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An Unlikely Beginning: A Fortunate Life

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Abstract

Elizabeth A. Bernays grew up in Australia and studied at the University of Queensland before traveling in Europe and teaching high school in London. She later obtained a PhD in entomology at London University. Then, as a British government scientist, she worked in England and in developing countries on a variety of projects concerned with feeding by herbivorous insects and their physiology and behavior. In 1983, she was appointed professor at the University of California, Berkeley, where her research expanded to a variety of topics, all related to the physiology, behavior, and ecology of feeding in insects. She was awarded a DSc from the University of London, and at about the same time became head of the Department of Entomology and regents' professor at the University of Arizona. In Arizona, most of her research involved multiple approaches to the understanding of diet breadth in a variety of phytophagous insect species.

Variety's the very spice of life,
That gives it all its flavour.

—William Cowper, 1785

AUSTRALIA

I was six when I fell in love with insects in the tropical Queensland garden that had been lovingly made by my parents. The little creatures jumped up at me with all their colors. They grabbed my attention with big green wings, delicate membranes, black horns, clubbed feelers, jeweled torpedo bodies, feathery texture, cold solid greenness, and light spots blinking in the night. My mother was happy that I was engaged with them, perhaps because I was so hopeless at school. During my teenage years, IQ tests pronounced me subnormal. "She had better just work to become a shorthand typist," the psychologist told my mother. I found relief from failure by wandering in the bush, watching butterflies feeding on nectar and leaf beetles making holes in eucalyptus leaves. The fascination with simply watching nature continued throughout my life, with long observations of behavior inspiring all my future questions and research.

I surprised everyone when I was finally an academic success. A crush on the math teacher was the cause, and suddenly, at 15, I was top of the math class. What excitement! And the thought of actually achieving anything and of making my mother happy gave me passionate motivation to get a scholarship to the University of Queensland. It is strange now to think that my early shortcomings became the root of my ambition and intellectual growth.

I was the first in my family to go to university and had no idea of all the opportunities I would find there after the limitations of an all-girls Presbyterian/Methodist school. University life was a tremendous novelty where I made lifetime friends and reveled in the exploration of art, plays, movies, seminars, bushwalks, and wild parties. The classes were often disappointingly dull, though I got good grades and came out with a degree in entomology and zoology. With some kind of accomplishment under my belt, I was ready to get away, to spread my wings and see the wide world. First though, I had to save for a year, so I got a job teaching high school physics, including weekly labs.

The momentous time was December 1963, and I was 22. The ship was the P&O liner *The Canberra*. It was birthed at Circular Quay in Sydney, waiting to engulf me in its massive whiteness for thousands of sea miles. It seemed as incongruous as an iceberg in a tropical forest, with giant lianas of ropes tethered below. At last, I climbed the gangplank and from the high deck threw my colored paper streamers into the thickly milling crowd below, and the hands of those little people caught them. Then lianas were undone and I saw the bobbing tugboat with its tall funnels pull us away so all the streamers tore apart and fluttered in the breeze.

Underway toward the harbor entrance, I looked back at the bougainvillea red of the wake, reflecting the setting sun, and the color caught on the distant wharf with the tiny people and on the rocks of Kirribilli Point, on gray puffs of cloud, and on the single torn streamer I still held in my hand.

Impatience during the long sea voyage changed to excitement as my friend Lucy and I disembarked in Gibraltar and hitchhiked around Europe. We had a carefree time, and I arrived in England with my head full of all that I had experienced and learned. In London at last, I had my year of Bohemian life before teaching high school in the East End. There, I learned rhyming slang and a lot more besides about Cockney life. Humor and self-deprecation was the norm, and I found it refreshingly new and funny after growing up in a humorless family. But after a year, I was ready, finally, to return to insects. I looked into biology courses at the University of London and found that, at a part of the university known as Birkbeck College, I could study at night while I was still teaching.

LONDON, ENGLAND

I got back into the entomological arena with a master's degree, and then, for my doctorate, I studied the great feat of hatching and molting in grasshoppers. I combined observation, filming, anatomy, and physiology to discover the process and control of the complex sequence of behavior and biochemistry (1–4). The many techniques I learned were perfect for someone who loves variety.

During my PhD studies, Reg Chapman, who was one of my teachers, took me off one summer to study food selection in British grasshoppers near Haslemere in Surrey (24, 25). It became love among the grasshoppers in that pretty English countryside, as we worked, side by side, counting plants on line transects, and identifying plants from their cuticular remains in the feces of captured specimens. The enjoyment of working together amid tons of laughter became the hallmark of our partnership.

1968 was a time when England was brimming with optimism, and the vitality was palpable. I found London thrilling; in that great city, with Reg and a career, I would never go back to Australia. After I obtained my PhD, we were lucky enough to work together on locusts and other pest insects as British government scientists at the Anti-Locust Research Centre. We were to work on anything at all that would improve knowledge of locust biology. There were no constraints and endless resources. Looking back, it is amazing what fun it was, and I never even had to write a grant proposal.

In our London lab, we focused for several years on feeding by grasshoppers and locusts. What plant chemicals influenced feeding behavior? What physiological mechanisms controlled feeding? We got a lot of answers, published a lot of papers, and, finally, developed a model system for control of feeding. Along the way was the excitement of unexpected findings and upturning of conventional beliefs. Among the projects and the two dozen papers we published, the topics that stand out to me now include showing that normally open taste receptors close in response to hormones produced during satiety (18, 26), the many physiological feedbacks controlling food intake (27), and the central role of plant deterrent compounds in determining food plant selection in locusts and grasshoppers (6, 8, 28).

When Reg and I joined the Centre, there was a close-knit group of entomologists and biogeographers, among them plenty of women and a number of eccentrics. We had a tearoom where everyone met mid-morning and mid-afternoon and where everything was discussed—work and travel and all the many sex scandals of the staff. We were in swinging London after all! Our papers were typed up from our longhand writings by typists—there must have been a dozen of them, before word processing took over and authors did their own typing.

Our fieldwork involved more practical projects on agricultural pests, and my longest African project concerned *Zonocerus variegatus*, an aposematic grasshopper decimating cassava crops in Nigeria. Looking back, the enjoyment of it all was working in a team to uncover unsuspected biological secrets in this colorful insect. For example, we noticed queen butterflies feeding on the fecal exudate of grasshoppers killed by fungus disease (34), and because these butterflies require pyrrolizidine alkaloids, the study led to finding that these chemicals were in the grasshoppers' food plants and were sequestered by them, providing protection from predators. In addition, the females used the alkaloids to make gregarization pheromones. This ensured mass egg-laying sites, which turned out to be a critical finding for nonchemical regulation of the pests, because when we marked such sites and dug them up later, population sizes the following year could be reduced by 95%.

The Nigerian project lasted several years and was a team effort, with no concern by anyone over who got credit or who were authors on papers but with tons of excitement-packed discoveries. Back in a London pub, our group retold stories of army ants and sodden plots, of work together and laughing in a tiny lab, of wild parties in a Lebanese restaurant, of shopping down in the market where a hundred voices loudly urged us to buy bananas, fried plantain, mangos, coconuts, chilies, okra, fly-covered bush meat, multicolored cloth, wooden carvings, and strings of beads.

Several projects on which I worked resulted in interesting or important findings, yet I was not an author, and at the time, it seemed irrelevant. We did our work as a team and something came of it, and that was what mattered. One of these projects concerned grasshopper populations in the southern Sahara, where desertification was increasing, aided by the ravages of these insects. Where did the grasshoppers come from, and how did they find the wadis where a little moisture collected and grass grew? Our team of biologists and radar physicists camped in northern Mali, home of the nomadic Tuareg people, and it was another world: extreme temperature, sandstorms, giving our precious water to sick nomads, walking long distances to get bathroom privacy, Tuareg women in my tent to watch me undress, and of course the interdisciplinary study of grasshopper flight patterns.

In short, swarms of grasshoppers fly downwind at night, whether the wind is from north or south. Where such winds meet, at the Inter-Tropical Convergence Zone, is where rain falls, and so the grasshopper flights take them to the zone from wherever they are, meaning that they thereby increase their chances of finding food. Now, when I handle the ancient stone tools I found there, I remember that time as one of such conviviality and friendship among 20 people surviving in a very tough place, with a French-speaking Malian cook. I remember that the generator running the radars and oscilloscope was also used for a small fridge, and the daily highlight in that hot, dry desert was the little bottle of beer we each got at sundown.

Back in the lab, I continued work on the chemistry of plant–insect interactions. Tony Swain at Kew Gardens, and various other plant chemists, wanted me to test chemicals on insect behavior. Undergraduates came to study antifeedants and their mixtures as a means of protecting crop plants. A plant chemist, Susan Woodhead, joined our team. Reg and I found that plant waxes could be detected by insects and were significant in their selection of a host plant (19, 20). We became engrossed in the overall role of plant chemicals in insect feeding behavior (28).

With such an interest in plant chemistry in the seventies, I became fascinated with the sudden surfeit of theories on patterns of plant defenses and the coevolution of plants and insects. I used locusts to test some of them and was disappointed at the time to find them wanting. Plant tannins were supposed to be the insurmountable plant defense, preventing digestion of protein, but I found they did not affect digestion (5). Plant phenols could even stimulate feeding, and in some species of insects were used as nutrients (46, 47). Further, many deterrent plant chemicals had no deleterious effects if ingested, casting doubt on their evolution as poisons to defend the plants (29, 53). I began to wonder about the popular overarching theories not based on empirical data, and my resulting publications became controversial.

But work abroad continued also. The Anti-Locust Research Centre became the Centre for Overseas Pest Research, and the research topics broadened. Among my overseas projects, one in India was my favorite. With Reg and others, I worked on pests of sorghum, including grasshoppers, plant hoppers, and caterpillars (66, 67). In particular, we worked on *Chilo partellus*, whose larvae feed on the growing point of the plant, causing what is referred to as dead heart. We had the task of discovering mechanisms of resistance to this pest, mechanisms that might be bred into high-yielding crop varieties. We examined plant extracts and specific chemicals for effects on development of larvae, and plant surfaces for effects on oviposition by the moths. But it was continuous field observation that led to success.

I learned that the mother moth laid her eggs at night at the bottom of the plant, and the tiny caterpillars climbed to the top where leaves are soft. They experienced their Everest in the first light of day, before the hot sun would shrivel them, before the dry wind could blow them into dust. I watched each hatchling emerge from its egg and orient upward and saw it struggle through the wax on the stem then crawl up the undersurface of a leaf only to discover it was not at the top of the plant. It would turn and find its way back down the long leaf to the stem and then continue on upward. After about an hour, it would reach the whorl at the top and scuttle down into its depths.

Parasites or predators inevitably destroyed eggs placed in a convenient place near the top of the plant, so I focused on early caterpillar life and found that on some resistant varieties, the tiny caterpillars were unsuccessful at the climb. They climbed but wandered out onto the undersurface of upright leaves and seemed unable to reorient back to the stem as they would need to do—this could be the key to the plant resistance.

With artificial replicas of stems and leaves, together with plant surface extracts, I found that with wax from susceptible plants, caterpillars crawling up the undersurface of the leaf blade always turned back down when they hit the leaf edge. With wax from resistant plants or wax from plants that were not hosts at all, caterpillars would reach the leaf edge as usual, but there they stopped and eventually parachuted away on threads of silk. If the wax didn't carry the right message to their tiny taste buds, they would hesitate instead of climbing up; they would spin their threads and blow off to their almost certain demise (32, 51, 55).

I recorded the travails of caterpillars out in the field, lying on the red soil, before the Indian women went to work and before the men walked up and down the rows in the fields watching over them, and it was here that I had my personal revelation. The plant genes could be tweaked to give wax the wrong message to make those baby caterpillars toss their own lives away.

Working in teams in different countries and ecologies was exciting, and learning about different cultures was part of it. Also, having time and freedom in the lab to venture into different topics was a luxury, but eventually, I hankered for an academic environment. One day, Reg saw an advertisement in *Science* for a job at the University of California, Berkeley to work on plants and insects. He felt it exactly suited me. I was first of all appalled. America! What of the violence and guns? What of racism? But I applied for the job anyway, and 18 months later, Reg and I landed in San Francisco with three suitcases and a cat. A future as Americans lay ahead of us.

UNIVERSITY OF CALIFORNIA, BERKELEY

I had no knowledge of America and was naive about the workings of American universities or writing grant proposals. I had arrived as a full professor with no startup funds and no equipment and a whole new culture to discover. But I soon learned about individualism, a trait that is well developed in Americans and amply found in Berkeley. It has to do with that all-important independence, confidence, and much-touted freedom, but also with the need to look after number one first. One professor even told me to work alone so I would get all the credit for anything I published. I was appalled.

But I became broader in my thinking, more flexible in my intellectual pursuits, and I thrilled to all the new ideas, seminars of visiting scientists, and the questioning students. I had to learn the rigors of writing convincing research grants and explaining why the work was important, a process that involved self-advertisement that had always been anathema to me yet ended up making me feel that I had a distinct place in the scientific world. The seminars and discussions, colleagues and students, took me into unknown places and brought me new ways to see theoretical problems. I began to actually feel the confidence that had seemed so unrelated to my life before I came to the United States.

With no facilities, I began with a study of insect learning (41, 48, 58, 59) and later spent long days observing behavior in the lab and field. How did physiology influence behavior, and what of the evolutionary implications of my findings? I found that learning by insects improves fitness (56). Also, in nature, when insects feed on plants, they are much more likely to be attacked by an enemy than when they rest (14). There had to be selection pressure for fast ingestion and fine tuning of mandible morphology to make feeding more efficient. I found contrasting foraging patterns, among and within species, with trade-offs between safety and optimal nutrition.

One summer, Reg and I traveled to the Southern California desert. We were fascinated by the unusual—in this case, two species of the grasshopper family Acrididae that confined their diets to a single plant species, *Larrea tridentata*, instead of the more common grasshopper habit of eating many different plant species.

There was *Bootettix argentatus*; it fed during the day on the leaves and hid among them, exhibiting a remarkable degree of camouflage. The insects were extremely difficult to distinguish among the clusters of creosote leaves, and looking at these insects, you knew they had to be specialists on creosote because they would have been too quickly found by predators had they ventured onto any other plant.

The other grasshopper species was *Ligurotettix coquilletti*; it is a gray insect that spends the daytime on the gray stems of creosote, again wonderfully camouflaged. Not surprisingly, this grasshopper feeds at night, creeping around the foliage where it would not be hidden in daylight hours.

Reg and I labored with a love of life as we worked day and night and dreamed up experiments in an old trailer, smelling creosote in the air whenever there was a hint of rain. We found that both grasshopper species are stimulated to feed by the smell and taste of strange chemicals in creosote bush and both have fewer taste and smell receptors than other grasshoppers, reflecting, perhaps, the simplicity of using a limited spectrum of special host-plant chemicals for choosing food instead of requiring input from a greater array of potential food plants (54).

I joined the ranks of biologists interested in the evolution of limited diet breadth that is a feature of most insect herbivores. The current theories at the time focused on the evolutionary battle between the plants and insects and on the notion that specialists would be more efficient than generalists in using their plant foods. But from spending hundreds of hours simply watching in the field in different habitats, I understood that parasites and predators are as abundant as herbivorous insects. How dangerous! What is a tiny reduction in growth rate compared with death from a predator? How critical to find ways of avoiding natural enemies! Crypsis, chemical protection, special avoidance behaviors, and vigilance all turned out to matter, and being a specialist provides the advantages for all of these. But it took years to obtain data that finally supported the idea.

Among the projects with students in Berkeley was our demonstration that feeding behavior was exceptionally dangerous—days-long observations in nature showed feeding enhanced the risk of being attacked by 40 times or more over any nonfeeding activity (14, 61). It is no surprise that mandibles are highly sophisticated organs, specialized for different plant structures and diverse leaf anatomies, so they can maximize ingestion rates (40). A series of experiments also demonstrated that generalist caterpillars were significantly more susceptible to predation than specialist caterpillars were (10, 11, 33, 38).

Among the plant defense theories of the time was the idea that plants evolved toxins for self-protection, yet I already knew that many potentially toxic plant chemicals were relatively unimportant for insects and many species had adapted to them and even sequestered them. What if deterrent chemicals were not toxic? To examine the potential toxicity of deterrent plant secondary compounds, we made micropills containing bad-tasting chemicals coated with sugar or plant wax and tested a range of grasshoppers and caterpillars for effects on growth and development (65). Few of the chemicals that deterred feeding had measurable post-ingestive effects. So were the chemicals supposedly significant as toxic plant defenses more important as signals that a plant containing them was the wrong species for surviving attack by natural enemies?

As I mulled these ideas, I dived into many sidelines that had captured my attention. For example, grasshoppers are able to learn to avoid a plant that produces either toxic effects or nutritional deficiencies (52). They also learn to use color in their foraging behavior. With surveys in the United States and Costa Rica, I found that plant-chewing insects had larger mandibles and mandible-closer muscles, relative to the size of their bodies, if their food was tough (39). Some species showed phenotypic plasticity in the size of their mandibles and larger ones relative to body size if they fed on plants that were hard or tough (7, 9, 12). Holometabolous insects have a nutritional advantage over hemimetabolous species owing to less investment in cuticular protein (8). It was fascinating to discover that small weevils could have most of their body protein tied up in the cuticle! With a postdoc and a German chemist, we showed that quinolizidine alkaloids were important in a caterpillar species, *Uresiphita reversalis*, on the weed French broom (62). We had worked on it as a potential weed control agent, but the ecology demonstrated that its sensitivity to high levels and intensity of rainfall limited its ability to control spread of the plant.

It was very exciting to have such variation in my work and enthusiastic students and postdocs to work with. The years in Berkeley provided the biggest learning experiences of my life, and each of the people who worked with me was quite special.

UNIVERSITY OF ARIZONA

In Berkeley, I had the professorship, but Reg was barred by nepotism rules from consideration for any job. We knew it would be the case, and I often wondered how many men would so happily give up their careers for their wives as he did. In 1989, we were both offered jobs at the University of Arizona, and it was not a difficult decision, especially as we loved the Sonoran Desert. At a dinner party to say goodbye to Rob Colwell, who was also leaving, our Chinese fortune cookie told us we would be going to the desert, much to the amusement of everyone there!

In Arizona, the atmosphere on campus was a big contrast to that in Berkeley. When I joined the faculty, the cooperative spirit was heady, with everyone from a dozen biology departments ready to do anything to help or work with one another. The interdisciplinary Center for Insect Science was flourishing, and it seemed that even the administration had a "can do" attitude to getting people together. As department head, I worked on the mandate I had been given, to make the entomology department one of the best. I also quickly settled in with the new lab and equipment—I knew how to bargain this time.

It was back to diet breadth, and we needed more comparative studies between specialists and generalists, closely related if possible. In one study, we chose two closely related species of *Heliothis* with different diet breadths and a predatory wasp to examine in detail. Both were fed on a host plant they had in common. In short, the generalist, *H. virescens*, was more vulnerable to predation but grew faster, while the specialist, *H. subflexa*, was taken less by the wasps but grew more slowly (57). Then, with *Manduca sexta*, field observations showed that there was a trade-off in host-plant use: plant quality for growth and survival versus plant features that enhanced protection from parasites and predators (60). The stories to support my overall ideas were building. Natural enemies provide a highly significant selection pressure for specialized diets at least in some insect herbivores.

With Reg, I turned to neurobiology, as he was set up to study chemoreceptors where he had his lab in the neurobiology department. We knew from our early work that among grasshoppers, grass specialists are behaviorally more sensitive to feeding deterrents than are the more polyphagous species, but caterpillars provided a more tractable system in terms of neurobiology. With them, we showed that the taste receptor neurons of specialists are more sensitive to chemicals that deter feeding than are the taste receptor neurons of generalists (42).

We also found that at least in some taxa, numbers of chemosensory receptors are fewer in specialists than in generalists (36). Further, it is well known that specialists among many insect taxa tend to have specific receptors highly tuned to chemicals of their particular host plants. In summary, there were fewer receptors, some deterrent receptors very sensitive to nonhost chemicals, and some feeding receptors especially sensitive to special chemicals of their hosts. I concluded that specialists evolved a neural system that is relatively simple and highly focused on detecting the plants of their narrow host ranges. Is there an adaptive basis for this difference? Does information processing take longer when there is a complex input than when there is a simple input, and does it matter? It seemed that in specialists, a reduced neural message was used in host-plant choice.

The question took me into the realm of decision-making and how streamlining it might matter. It led to experiments with grasshoppers, aphids, whiteflies, and caterpillars, with colleagues elsewhere working on butterflies. Simple comparisons in different taxa showed that specialists do make faster decisions than generalists when it comes to food choice (16, 22, 35, 49, 50).

Homing in on this issue, there was a need to find out more without the complication of other possible genetic factors in comparisons, and to do so, I focused experiments on a single species—the generalist grasshopper, *Schistocerca americana*. I exploited their learning ability in order to raise individuals with different feeding habits so that they were effectively generalists and specialists by training, rather than by genetic predisposition.

Each insect was raised in its own cage. In one experiment, there were two main treatments. One involved six dishes of artificial diet, each with a different added odor. The other involved six dishes all with the same odor. Grasshoppers learned that food came in six flavors or one flavor, and they became either generalists (mixing their variety of foods) or specialists (learning that one flavor meant food). The training period lasted a month, and then I tested my hypothesis that generalists take longer to make decisions than specialists do. On the big test day after the month of training, I presented each grasshopper in turn with six dishes to choose from. This time though, all individuals got variety—six different flavors, including one flavored dish that the specialists knew from experience to be the "only" food. Through close observation of every move, I found that among the specialists, decision times to choose were decreased and feeding was markedly faster with many fewer hesitations throughout the meal (15).

Actually, it is nothing new among humans and other animals that the more items to choose from, the longer it takes to make a choice. The demand on our mental ability to make a selection among choices shows in many, often trivial, ways. It takes longer to select an item on a tray of diverse finger foods at a party than a tray with just two foods. It takes time to choose what to wear unless one has only a single set of clothes (45).

No animals, including people, can take in everything about a whole scene at once. Instead, attention to parts of the scene changes over time. In general, it is the conspicuous items that are detected first. When items stand out strongly—for example, with a bright color or unusual shape—we attend to them selectively so that fast and accurate judgments can be made in the same way as when the choices are few. Selective attention to subsets of inputs from the senses is normal for our ordinary behavior. Where chemicals are involved, enhanced attentiveness to specific odors or tastes matters.

The study with grasshoppers showed a 20% increase in time taken to eat a meal by generalists making choices, and this could be critical. Feeding per se is dangerous. But also, in processing so much information, they would necessarily have reduced vigilance with respect to risks and as a result would fall prey to a multitude of predators and parasites (17).

In the natural world, a plant-feeding insect that is a specialist must still find, detect, and then select the host among a multitude of different plants. So they have smell and taste organs that are hypersensitive to the key chemical characteristics of their hosts. Many flies, beetles, moths, and butterflies have been shown by others to have especial sensitivity to unique chemicals that indicate their host plants. The particular plants they will lay eggs on or need to eat are thereby made conspicuous in the sea of plant chemicals that fill the air, aiding selective attention (13). My intelligent grasshoppers reared with one main chemical learned to use that chemical in their foraging behavior, and it turns out that caterpillars also get hooked on a particular set of plant chemicals, making it easier to locate and select a similar plant in a process commonly known as host-plant conditioning. Such strong signals allow the insects with their neural limitations to selectively focus on feeding without distraction so as to complete their meals in the fastest possible time.

My reading about neural limitation issues with birds and mammals, including humans, influenced my thinking about insect decision-making and how it matters in host affiliation. In recent years, animal behaviorists have rejected the idea that other animals are very different from us or that we must avoid anthropomorphism at all costs. This has allowed us to appreciate all animals' faculties and limitations. As a result, objective experiments can be designed to study the impact of benefits and constraints of physiologies and behaviors that were once considered to be specific to humans or perhaps primates, and then perhaps other mammals and birds. I am thankful that the breadth of my reading, and the changing fashions in the study of behavior, have assisted me in my study of specialization. Already, the work of others has found many of my ideas on the critical importance of neural limitations to also have relevance to butterflies and flies.

Of course, one has to ask why there are generalist insect herbivores at all, given the apparent importance of specialization. There are obvious ecological factors such as the availability of foods allowing flexibility in varying weathers and habitats, and the ability of generalists to extend their geographic ranges, but is that all? One of my students, M.S. Singer, has focused on strategies of generalist caterpillars, especially those in the subfamily Arctiinae. Some of the last projects of my career were with him and other collaborators. Earlier, others had worked with me on foraging by various extreme generalist grasshoppers. And some patterns have emerged common to some of the grasshoppers and caterpillars. A conspicuous pattern concerns species that are highly mobile, foraging actively among whatever host plants are available at a particular site. It appears that individuals are actively selecting food mixtures that improve nutrition.

We also studied *Melanoplus sanguinipes* grasshoppers in the lab and found that they do maximize nutrition by dietary mixing (21, 43). Interestingly, individuals tend to have one of two strategies: being timid in moving across space to get a good mix of foods or bold in doing so, ending with a better mix. The latter individuals grew bigger and faster, suggesting a trade-off between improved nutrition and avoidance of risk. *Taeniopoda eques* grasshoppers can sequester a wide range of noxious plant chemicals, which provides protection from a wide range of potential predators. Individuals move actively from plant to plant, apparently preferring plants with toxic chemicals (37, 63). Experiments with *T. eques* and a related species demonstrated that the switching between foods was stimulated by novelty (23, 37), which ensures a big mix of foods and a big mix of protective chemicals in their bodies.

Among polyphagous arctiines, individuals can vary the ingestion of various secondary metabolites in plants that protect them from a variety of natural enemies. Some arctiines have taste receptor neurons driving feeding that are sensitive to a variety of toxins, including pyrrolizidine alkaloids, to which they respond neurally at a concentration of 10^{-12} M (31). Plants with these compounds are thus highly preferred, but when levels ingested become too high, these neurons cease functioning and other plant compounds become more dominant in behavior (30). In addition, parasitization of the caterpillars can induce greater ingestion of these chemicals, which then protect them from death by the parasitoid. In effect, there is a kind of self-medication (44, 64).

ENDNOTE

Now, in my retirement, I look back on my varied career, my diverse projects over the years in countries all around the world, and my role in the study of entomology. I was lucky enough to be a generalist with varied topics of work in physiology, behavior, and ecology, and I believe each discipline provided insight for the others. Fancy being paid to have such a good time! Much of my work was initiated by a thirst for finding things out and solving problems and a curiosity about life itself, with hypothesis-testing coming later. I think that the curiosity-driven work has the advantage of being more objective because there is no particular "desired" result, while hypothesis testing requires especially rigorous protocols for working "blind" because of the human tendency otherwise to get the results hoped for. But with all the projects I was involved in, it seems clearer than ever now that observation of behavior is the starting place for understanding the lives of animals.

I am grateful to Reg Chapman, who died in 2003. I was lucky to have an admiring, loving husband and vigorous critic, without whom I would not have had such a fortunate life. We had such exhilaration thinking about where the data was taking us—always open to new paths, always excited by unexpected results. I often had the new wild ideas, but Reg would keep me on the path of reason. Together, we shed rays of light on small biological questions, but the payoff in our lives was in gold. I am so grateful to the numerous wonderful students, postdocs and colleagues who made work life so rewarding and such fun. They contributed immeasurably to the work. The memory of their helpful criticisms, excited involvement, and entertaining wit is with me still.

DISCLOSURE STATEMENT

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