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Sex, Drugs, and Butterflies

For male milkweed butterflies, a dead, withered leaf may have a chemical allure no pretty flower can match

Observe the butterflies, sombre black fellows[...]flying in a crowd round a shrub with thick silvery-looking leaves. It is the Tournefortia Argentifolia, a tree that I see on almost every seashore that I have visited throughout the Pacific.[...] A branch is broken, and the leaves are hanging dry and wilted. The butterflies settle on the dead leaves in swarms, almost pushing and jostling one another to get a good place. Notice that it is the withered leaves and flowers that they prefer, and seem to become halfstupid in their eagerness to extract the peculiar sweetness, or whatever it is, that the leaves contain.

Since these observations were published in 1890 by C.M. Woodford, in A Naturalist Among Headhunters, other reports in the scientific literature have described butterflies apparently sucking at dead parts of Tournefortia trees and a number of other, unrelated plants. For nearly a century, these reports were a great puzzle to naturalists and scientists: first, because dead plants are dry and butterfly mouthparts are designed to suck up liquids, and second, because only male butterflies were seen at the dead leaves. Only in the last few decades have scientists in Australia, Europe, and the United States pieced together an explanation involving complex interactions of sexual communication and chemical protection.

The butterflies Woodford watched were members of the genus Euploea (commonly known as crows) in the milkweed butterfly subfamily, Danainae. Other family members include the tiger, queen, and monarch butterflies. Males of all danaines possess hairy glandular organs. Nineteenth-century naturalist Fritz Mller proposed that all these "pencils, tufts or manes of hair," which he found in a variety of forms in the males of many butterfly species, were odoriferous organs serving "as an excitement to the opposite sex." The proof came nearly one hundred years later. In the mid-1960s, studies by Lincoln Brower (now at the University of Florida, but then at Amherst College) and his coworkers showed that male Florida queen butterflies locate females visually and, once they are within close range, emit chemicals from these glandular organs, or hairpencils, to seduce them. Such chemical sexual stimulation is widespread in butterflies and moths, but the danaines exhibit one of the most elaborate chemical communication systems known among the Lepidoptera. (The American monarch, Danaus plexippus, is an exception. In the mating strategy of this species, chemical communication plays a minor role. Male scent organs are much reduced and rarely employed in sexual interactions, which appear to the human eye more like rape than seduction.)

During courtship, a danaine male hovers above a female. He extrudes his hairpencils (usually hidden inside his abdomen) close to her antennae and then expands them, often for just fractions of a second. In many species, the sudden protrusion and expansion of the hairpencils delivers tiny, pheromone-laden particles to the female's antennae, which are lined with olfactory receptors. Without adequate pheromonal stimulation, the female would reject her suitor.

Not all danaine pheromones smell alike, and the human nose can detect some differences in the male perfumes of milkweed butterfly species. Mostly they smell strong but pleasant to us: some, sweet like chocolate; others, more like pineapple. However, for a more precise identification of the pheromone composition, sophisticated technical equipment is needed. Jerrold Meinwald, of Cornell University, and Stefan Schulz and Wittko Francke, of the University of Hamburg, have analyzed the chemistry of hairpencil extracts taken from many species and found that the pheromones are species-specific bouquets made up of twelve to fifty volatile components, most of which are "unsmellable" by the human nose.

What is the male telling the female with this fanfare of pheromones? Danaine butterflies locate one another by sight, so the pheromones cannot be long-range attractants. However, mimicry is very common among these butterflies, so something more than just visual inspection may be necessary to allow members of a species to recognize one another. At close range, the female may use the male's perfume to determine which species her suitor belongs to: "Let me smell you so I can know who you are."

But there appears to be more than species recognition to the story. Certain chemical compounds are common components in the pheromone bouquets of many danaine species and thus are unlikely to contribute to species specificity. Called dihydropyrrolizines, these chemicals often make up the largest proportion of the hairpencil volatiles, with up to 500 g (a half thousandth of a gram) in a single pair of hairpencils, an enormous amount compared with that of pheromones in other insects. These chemicals must serve a different purpose.

Studies with field-caught male danaines revealed that the amount of dihydropyrrolizines varies greatly from individual to individual. Freshly hatched males possess various other pheromone components but lack dihydropyrrolizines entirely, and as Thomas Pliske and Thomas Eisner, of Cornell University, discovered, male queen butterflies lacking this type of compound are much less successful in getting accepted by a mate. These findings suggested that the chemicals played an important role in the lives of the butterflies, but no one knew just what that role was or where the dihydropyrrolizines were coming from.

The answers to these questions began to come in the mid-1970s, from scientists working independently (John Edgar, with the Commonwealth Scientific and Industrial Research Organization in Australia) and collaboratively (Jerrold Meinwald and others at Cornell, and Dietrich Schneider and me at the Max Planck Institute for Behavioral Physiology). We now know that adult male milkweed butterflies utilize certain secondary plant compounds, known as pyrrolizidine alkaloids (PAs), as chemical precursors for synthesizing dihydropyrrolizines. (Secondary plant compounds are chemicals that are not part of the plant's essential molecular makeup but that frequently have a defensive function and lead to better survival.)

The butterflies use their sense of smell to locate the dry, withered, or damaged parts of certain plants that contain pyrrolizidine alkaloids. After landing on an appropriate plant, the butterflies walk about, probing the surface here and there with their proboscises. Eventually they settle down at one spot and release drops of fluid on the plant. They then reimbibe the fluid mixture and, with it, some of the plant's PAs. Butterflies often congregate in small groups and fight over spots previously wetted by others. What Woodford saw a century ago was undoubtedly such an incident, for Tournefortia trees contain pyrrolizidine alkaloids. (Other PA plants include Crotalaria, or rattlebox, in the pea family; Senecio, or groundsel, in the aster family, and Heliotropium in the borage, or forget-me-not, family.)

These alkaloids occur in living as well as dead plants, but in live tissue, the compounds are sealed within cell vacuoles, where the butterflies cannot detect them. If, however, a leaf has been damaged by, say, leaf-feeding beetles, it may attract male milkweed butterflies, which, chickenlike, scratch at it with their legs, creating fresh tears in the plant tissue and thus gaining access to the alkaloids within.

Using pyrrolizidine alkaloids purified from plant extracts, we have demonstrated that the butterflies are after the PAs and not any other plant compounds. And their interest in these chemicals is independent of any nutritional requirements: their sole reason for visiting PA-containing plants is to gather the alkaloids. These butterflies, then, visit two groups of plants: those they feed on, which could be thought of as grocery stores, and those they gather secondary chemicals from, which could be considered pharmacies.

Why do males engage in these efforts? Some twenty years ago, biologist Miriam Rothschild studied moth larvae feeding on fresh PA plants and proposed that insects are capable of stockpiling the alkaloids to protect themselves from predators. In the years since her suggestion, chemical analyses conducted by several separate research groups have revealed that pyrrolizidine alkaloids gathered by adult butterflies from dry plants are used for the same purpose. The insects' storage capacity is impressive: up to 15 percent of a butterfly's dry weight may be made up of unconverted pyrrolizidine alkaloids extracted from dry plants.

Behavioral tests of butterfly predators have shown that the stockpiled PAs can provide the insects with protection from many enemies. These chemicals, which become toxic once ingested, taste bad and have been found to be repellent, to varying degrees, to some mice, bats, lizards, spiders, birds, and all unadapted insects.

Some members of the milkweed butterfly family -monarchs and queens -are protected by other chemicals unpalatable to predators. Unlike PAs, these chemicals, known as cardenolides, have an immediate effect on heart rate and blood pressure. Neither egg-laying females nor larvae specifically seek out cardenolides, but if the larval host plant contains them, they are ingested along with food. Stored in the larval body and retained into adulthood, these cardenolides deter several predators, as has been well documented during the last twenty-five years. Film footage based on Lincoln Brower's studies with blue jays provided the most memorable proof: blue jays eating with gusto and then immediately vomiting up monarch butterflies that had been reared as larvae on cardenolidecontaining plants.

For certain milkweed butterfly species or individuals, then, pyrrolizidine alkaloids add another dimension to their unpalatability, while for others, the alkaloids may be the only defensive compounds. In all cases, however, these plant chemicals play a dual role in the lives of danaines: they help males seduce females, and they act as potential lifesavers. Thus, males have good reason to pursue pyrrolizidine alkaloids. But why is a female so interested in whether or not a suitor smells of the PA-derived dihydropyrrolizines? And why does she seem to use them in selecting a mate?

As the research teams of Thomas Eisner and Keith S. Brown, Jr., have demonstrated, male milkweed butterflies transfer more than just sperm to the female during copulation: included in the ejaculate is a mass of pyrrolizidine alkaloids, previously collected by the adult male from plants. This nuptial gift varies from male to male: the more of the alkaloids a male has taken in, the more his personal perfume will smell of dihydropyrrolizines and the more PAs he has to offer a female. Thus, if a male's aroma is an indication of the size of the nuptial gift he is likely to present, the female may have a meaningful basis for choosing a mate: the more alkaloids she can get from the male, the more she will possess to protect herself and to incorporate into her eggs for their protection, too.

Studies of the chemical ecology of milkweed butterflies led to a better understanding of other insects that utilize PAcontaining plants as grocery stores and pharmacies at the same time. The larvae of several tiger moth species (family Arctiidae) store PAs for their protection, and some also use them as pheromone precursors. Although many are specialized to feed on PA plants exclusively, not all are capable of detecting PAs directly. Among the most interesting of the PA moths are those such as Creatonotos species, which respond to PAs behaviorally, as danaines do. The larvae of these moths can feed and develop perfectly well on a variety of shrubs, including some that contain PAs and others that do not. Under experimental conditions, however, these caterpillars show a definite interest in the alkaloids, feeding eagerly on almost any material, including fiberglass disks, as long as the material has been first impregnated with the chemicals. As with the milkweed butterflies, their enthusiasm for these chemicals is independent of their nutritional requirements.

Creatonotos moths exhibit some striking similarities to danaine butterflies. Males possess eversible scent organs, called coremata, that emit a dihydropyrrolizine derived from pyrrolizidine alkaloids, and they, too, stockpile unconverted PAs for protection and transfer them to females. However, there are some basic differences. Both male and female Creatonotos feed on PA plants, gathering the protective compounds together with food, and they do so only as larvae (the shortlived adults do not feed at all). So while milkweed butterflies accumulate PAs as adults only, Creatonotos moths hatch with a fixed amount of pheromone and protective chemicals. In both groups, the degree of protection varies from individual to individual, as does the amount of male pheromone.

The dihydropyrrolizines of many danaines and Creatonotos are structurally identical, but their roles in influencing the behavior of conspecifics are quite different. In most butterflies and moths, males expand their scent organs only in the final phase of courtship, after the sexes have come together through sight (butterflies) or smell (moths). Creatonotos males, in contrast, display their organs for hours, starting at dawn, whether any females are around or not. The pheromones the males release appear to lure both females and males, leading to the establishment of mating aggregations, or leks. Since Creatonotos females also produce pheromones to lure males (as is typical among moths), the genus appears to use two markedly different means of bringing the sexes together.

We have not yet been able to conduct a detailed field study of these rare, nocturnal, and quite small moths, but one aspect of their biology has already added a fascinating element to the complex story of plant alkaloids and insects. In the field, some Creatonotos individuals have gigantic coremata, exceeding the insects' wingspan; others of the same species have coremata so tiny they are almost invisible; and yet others exhibit intermediate sizes. In the laboratory we have experimented with feeding Creatonotos larvae different amounts of pure PAs and have demonstrated a direct correlation: the more PAs a moth took up while it was a larva, the larger its coremata and the more PA-derived pheromone it produces. (No other part of the moth is affected by these dietary changes.)

Available phylogenetic evidence indicates that adaptations to utilize pyrrolizidine alkaloids evolved several times in various insect groups. Certain leaf beetles, grasshoppers, and chloropid flies, for instance, as well as numerous other species of butterflies and moths, seek out these chemicals independent of feeding. Experiments have demonstrated that these insects are attracted to the alkaloids, whether they are presented in the form of dry plants or laboratory dishes impregnated with the chemicals. Not all these insects possess male scent organs, so the chemicals' role as a pheromone precursor is limited, and not all insects that need them to produce pheromones use them in the same way in sexual communication. By improving their chances of survival and perhaps by increasing their reproductive success, however, all do better with PAs. For these insects at least, purloining plant poisons pays off.

PHOTO: Male crow and blue tiger butterflies congregate on a bundle of dried Heliotropium plants, in search not of food but of pyrrolizidine alkaloids. (Edward S. Ross)

PHOTO: Numerous other insects, such as the snouted tiger moth are attracted to the dried parts of plants containing these protective compounds. (Edward S. Ross)

PHOTO: The crow caterpillar may gather and store certain noxious plant compounds, such as cardenolides, while feeding on its host plant. (Michael ***Boppre***)

PHOTO: The chrysalis of a friar butterfly has a strong metallic luster, the effect of light reflecting off many thin layers in the cuticle. (Michael ***Boppre***)

PHOTOS (2): After scratching at a beetle-damaged Heliotropium leaf, two blue tiger males, below, gain access to the pyrrolizidine alkaloids within. These butterflies must also continue the regular business of feeding on nectar, right. (Michael ***Boppre***, Tim Laman; The Wildlife Collection)

PHOTOS (2): Male milkweed butterflies and male Creatonotos moths use pyrrolizidine alkaloids for protection and in the synthesis of sex pheromones. The butterflies emit pheromones from glandular organs known as hairpencils, below. The size of a moth's scent organs, or coremata, right, depends on the amount of PAs it gathered as a larva. (Michael ***Boppre***)

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By Michael ***Boppre***
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