc. The soft-walled edible forest seeds are usually mast-seeding species the world over (bamboo, dipterocarps, niloo, oaks, conifers, beech, pecans, hickory nuts; Janzen, 1971, 1974, 1976a) and even many of these have relatively hard shells. Clams are the turtles and nuts of the invertebrate world

unless they happen to have been feeding on toxic small invertebrates. In short, even in sedentary organisms, a very hard or tough castle can act as a substitute for other defences such as stings, toxins and indigestibility.

The organisms that specialize at being truly defenceless appear to live largely in two quite different ways. First, there are those things that live in largely predator- or parasite-free habitats; islands offer the most striking examples. Many species of island plants have been gobbled down to extinction by introduced mainland herbivores like goats and pigs. Galapagos tortoises would not survive one week in Africa and ground-nesting birds are commonly extirpated when cats and/or rats are introduced to oceanic islands. But there are other kinds of islands. Penguins would be 'sitting ducks' for any predator that could get to Antarctica and survive long enough out of water to find them. The tops of tropical mountains and some extremely nutrient-poor terrestrial habitats have vines with above-ground storage tubers, presumably owing to a lack of the sorts of rodents or other climbing herbivores that would gobble them up in a lowland site. When hunting humans hit the North American island, they appear to have encountered a megafauna that was defenceless against tools and weapons, and many species suffered extinction before they could evolve fear of man (Martin, 1973).

Second, there are those things that make their own predator-free habitat by doing something in such concentrated synchrony with their conspecifics that defences are not needed; every available predator has its stomach long since stuffed with food by the time the average individual arrives on the scene. We have predator satiation at the population level in wildebeest calving, 13- and 17-year cicadas, bamboos, northern conifers and Fagaceae, mayflies, termite mating swarms, salmon spawning and passenger pigeon nesting. The ingredients are the physiological ability to synchronize by counting intrinsically (e.g. bamboo; Janzen, 1976a) or by cueing on weather events (e.g. Dipterothraupidae, conifers and Fagaceae; Janzen, 1971, 1974), to store the resources to breed or otherwise appear in huge numbers at one point at long intervals, to co-occur in large enough numbers that the predators are satiated and to put all the resource into production of individuals and virtually none into individual defences. A periodical cicada, salmon egg, bamboo seed, etc. is essentially defenceless. There is also predator satiation at the level of the individual, such as when a tree produces 100 000 seeds which are on the average located by only 100 weevil females, each of which can only lay 200 eggs, or when on the average a grazing elk is found by only enough mosquitos to lose 10 cm³ of blood every 24 h. Here, the organism gains more by producing

more seeds or more blood than by being chemically or behaviourally defended. The process is extremely common in defence-attacker systems. In short, a defence is not going to arise evolutionarily unless the return is greater than the cost. This is something well reflected in the high prices that housewives pay for unblemished fruit, a fruit type that is very costly in pesticides to produce.

At a more moderate level, it seems reasonable that in many simple defence systems the intensity and diversity of personal defences carried by the prey or host will be proportional to the probability of being found. It has been reasonably argued that plants which carry large crowns of long-lived leaves among many conspecifics on the same terrain for many years are maximally 'apparent' to herbivores and will have to possess a particularly good defence, one that is hardly penetrable even by a specialist. Digestion inhibitors in northern forest tree leaves and in desert evergreens are good examples. At the other end of the scale there are small plants that are scattered among other plants and often occupy a site for only a short time. These escape somewhat in space and time, as do, for example, the very new leaves of trees. Here the challenge is the specialist who searches out a particular species and concentrates evolutionarily on keeping up with its defences. Such plants are expected to be defended by toxic molecules that will stop the occasional generalists, but will be of little use in deterring the specialist (from which escape is largely by playing geographical and temporal hide and seek) (Feeny, 1976; Rhoades & Cates, 1976). However, Freeland points out (personal communication) that the same result can be obtained if we note that the small 'unapparent' plant can ill afford to lose 100 g of leaves to a generalist such as a deer while a large and 'apparent' tree that loses 100 g of leaves to a deer has hardly been touched.

No organism has a defence system that is impenetrable to all attackers. All organisms must escape to some degree in time and space, and aphids more so than elephants. But then again aphids, producing a large number of highly-edible individuals, display yet another kind of defence. In essence, an aphid clone is a highly subdivided camel (Janzen, 1977a); yes, the parts are highly edible, but usually no predator or predator population can find a large proportion of the members of the clone, many of which are rapidly multiplying even as some are being found. The same can be said of grasses, highly evolved to be burned, or grazed by vertebrates (and lawn mowers!). Such organisms have the defence of being able to subdivide and multiply faster than they can be eaten.

6.11 DEFENCE HIERARCHIES

Since many defence traits have multiple functions and origins, and since most organisms have more than one kind of personal defence, it is hard to organize progressions of defences along single axes. Clams are hard on the outside but unprotected on the inside (as are most large tropical nuts), conversely sea cucumbers are soft but well protected inside (as are many large tropical seeds). However, if we construct a scale along the gradient between clams and sea cucumbers, an annoyingly large number of organisms need to be placed in two or more places on the scale. Kentucky coffee bean (*Gymnocladus dioica*) seeds are rock hard and very poisonous inside; aphids are soft and unprotected inside. We are forced to view each organism as sitting at a point in the now famous n -dimensional hyperspace; each axis of the hyperspace is a gradient between only two opposite defence traits or allocation behaviours. Just as the r and K selection dichotomy was clearly inadequate to deal with organisms with complex life cycles; defence repertoires usually cannot be arrayed along a single general-purpose axis.

However, at the level of higher taxa, and often at the interspecific or intergeneric level, the size of the repertoire of chemico-morphological defences is directly proportional to the sedentariness of the individual. In addition to the best-known botanical defensive compound of all, indigestible cellulose, plants offer literally millions of kinds of toxic defence compounds, urticating hairs, fibrous tough covers, stone cells, in striking contrast to the sprinkling of chemical defence analogues offered by the mobile animal world. Where are the really potent chemico-morphological defences among animals? Sessile marine invertebrates (molluscs and soft, exposed organisms like sea cucumbers; see Ruggieri, 1976), social Hymenoptera (see Akre & Davis, 1978), and turtles/armadillos/pangolins/puffer fish/glyptodonts/bird eggs are distinctly non-cursorial. Conversely, if you can run you do not need so much armour. The economic trade-offs are generally clear but specifically unfocused. Does a box turtle make better use of its resources by lumbering about in its castle than does a threatened ctenosaur lizard who runs like hell for its castle? If the ctenosaur is more than about 80 m from its hole in a tree or rocks, it's dead; if the threat is big enough to swallow or crush the turtle, it's dead.

6.12 COST DOES NOT EQUAL EFFECTIVENESS

There is an extremely complex relationship between the cost of a defence and its effectiveness, a complexity that occurs by and large because each organism is defending itself against many different kinds of attacker and because the

same defence resources are differentially hard for different organisms to obtain. A few milligrams of caffeine per gram of seed may be as effective a defence against a rodent as 300 mg of tannin per gram of seed, but the caffeine may be worthless as a defence against a caffeine-resistant seed-boring insect. If the plant is in a light-rich and nitrogen-poor habitat, the few milligrams of caffeine may be more difficult to obtain than 300 mg of tannin. But this physiological approach ignores the most serious problem of all in studies of defence costs. True defence costs can only, if ever, be measured by the changes in fitness of the organism (or hopefully some close approximation of fitness like the number of offspring fledged) that occur when the defence trait is present or absent. An enormously expensive defence may be highly selected for if it confers an equally great increase in fitness. The trait called 'a protective ant colony on an ant-acacia' costs at the very least the energy, building blocks and genetic programming and maintenance of Beltian bodies, thorns, extra-floral nectaries and dry-season evergreenness. The gain from this large physiological cost can be eliminated by removing the ants, and the consequence is death for the ant-acacia (Janzen, 1966), a rather high loss in fitness. Yet a very cheap defence may also greatly increase the fitness of an organism. I suspect that the physiological cost of those pigments in an insect's cuticle which gives it such marvellous camouflage is probably a trivial part of the animal's total defence budget. Likewise, the production of cactus spines may be a major part of the growth costs of a cactus shoot tip, but they are dead tissue and once produced bear no maintenance charges. Cactus spines also illustrate yet another aspect of cost/fitness heterogeneity. They may evolutionarily arise rapidly in the face of intense herbivory, but disappear very slowly once that selective pressure is removed simply because they are such a small part of the plant's defence budget. The rate of appearance and disappearance of defence traits in the face of fluctuating selection pressures will depend on both the physiological cost of the trait and the intensity of selection for it.

It is often not appreciated that many kinds of defences bear a cost of preventing the organism from following some kind of resource-gathering behaviour. Selection for downward pointing petioles, few lateral branches, and entire leaves as a morphological way of discouraging vines, cuts down severely on the light-gathering options of a self-supporting plant. But then again, by living this way in the vine- and light-rich habitats of early succession in tropical tree falls, it is occupying a habitat where restricted light-gathering options are of minimal consequence. When aculeate Hymenoptera females evolved a sting out of their ovipositor (the egg lubrication gland became the venom gland) they lost the ability to place their eggs deep in host tissue, but they gained the

abilities to immobilize their host and protect themselves. Turtles cannot run well but then their suit of armour works well against the majority of predators and apparently turtles rarely eat highly mobile prey. Vomiting is a good solution for getting rid of an unwanted toxin or microbial contaminant, but the meal is lost as well.

6.13 NO DEFENCE STOPS ALL

Defences are not absolute in their effectiveness. The likelihood of their being penetrated in ecological or evolutionary time is a function not only of their imperviousness or toxicity to living organisms, but of the value of what they are protecting. While a few milligrams of tannin per gram wet weight might stop a colobus monkey from eating a leaf, that same amount of defence would not necessarily stop it from eating a seed (McKey *et al.*, 1978). A well-fed tiger may be deterred by the spines of an Indian porcupine, but a starving one may be willing to pay a fair amount of pain and blood to get a porcupine for dinner.

Another aspect of the same problem is offered by the observation that toxicity (and therefore defence) is not an intrinsic trait of any compound (or structure). Canavanine may be a very toxic uncommon amino acid when incorporated in the diets of a variety of insects and vertebrates, yet for a particular beetle, the bruchid *Caryedes brasiliensis*, it is not toxic (though at a cost). *C. brasiliensis* has tRNA which avoids incorporating canavanine in the place of arginine in growing protein chains. Canavanine is even degraded and used in the beetle's protein synthesis (Rosenthal *et al.*, 1976, 1977, 1978). This is just another way of noting that the horns and hooves of bovids do not defend against ticks and mites. The newly-germinated seeds of *Enterolobium cyclocarpum* are such good food for *Liomys salvini*, pocket mice, that they maintain their body weight and even grow fat on a pure diet of them; *Sigmodon hispidus*, another common small seed and leaf-eating rodent in the same tropical deciduous forest habitat, dies within 2–4 days on a pure diet of these seeds (Hallwachs & Janzen, *submitted for publication*).

6.14 DEFENCE VARIANCE

Not only are defences species-specific in their context, but their effectiveness (in terms of fitness outcome) is highly variable among individuals. A fat and well-muscled East African buffalo appears to be little affected by its blood parasites, but if the animal is subjected to a normal dry season it loses weight and the blood parasites become a severe drain (lethal if at high density) (Sinclair, 1975).

Clearly the body weight of the animal itself is a kind of defence, and one that has as real a cost as horns, hide and fleeing behaviour. Again, a zebra's defences are down when she is heavily pregnant, a fact which has led to many a hyaena's full stomach. A plant growing in the shade may have a quite different content of defensive chemicals. Something happens to the defences of an *Enterolobium cyclocarpum* seed when it germinates; agoutis eat the swelling, germinating seed like candy but will refuse the seedling once it has ventured a few centimetres out of the seed coat.

Not only do defences have to be paired off against their protagonists before it makes sense to speak of them, but they also are dosage-dependent. This seems self-evident when speaking of rabbit speed when running away from coyotes, or palm nut hardness when faced with the molars of mastodons, but it also applies to plant poisons. Digitalis, cortisone, cannabitol, morphine, caffeine, theobromine, capsaicin, rotenone and many other familiar botanical drugs are mild perturbers of human neural systems at one dose and lethal at higher doses. When various uncommon amino acids were incorporated into the normal seed diets of larvae of a bruchid beetle, at 1 % concentration, 32 % had a lethal effect, while at 5 % concentration 90 % did (Janzen *et al.*, 1977). Viewed from the cost aspect, however, we encounter yet another source of non-linearity. Once the enzyme and substrate chains are set up (evolved) for the production of say 0.1 mg per gram of seed tissue, I suspect that the cost to raise it to 50 mg per gram of seed tissue is much less per milligram than were the factory expenses of the first 0.1 mg. The evolutionary invention of a spine, and the evolutionary lengthening of a spine are acts of quite different physiological, as well as genetic, costs.

6.15 HOSTS AS ISLANDS

Just as parasites compete with each other through the resource budget of their host plant or animal (Janzen, 1973b), they also influence each other through selecting for a defence which then incidentally hurts another parasite (or even predator). There are two components to this. First, several species of parasite may produce in concert a sort of diffuse selection pressure that favours a trait which reduces the intensity of damage from their combined impact. Neither alone might provide enough selection pressure to do this. Ironically, the final outcome might even be the loss of one parasite species from the plant's herbivore load, and this one would not necessarily be the newcomer that caused the significant increase in selection pressure. Second, a major parasite may select for a trait which removes parasites which individually are quite

trivial reducers of host fitness. While an example is not at hand, I suspect that this is very common among small foliage-eating insects in tropical forests.

6.16 DEFENCE CONVERGENCE

Convergence in defences is an extremely common phenomenon. There are over 80 genera of small mammals in the world that have (probably independently) evolved spines out of their dorsal hairs (compilation from Walker, 1964), not to mention spiny lobsters, cacti and sea urchins. The urticating spines of *Automeris* silk moth caterpillars and the urticating spines of stinging nettles (*Urtica*) both contain a mixture of acetylcholine and histamine that is injected by hydrostatic pressure through a spine whose top breaks off after puncturing the victim; neither chemical by itself is painful when injected. Eye spots closely resembling the eyes of (presumably threatening) vertebrates have evolved independently on lepidopteran wings many thousands of times. Many secondary compound defences in plants are made by several different biochemical pathways, strongly implying that they are independently (convergently) evolved. All these convergences stem in part from the fact that many different organisms are confronted by the same predators or parasites. Different species of predators and parasites very commonly share vulnerability to defences at the same points. Caffeine in a seed probably acts as effectively upon a mouse as on a boring beetle larva. But convergences are probably also due to the fact that the most economical steps in the evolution of secondary compounds, and other defences, are similar in similar organisms. We find eye spots, and not pictures of mouths full of jagged white teeth on the faces of butterfly wings, because the way lepidopteran wings develop leads easily to patterns of wavy lines, loops and circles with different colours inside and outside the lines. The prominence of polyphenolic digestion inhibitors in plant foliage is a reflection not only of the similarity of digestive processes in herbivores, but the ubiquity of phenolic molecules in plant primary biochemical systems.

An area that requires study in defence biology is recognition of similarity of defence function among very different structures. A straightforward example is fever in a sick adult rabbit and the heat-seeking behaviour of its sick juvenile. Less obvious is that of the ostiole of a fig whose entrance hole is plugged with overlapping scales. The ostiole restricts entry to only a certain size of pollen-bearing wasp and strips the wasp of dirt as it passes through. It is as much a defence against interspecific rape and microbial contamination of ovules as is the stigma and style through which the pollen tube must grow in an

ordinary flower (Janzen, 1979b). A colony of social wasps or bees that 'pays' workers to keep out a bird, bear or army ants is no different than a mammal that 'pays' phagocytes, antibodies and leucocytes to keep out microbes. The fungus that produces aflatoxin to protect its grain from the rodent that made the cache (Janzen, 1977b) is no different from the farmer who sprays her apples with parathion to keep out codling moths. Ear wax is probably a powerful antibiotic against the numerous bacteria and fungi that could do so well in that nutrient and moisture-rich incubator; it begs analogy with the intense secondary compound deposition in the walls of holes in the trunks of trees, or the walls of holes to be (Janzen, 1976b).

6.17 WHERE ARE THE DEFENCES?

Categories of defences are certainly not uniformly or randomly distributed over the earth's surface. There appear to be more poisonous snake species per species of snake in Africa than in the neotropics, and I suspect that the reason is that African snake populations have been subject to more intense continuous selection by snake-eating vertebrates than have the neotropical forms (Janzen, 1976c). Such guesses must be made with care, however; nearly 100% of Australia's snakes are poisonous but for a quite different reason. It appears that the first to arrive were Elapidae, a family containing only poisonous species throughout the world. All but a very few of the spiny mammals mentioned earlier are tropical, while there appear to be just one or two species of skunk in each major habitat type. The Asian rainforest tropics are famous for their terrestrial leeches, parasites that are absent from the African and New World tropics; presumably antibody, mechanical and behavioural defences against their effects are likewise absent from the terrestrial vertebrates of Africa and the New World. We can even predict that terrestrial small rodents would have a very difficult time nesting on the ground in a leech-infested Asian rainforest. Likewise, the northern latitudes are famous for their horrible concentrations of vertebrate-biting mosquitos and other flies; except for certain swamp-rich habitats, many tropical forests are comparatively extremely poor in mosquitos that descend in hordes on large vertebrates. Again, I suspect that the native animals in these sites lack the defences that their northern relatives have. Why is the tapir's tail so short and its hair so thin? Levin (1976b) seems to have located a latitudinal gradient in alkaloid frequency and concentration in plants, and it is clear that the tropics are generally a much greater source of pharmacological drugs than is extra-tropical vegetation (though this may not be much more than a reflection of the much greater species richness of plants in the tropics).

6.18 IN CLOSING

Defences dear to our own way of doing things will long receive attention from humans. On the one hand, the detailed studies of how one organism protects itself from its attackers (e.g. Snyder, 1967; MacConnell, Blum & Fales, 1970; Eisner, van Tassel & Carrel, 1967; Eisner & Shepherd, 1966; Finkelstein, Rubin & Tzeng, 1976; Eisner & Dean, 1976; Eisner & Adams, 1975; Eisner, Kriston & Aneshansley, 1976; Rothschild *et al.*, 1979) are still of great importance. On the other hand, it is clear that we need a much greater understanding of two areas: what do those defences cost in resources and options, and how much is the fitness of the organism that lacks them depressed? For a long time we have been deluded in believing that tightly interacting members of the habitat are likely to be co-evolved, that defence effectiveness is related to defence amount, that the impact of the herbivore array is measured by its size or the amount it eats, etc. A change in attitude is required, instead of more descriptions of yet another alkaloid or its concentration in a tree's foliage. Above all, we need field experiments to tell us the fitness gains and costs that the organism accrues with and without its defences.

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