The Nature of Defense: Coevolutionary Studies, Ecological Interaction, and the Evolution of 'Natural Insecticides,' 1959-1983

A DISSERTATION
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF THE UNIVERSITY OF MINNESOTA
BY

Rachel Natalie Mason Dentinger

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

Mark Borrello

December 2009

Acknowledgements

My first thanks must go to my advisor, Mark Borrello. Mark was hired during my first year of graduate school, and it has been my pleasure and privilege to be his first graduate student. He long granted me a measure of credit and respect that has helped me to develop confidence in myself as a scholar, while, at the same time, providing incisive criticism and invaluable suggestions that improved the quality of my work and helped me to greatly expand its scope.

My committee members, Sally Gregory Kohlstedt, Susan Jones, Ken Waters, and George Weiblen all provided valuable insights into my dissertation, which will help me to further develop my own work in the future. Susan has given me useful advice on teaching and grant applications at pivotal points in my graduate career. Sally served as my advisor when I first entered graduate school and has continued as my mentor, reading nearly as much of my work as my own advisor. She never fails to be responsive, thoughtful, and generous with her attention and assistance.

My fellow graduate students at Minnesota, both past and present, have been a huge source of encouragement, academic support, and fun. Even after I moved away from Minneapolis, I continued to feel a part of this lively and cohesive group of colleagues. The sense of camaraderie created by the Minnesota connection is undeniable, and I anticipate many more years of intellectual exchange and friendship with these colleagues, especially Georgina Montgomery, Christine Manganaro, and Nathan Crowe. Most importantly, I thank my lucky stars that I entered the history of science and technology program in the same cohort as Gina Rumore. I can't even imagine what

graduate school would have been like without her. I am proud to have shared these years with this great historian, role model for balancing motherhood and scholarship, and dear friend.

Support for my graduate work has come from the Program in the History of Science and Technology, which employed me as a teaching assistant for three years. This support was much more than financial—in particular, my experiences as a teaching assistant for Sally Gregory Kohlstedt, Susan Jones, and Mark Borrello enriched me as a scholar and as a teacher. Further financial support for both living and research expenses came from the University of Minnesota Graduate School. My graduate program and the Graduate School, in addition to the National Science Foundation (Doctoral Dissertation Research Improvement Grant #0724244), all provided the funds that enabled me travel to various corners of the United States, visiting archives and conducting oral history interviews.

The generosity of my interview subjects, in taking time out of their invariably busy schedules to share their experiences and insight with me, can't be underestimated. Thank you, May Berenbaum, Paul Ehrlich, Paul Feeny, Dan Janzen, and Peter Raven. In addition, the archivists and librarians in charge of many collections have been extremely helpful—but none more so than Laurie Hannah of the C.H. Muller Library in the Cheadle Center for Biodiversity and Ecological Restoration, who opened the C.H. Muller collection and her own home to me when I traveled to Santa Barbara for the first leg of my dissertation research in 2007. Both she and Jennifer Thorsch made this one of the most satisfying and useful archival trips of my graduate research.

My friends and family deserve much credit for their unfailing support of my academic pursuits, even when the purpose of spending so much time in school may not have always seem entirely clear to them! I often feel unworthy of the faith that these loved ones bestow on me. I sorely wish that I could have shared this success with my deeply missed grandmother, Lee. Nevertheless, her presence at my dissertation defense could be felt with the amazing showing that my fantastic family made in support of my work. Thanks for coming and cheering me on. My in-laws, the Dentingers, and my oldest and dearest friends, especially Angela and Beth, are living proof that the love of true family need not emerge from shared ancestry.

Ever important, since the very beginning of my academic career almost three decades ago, has been my mother's steadfast emotional, intellectual, and technical support. Nothing seems to deplete her ability to give generously of her love and assistance—even when I call her with a desperate last-minute proofreading request! Together, her certainty of my success and her very practical help and advice have provided the firm foundation from which I still work today.

There is no question that the years of my graduate work have been most profoundly shaped and fueled by the love and partnership of my husband, Bryn. A graduate student himself when we first met, he knew just how to encourage me at those moments when I was pretty sure that I was not going to make it past the next milestone. His understanding of my work in the history of science, as well as his own experiences as a scientist, have provided a wellspring of knowledge for me to draw on throughout my dissertation work. For both of us, graduate school was a test of our confidence and our resolve, and in facing these challenges jointly, we built our relationship with the *mutual* confidence and resolve that now carries us into the next phase of our life together. I think that Bryn will agree, though, that in the final stretch of this dissertation, the person most responsible for urging me on to completion was one that I have yet to meet—the baby in my belly, whose due date fast approaches now. Thank you, both Baby and Bryn, for helping me keep things in perspective during those times when it's been all too easy to become overwhelmed by the work at hand.

This dissertation is dedicated to Bryn and to Baby M.D., whom we can't wait to meet!

Table of Contents

List of Figures

Introduction

This dissertation is a historical account of one of the most compelling concepts in evolutionary biology in the last half of the 20th century: the notion that organisms of different species, and even different kingdoms, can evolve in close, reciprocal response to one another. At the same time, it is an examination of some of the ways that human action in the natural world can change how biologists understand nature. Coevolutionary theory has deep roots in the history of biology. Darwin himself was fascinated by what he called "coadaptation," particularly between flowers and their insect pollinators. These intricately specialized adaptations provided him with evolutionary stories that continue to capture our imaginations in the present day. Yet the field of "coevolutionary studies" was something different. Becoming a vigorous domain of discovery in the 1960s, its practitioners were direct inheritors of the modern evolutionary synthesis of the 1940s. They were also direct inheritors of a natural environment that seemed increasingly on the decline, thanks primarily to the destructive actions of humans. Thus, in my account, *knowing*—the pursuit of knowledge about the natural world—is inextricably interwoven with *doing*—the practical business of interacting with and altering the natural world, for better or worse.

While this dissertation falls solidly within the domain of the history of biology, it also draws significantly from the recent work of environmental historians, whose interrogation of the relationship between nature and human culture has proved an invaluable resource. Through his history of the Columbia River, Richard White writes of "knowing nature through labor," where the process of work, of exerting the human presence upon nature, whether mediated by technology or not, not only teaches us what nature is, but also embeds human beings in the natural world "so thoroughly that they can never be disentangled."[1] Similarly, Edmund Russell's work on the development of chemical warfare, against humans and against insect pests, shows how technology transformed our views of both nature and of ourselves. In the past, "we have seen war and interactions with nature as separate, even opposite endeavours," Russell writes, but "the control of nature expanded the scale of war, and war expanded the scale on which people controlled nature. More specifically, the control of nature formed one root of total war, and total war helped expand the control of nature to the scale rued by modern environmentalists."[2] Critically, both Russell and White explore the multiplicity of meanings of "nature," revealing permeability in the supposedly reliable boundary between the natural and the technological. Environmental historian Joshua Blu Buhs investigates the same porous boundary, defining nature in three "distinct but interrelated ways," namely: nature as "something independent of humans," which would exist with or without *Homo sapiens*; nature as it "exists in our heads," when we "analyze and divide the world around us according to our preconceived notions, our place in society, and our experiences with the world"; and, finally, nature as "something we do." With "our

---

[1] Richard White, *The Organic Machine: The Remaking of the Columbia River* (New York: Hill and Wang, 1995), 7.

[2] Edmund Russell, *War and Nature: Fighting Humans and Insects with Chemicals from World War I to Silent Spring* (Cambridge: Cambridge University Press, 2001), 2.

capacity to dominate the environment," he writes, "we increasingly shape the world around us," thus making nature something that we enact.[3]

In this dissertation, I employ the concept of "nature" in all three senses. Nature as it *is*, "independent of humans," plays a large role in my account, as it constitutes the central focus of investigation in the field of coevolutionary studies.[4] Put more strongly, nature is itself an actor in this account. The precedent of granting historical agency to natural, nonhuman entities has already been set by environmental historians and by those social constructivist scholars who approach science from a perspective of "pragmatic realism."[5] The latter group, while framing science as a product of human culture like any other, emphasizes that the real world steers and constrains the construction of human knowledge. As Andrew Pickering presents it, the process of scientific modeling is extremely "open-ended": "One can try to extend a given scientific culture in an indefinite number of ways." However, "most of those ways do not work." The real world exists—and it *resists*. Thus, knowledge emerges in a "dialectic of resistance [by the real world] and accommodation [by the scientist and her models]."[6] Thus, in science, the second sense of nature, how humans "analyze and divide the world," interacts with the first sense of nature, the world as it really is.

---

[3] Joshua Blu Buhs, *The Fire Ant Wars: Nature, Science, and Public Policy in Twentieth-Century America* (Chicago: University of Chicago Press, 2004), 3.

[4] See "Note on terminology" below for an explanation of my usage of "coevolutionary studies," "coevolutionary theory," and the various terms used to describe scientists practicing under the coevolutionary umbrella.

[5] Andrew Pickering, *The Mangle of Practice: Time, Agency, and Science* (Chicago: University of Chicago Press, 1995), x.

[6] Ibid., xi. For a more wide-ranging review of this literature, see: Jan Golinski, *Making Natural Knowledge: Constructivism and the History of Science (with a New Preface)* (Chicago: University of Chicago Press, 2005).

This "dialectic of resistance and accommodation" can be seen even more clearly when considering the third sense of nature, as "something we do." For it is in the act of doing, of intervening in the real world, that we feel its resistance most strongly. This dissertation is an account of how human technological intervention in the real world fed back upon nature both *as it is* and *as we conceptualize it*. Like Buhs and Russell, I examine human technological intervention in nature with chemicals, the insecticides of agriculture and economic entomology that have had such dramatic effects upon our natural environment. As a historian of science, however, my account diverges dramatically from theirs. Both scholars are focused primarily upon cultural ways of knowing and understanding nature. And while scientists play critical roles in shaping the cultural understanding of insect pests and motivating further technological intervention in both accounts, the relationship is mostly unidirectional. But what factors influence science itself? How are scientific theories about biological change shaped and influenced not only by nature as it is, but also by nature as we enact it? These are the questions that my history of coevolutionary studies pursues.

My argument, outlined in more detail below, may be put simply: The act of changing nature through technological intervention with chemical insecticides profoundly changed the way that biologists understood the natural world and the way that humans understood our own place in the natural world. In building this argument, I draw not only from the environmental historians and science studies scholars cited above, but also from historians of science who have examined the boundary between nature and technology. Of particular value is the work of the late Philip Pauly, whose formulation of the "engineering ideal" in early-20th-century experimental zoology offers a lens through which to examine the work of coevolutionary scientists. Pauly's conceptualization of the engineering ideal embodies, simultaneously, both so-called "pure" scientific knowledge, about nature as it is, and so-called "applied" science, where the objectives of manipulation and control make nature into "something we do."[7] Thus, I spend a significant amount of time in this dissertation analyzing the relationship between pure (or "basic") science and applied science, as one way of accessing the relationship between these different senses of nature. I find that the values of control and intervention that are implicit in the applied sciences can have a direct, substantive effect on shaping the direction and form that basic science assumes.

At the heart of coevolutionary studies is the central principle of *interaction*. More than any other concept, interaction represents the subject of coevolutionary studies, as well the theoretical framework and value system within which the field itself unfolded. Thus, not unlike classic accounts of the “Darwinian revolution,” the story that coevolutionists tell about their own field is one of dismantling a static, one-sided view of nature and replacing it with a perspective based upon dynamic, interactive change, imbued fully with all of the elements of chance and history that make natural selection such a formidable and creative mechanism for evolutionary change. My account concurs in large part with that of the coevolutionists. In shifting their scientific focus from one or another species of organism to the space between multiple species, they did indeed

---

[7] Philip J. Pauly, *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology* (New York: Oxford University Press, 1987).

challenge a number of static and one-sided views that has established strongholds within biology, in particular, in the disciplines of botany and ecology.

More importantly, however, I extend their account of the power of interaction, examining how coevolutionary theory was predicated on the role of humans as participants—interactors—in the very natural systems that coevolutionists strove to understand. To this end, I analyze how methods, metaphors, and materials derived from the applied sciences of economic entomology and agronomy formed a foundation for coevolutionary studies. It is no coincidence that most of the scientists in this narrative were disciplinarily rooted in entomology or insect physiology, two fields where potent toxins aimed at destroying insects were of significant importance. These insect scientists were intimately familiar with the methods, metaphors, and materials used to intervene technologically in the operation of nature. Moreover, the model of chemical activity, of the causal agency of potent molecular tools, which dominated both insect physiology and economic entomology, shaped the model of biochemical interaction that drove early coevolutionary studies.

In the first chapter, I introduce two biological approaches that began to converge in the 1950s, creating a dialectic that was foundational to coevolutionary studies in the 1960s. Scholars have identified molecularization as the historical process by which early-20th-century physiologists transformed biologically active compounds with vague "functional ascriptions" into highly specific molecular agents that could be isolated and analyzed using increasingly sophisticated chemical techniques.[8] Typically regarded as a reductionist trend in biology, the molecularization of insect physiology actually provided a fertile ground for evolutionary theorizing about biochemical relationships between insects and plants. Modern evolutionary biology developed independently from molecularization and is often seen as an integrative antithesis to reductive molecular causation. But in the work of prototypical coevolutionary scientists, the loci of causation offered by these two approaches—one molecular and proximate, the other organismal and historical—proved complementary. I follow the development of this dialectic between molecularization and evolutionary theory through the career of insect physiologist Gottfried Fraenkel, who was among the first to proffer a reciprocal evolutionary solution to the problem of insect-plant relationships. Though Fraenkel and his colleagues in insect physiology were basic research biologists working in academic institutions, the importance of agricultural data and societal problems, which nourished and motivated their research, builds my case that the applied sciences provided the very backbone of the nascent field of coevolutionary studies.

In Chapter Two, I focus more closely on the evolutionary locus of causation, introducing a new generation of evolutionary ecologists, which strove to provide evolutionary explanations for ecological phenomena. These scientists moved, inversely to the insect physiologists, from the evolutionary history of organisms toward an understanding of their biochemical interactions. The dialectic between these two

---

[8] Harmke Kamminga, "Vitamins and the Dynamics of Molecularization: Biochemistry, Policy and Industry in Britain, 1914-1939," in *Molecularizing Biology and Medicine: New Practices and Alliances, 1910s-1970s*, ed. Soraya de Chadarevian and Harmke Kamminga (Amsterdam: Harwood Academic Publishers, 1998).

approaches continued, integrating molecular and evolutionary explanations, as well as basic and applied approaches to science. In fact, the influence of agriculture upon the development of coevolutionary theory was felt particularly strongly in the case of insecticide resistance, an example of real-time evolution in insect populations. For evolutionary biologists like Paul Ehrlich and Daniel Janzen, insects' ability to evolve rapidly in response to anthropogenic toxins appeared to mirror their ability to evolve in response to plant-generated toxins. A notion of “natural insecticides,” adaptively evolved by plants over millennia in order to evade herbivory by insect predators, indelibly linked the biochemical evolution of plants in nature and the human application of artificial poisons in agriculture. Here, then, the realm of applied sciences imbued basic evolutionary theory with the substance of human intervention and control.

In the third chapter I further explore the disciplinary linkages that coevolutionists attempted to build through their work. Considering natural relationships on both an ecological time scale and an evolutionary time scale was not easy and, unsurprisingly, linking the fields of ecology and evolutionary biology was part of the challenge of studying coevolutionary phenomena. However, by arguing that interactions were themselves evolutionary adaptations, coevolutionists made great strides in this direction. As in Chapters One and Two, biochemical methods were also invaluable in linking the disciplines. Janzen and Paul Feeny were particularly instrumental in creating interdisciplinary connections, the former by creating collaborations between biologists and chemists, and the latter by generating research methods that actively joined the separate disciplines within his own work. Thus, as in past chapters, biochemical and organismal methods worked complementarily, providing molecular traces with which present day ecological interactions might be followed back through evolutionary time.

Chapter Four examines the conflict and collaboration that arose between botanists and entomologists as coevolutionary studies developed. While botanical/entomological collaborations were critical to making the field viable, entomologists still primarily dominated it. What's more, some botanists and plant ecologists maintained perspectives on plant evolution that conflicted directly with coevolutionary accounts. These botanists and ecologists actively defended their disciplinary boundaries against the incursions of insect scientists. Much of this conflict was played out through the potent, polarized language that came to dominate coevolutionary studies. Here I analyze this language, especially the tropes of warfare and insecticide used by coevolutionists, in light of scholarship that suggests that language can play a critical role in influencing the success and failure of particular scientific theories and disciplines. I use material from large conferences on biochemical interactions to illustrate how different ideological and theoretical perspectives on plant and insect evolution could fruitfully convene, while contrasting these successful collaborations with the conflict that arose between plant ecologist Cornelius Muller and coevolutionists Ehrlich and Janzen. Muller's commitment to the theory of allelopathy, which held that plant toxins were merely "waste" products, excreted non-adaptively into the environment, contrasted sharply with the coevolutionary perspective that plant toxins were adaptively evolved "weapons." The clash between these two perspectives demonstrates how language can shape scientific conceptions of nature, particularly in the level of agency attributed to particular species within their ecological communities.

In Chapter Five, I assess the further spread of the concept of coevolution in the 1970s and beyond—and in evolutionary biology and beyond. Indeed, enthusiasm for coevolutionary as an explanation for interactions between species, as well as for human cultural phenomena, grew among scientists and non-scientists alike. Coevolution seemed a straightforward byword for the importance of interaction to health of the ecological communities. In fact, coevolutionists like Ehrlich, Janzen, and ecologist Robert Whittaker developed lessons for human society based upon coevolutionary theory. Janzen, in particular, developed a philosophy for conservation based upon human coevolution with other organisms. Coevolution came to represent the hope that human cultural evolution—especially evolution in our use of technological tools—could more closely resemble the coevolutionary systems seen in nature. Significantly, this view of humans as coevolved oragnisms blurred boundaries between supposedly artificial and natural phenomena, a process begun decades earlier when coevolutionary studies sprang up from human agricultural experiences. Yet coevolutionists, even as they encouraged this expansive application of coevolutionary theory, also tried to reform their field, demanding clearer definition, testable hypotheses, and stronger, more generalizable theoretical structures. These attempts at preserving the specificity and scientific utility of the term "coevolution" encouraged the development of sophisticated model systems for the study of coevolution, exemplified here by the work of Feeny's student May Berenbaum. More recently, Berenbaum has helped to shape a global perspective on coevolution, a framework that accommodates both local studies of coevolved systems and global coevolutionary patterns. Through such developments, coevolutionists have struck a balance between expansive extrapolation and reform of coevolutionary ideas.

Note on terminology:

Throughout this dissertation I use the term "coevolutionary studies" to refer to the general body of research undertaken by a disciplinarily diverse set of researchers interested in the phenomenon of coevolution. The term "coevolutionary theory" is meant just as broadly, referring to a loosely bound group of theoretical constructions about the process and products of reciprocal evolutionary change. That said, this dissertation is primarily about biologists who studied (and continue to study) *antagonistic* relationships between insects and plants, such as those that characterize crop plants and their insect pests. It was within this context that coevolutionary studies as we know it today developed, though the field now subsumes a panoply of interactions, from the apparently benign mutualisms of pollination to the outright exploitations of parasitism. Nevertheless, the interactions between butterflies and their food plants motivated the first use of the term “coevolution” in 1964, and rarely did scientists use the term in pollination research during this period. The word “co-evolution” was used by a parasitologist in 1958,[9] but does not seem to have gained much usage immediately thereafter. It was only

---

[9] Charles J. Mode, "A Mathematical Model for the Co-Evolution of Obligate Parasites and Their Hosts," *Evolution* 12, no. 2 (1958).

in 1964, with the publication of Ehrlich and Raven's seminal paper,[10] that the use of the term became common, and then only within the context of relationships between plants and their insect herbivores. To describe the scientists who participated in the development of coevolutionary studies, I use the terms "coevolutionary scientist," "coevolutionary biologist," "coevolutionary researcher," and "coevolutionist" interchangeably.

---

[10] Paul R. Ehrlich and Peter H. Raven, "Butterflies and Plants: A Study in Coevolution," *Evolution* 18, no. 4 (1964).

Chapter One

Molecularizing Plant Compounds, Evolutionizing Insect-Plant Relationships: Gottfried S. Fraenkel and the physiological study of insect feeding in the 1950s

In 1910, "The cause determining the selection of food in some herbivorous insects" was published in the *Proceedings of the Royal Academy of Amsterdam*. The cause at issue, wrote Éduard Verschaffelt,[1] a botany professor at the University of Amsterdam, were the pungent chemicals produced by the cabbage, which become obvious whenever its leaves are bruised or torn. But Verschaffelt based this hypothesis on more than just the sensitivity of his nose; the experience of farmers and horticulturists showed that cabbage butterflies are choosy about their host plants, feeding only on particular species of crucifers or on unrelated groups of plants that share the same chemical profile.[2] In a series of feeding experiments, Verschaffelt demonstrated that mustard oils extracted from these plants could induce cabbage butterfly larvae to feed on erstwhile unattractive plants and even on filter paper.[3]

Verschaffelt's paper appears notable to biologists today as an early contribution to the study of highly specialized relationships between insects and plants, made even more remarkable by the historical mystery it suggests: After Verschaffelt argued for the

---

[1] E. Verschaffelt's first name, Éduard, was inferred based on a biography of the physicist Jules-Émile Verschaffelt, who I believe was his brother. "Scientists of the Dutch School: Verschaffelt," Royal Netherlands Academy of Arts and Sciences, http://www.knaw.nl/waals/verschaffelt.html.

[2] E. Verschaffelt, "The Cause Determining the Selection of Food in Some Herbivorous Insects," *Proceedings of the Royal Academy, Amsterdam* 13 (1910): 536. (Note: This journal is now named the *Proceedings of the Royal Netherlands Academy of Arts and Sciences*.)

[3] Ibid.: 538.

chemical causation of insects' host-selection behavior in the early 20th century, why did such work fall by the wayside until insect physiologists in the mid-century revived interest in the phenomenon?[4]

In part, Verschaffelt's works appears to have been hardly controversial at the time; the notion of chemical causation in plant-insect relationships verged on the commonplace, simply a confirmation of what was generally thought to be the case. It had long been known that plants contain compounds that either attract or repel insects, and the latter function had been well exploited in the creation of the first insecticides.[5] A few European scientists in the late 19th century had even suggested that the biological function of plant compounds was protection against predation by insects or snails.[6] Furthermore, farmers were well aware of the selective eating habits of herbivorous insects, as the common names of crop pests like the tobacco hornworm or corn earworm suggest. In other words, both the chemical variety of plant life and its possible influences on animals were part of an uncontroversial body of knowledge tied, in particular, to the development of agricultural practices.

But in the 1940s and 1950s, insect physiologists picked up the thread of Verschaffelt's research, lamenting that his insights had lain fallow for so long. They

---

[4] For example, Vincent G. Dethier, "Host Plant Perception in Phytophagous Insects," in *Symposia of the Ixth International Congress of Entomology (Amsterdam)* (Amsterdam: DR W. Junk, Publishers, 1953), 81.; R.F. Chapman, "Entomology in the Twentieth Century," *Annual Review of Entomology* 45 (2000): 270.

[5] Edmund P. Russell, *War and Nature: Fighting Humans and Insects with Chemicals from World War I to Silent Spring* (Cambridge: Cambridge University Press, 2001), 5.

[6] Leo Errera,Maistriau, and G. Clautriau, *Premières Recherches Sur La Localisation Et La Signification Des Alkaloids Dans Les Plantes* (Brussels: Henri Lamerin, 1887); Ernst Stahl, *Pflanzen Und Schnecken : Eine Biologische Studie Über Die Schutzmittel Der Pflanzen Gegen Schneckenfrass* (Jena: G. Fischer, 1888).

drew the uncontroversial body of agricultural knowledge about insects and plants into a new context, where Verschaffelt's search for chemical causation was lent a richer meaning. In this chapter, I argue that interest in the chemical relations between insects and plants was revived in the mid-20th century as part of two new biological frameworks that began to rewrite the methods and goals of biological research. What had been an unremarkable phenomenon was transformed into a compelling biological problem through the concurrent developments of molecularization and modern evolutionary biology. Immediate chemical causation, easily perceptible through simple experimentation, was displaced by two more elusive loci of causation: the molecular level and the evolutionary past. I use the work of insect physiologist Gottfried S. Fraenkel to illustrate how the new frameworks of molecularization and evolutionary biology reinvigorated the study of chemical interactions between plants and insects and provided the foundation for the emergence, in the 1960s, of coevolutionary studies of plants and insects.[7] The early-20th-century empowerment of molecules—as concrete causal agents—influenced how biologists in the mid-century came to study, conceptualize, and employ the chemicals of plants. This was the beginning of the transformation of the generic and unremarkable chemicals of plants into "chemical defenses" and "natural insecticides," identities that implied both an evolved biological function and the potential for human application. These specific molecular agents of biological activity were exemplars of a new conception of natural technology.

Fraenkel was a member of the first generation of insect physiologists. In tracing the course of his career, I map the early development of 20th-century studies of plant-insect interactions. His work illustrates how the new molecular paradigm, considered by most historians of biology to epitomize the power of reductionism in 20th-century biology, could be both fully embraced and also subverted: molecules became central to biology, but they were also tools, used in service to the study of the evolution of higher-level interactions between distantly related species. This dialectic, between reductionism and holism, is reflected in the conceptualization of molecules as agents for immediate human intervention into nature and, at the same time, products of an integrative coevolutionary process occurring over millennia.

Fraenkel's hormone work: Molecules as the "actual forces" of causation

The discipline of insect physiology did not yet exist when Gottfried Fraenkel began his study of biology at the University of Munich in the 1920s. He first made his name by identifying medusae statocysts, the organs allowing orientation and balance in the sea, which he discovered while at a marine laboratory in the Bay of Naples.[8] In 1928, soon after finishing his Ph.D., Fraenkel took a job at Hebrew University in Jerusalem, where he would very soon delve into insect physiology: Within a year, Palestine was struck with its first locust invasion in fourteen years and Fraenkel joined the British

---

[8] Gottfried S. Fraenkel, untitled typed notes from folder, "80th Birthday Recollections & Greetings, April-May 1981," Gottfried S. Fraenkel Papers, Series 15/8/22 (henceforth: GSF Papers), University of Illinois Urbana-Champaign Archives (henceforth: UIUC Archives); C. Ladd Prossert,Stanley Friedman, and Judith H. Willis, "Gottfried Samuel Fraenkel," *Biographical Memoirs of the National Academy of Sciences* 59 (1990): 170.

Department of Agriculture's anti-locust control team. In this investigation of locust swarms, he embarked on his first examination of the sensory physiology of insects.[9]

Yet, while sensory physiology continued to fascinate him,[10] the trajectory of his research soon shifted to the study of insect hormones. Leaving Jerusalem in 1932 (initially, for a short-lived lectureship at the University of Frankfurt),[11] Fraenkel became a research associate at University College in London by 1933. Here his hormone research began in earnest and, with it, a deepening of his experience with the nascent molecular paradigm, which was transforming vertebrate hormone research.[12]

While vertebrate hormones were already being recast as molecular tools, the very reality of insect hormones was still under debate in the 1930s. In the previous decade, their existence had been posited,[13] yet the consensus remained that insect produced no hormone and this hypothesis was considered more or less "heretical."[14] British insect

---

[9] Fraenkel, "80th Birthday Recollections"; Ibid.: 171-172.

[10] See, for e.g., Gottfried S. Fraenkel and Donald L. Gunn, *The Orientation of Animals, Kineses, Taxes and Compass Reactions* (New York: Dover Publications, 1961).

[11] Later in life, however, he would reprimand a *Minneapolis Star* reporter for identifying him as a "German scientist"; his career as a German scientist was short-lived, since he came of age, a promising young Jewish physiologist, just as the Nazis were coming to power, and was forced to leave Germany soon after. Wendell Weed of *The Minneapolis Star* to Fraenkel, 21 May 1947, GSF Papers, UIUC Archives.

[12] On Fraenkel's biographical details: Prossert,Friedman, and Willis, "Gottfried Samuel Fraenkel." On vertebrate hormone research: Merriley Borell, "Organotherapy, British Physiology, and Discovery of the Internal Secretions," *Journal of the History of Biology* 9, no. 2 (1976); Bernice L. Hausman, "Ovaries to Estrogen: Sex Hormones and Chemical Femininity in the 20th Century," *Journal of the Medical Humanities* 20, no. 3 (1999); Nelly Oudshoorn, "On the Making of Sex Hormones: Research Materials and the Production of Knowledge," *Social Studies of Science* 20, no. 1 (1990).

[13] S. Kopec, "Studies on the Necessity of the Brain for the Inception of Insect Metamorphosis," *Biological Bulletin* 43 (1922).

[14] John S. Edwards, "Sir Vincent Wigglesworth and the Coming Age of Insect Development," *International Journal of Developmental Biology* 42 (1998): 471.

physiologist Vincent B. Wigglesworth is typically credited with establishing the existence of the first insect hormone in his discovery, in the 1930s, of the hormone triggering insect metamorphosis.[15] Though Fraenkel's early hormone research is granted nary a footnote in this history, his personal recollections assert, and the publication record confirms, that his own discovery of the same insect hormone, later known as ecdysone, was nearly simultaneous with Wigglesworth's discovery.[16]

Fraenkel would later recall that he began his hormone research with "a vague idea [of] finding out what directed metamorphosis,"[17] an impulse that would lead him to apply the methods of molecular manipulation from vertebrate hormone research to the bodies of insects. The project began with a carefully nurtured blowfly culture, started serendipitously after a single blowfly (*Calliphora erythocephala*) came in through his lab window and laid its eggs on a piece of meat. Though the culture was "extraordinarily smelly" and generated "many complaints," it gave Fraenkel a chance to develop his insect rearing skills and practice making ligatures, tying off sections of larvae to watch the effects of reduced circulation between them.[18]

Sometime in early 1934, Fraenkel found that a single ligature separating the anterior and posterior sections of a blowfly larva just as it was about to pupate had a startling effect. While the anterior end would begin to pupate, the posterior would remain in the immature, pre-pupal stage. Not only did it appear that an element circulating through the

---

[15] Ibid.

[16] Fraenkel, "80th Birthday Recollections"; Gottfried S. Fraenkel, "Pupation of Flies Initiated by a Hormone," *Nature* 133 (1934).; Vincent B. Wigglesworth, "Factors Controlling Moulting and 'Metamorphosis' in an Insect," *Nature* 133 (1934).

[17] Fraenkel, "80th Birthday Recollections."

[18] Ibid.

larva must “direct” the stages of metamorphosis, but it also seemed to originate in some center in the front of the larva.[19] To preclude the possibility that pupation was caused by a “nervous stimulus,” a hypothesis long supported by many entomologists,[20] Fraenkel extracted blood from a pupating larva and injected it into the posterior of a ligatured pre-pupa. This injection stimulated pupation, demonstrating experimentally that pupation was not caused by the diffuse signaling of the larva’s nervous system, but by a specific—and likely isolable and manipulable—agent in the bloodstream.[21]

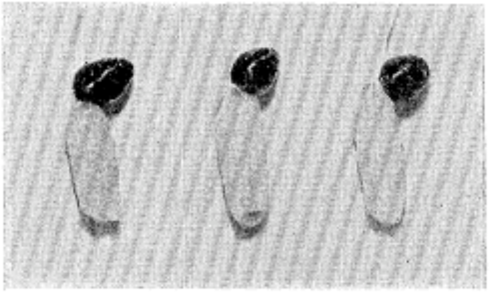

Figure 1. Ligatured blowfly larva with anteriors pupating and posteriors remaining in the pre-pupal stage.[22] (Image reprinted by permission from The Royal Society.)

“Excellent descriptions exist of the morphological and chemical changes in the metamorphosis of insects,” Fraenkel wrote in 1935, “but until the last few years practically nothing was known about the *actual forces* which induce, initiate, or control

---

[19] Ibid.; Fraenkel, "Pupation of Flies Initiated by a Hormone."

[20] Edwards, "Sir Vincent Wigglesworth and the Coming Age of Insect Development."

[21] Fraenkel, "Pupation of Flies Initiated by a Hormone."

[22] Gottfried S. Fraenkel, "A Hormone Causing Pupation in the Blowfly *Calliphora Erythrocephala*," *Proceedings of the Royal Society of London. Series B, Biological Sciences* 118, no. 807 (1935).

moulting and pupation."[23] Fraenkel shared with his contemporaries a sense that the methods of experimental physiology might allow them to finally access and manipulate these "actual forces" directly. As historians of biology have asserted, this type of approach in the laboratory transformed hypothetical biological chemicals, defined via "functional ascriptions" alone, into the highly specific molecular tools of the next generation of scientists.[24] These molecular tools were elements of, in the words of historian Lily Kay, the new "molecular vision of life,"[25] which historians of science have extensively examined in recent years. The "molecularization" of the life sciences was more than just the improvement of laboratory techniques, allowing scientists to investigate the microscopic makeup of the biological world with finer and finer resolution.[26] It was also the transformation of "hypothetical explanatory devices"—

---

[23] Ibid.: 1. (my italics).

[24] Harmke Kamminga, "Vitamins and the Dynamics of Molecularization: Biochemistry, Policy and Industry in Britain, 1914-1939," in *Molecularizing Biology and Medicine: New Practices and Alliances, 1910s-1970s*, ed. Soraya de Chadarevian and Harmke Kamminga (Amsterdam: Harwood Academic Publishers, 1998).

[25] Lily E. Kay, "Life as Technology: Representing, Intervening, and Molecularizing," *Rivista di Storia Della Scienza* 1, Series II, no. 1 (1993): 85.

[26] See, for example: Soraya de Chadarevian and Jean-Paul Gaudillière, "The Tools of the Discipline: Biochemists and Molecular Biologists," *Journal of the History of Biology* 29 (1996); Soraya de Chadarevian and Harmke Kamminga, "Introduction," in *Molecularizing Biology and Medicine: New Practices and Alliances, 1910s-1970s*, ed. Soraya de Chadarevian and Harmke Kamminga (Amsterdam: Harwood Academic Publishers, 1998).; Jordan Goodman, "Plants, Cells and Bodies: The Molecular Biography of Colchicine, 1930-1975," in *Molecularizing Biology and Medicine: New Practices and Alliances, 1910s-1970s*, ed. Soraya de Chadarevian and Harmke Kamminga (Amsterdam: Harwood Academic Publishers, 1998); Kamminga, "Vitamins and the Dynamics of Molecularization: Biochemistry, Policy and Industry in Britain, 1914-1939."; Lily E. Kay, "'Biochemists and Molecular Biologists: Laboratories, Networks, Disciplines': Comments," *Journal of the History of Biology* 29 (1996); Sara Shostak, "The Emergence of Toxicogenomics: A Case Study of Molecularization," *Social Studies of Science* 35, no. 3 (2005).

chemical substances conceived to make sense of gross biological phenomena—“into molecules that could be isolated, identified, manipulated and synthesised by scientists.”[27] In other words, when the “internal secretions” of the late 19th century became the “hormones” of the early 20th century, it was not just a revision of scientific vocabulary; it was the reconceptualization of a chemical cause, which had been pervasive, vague, and difficult to detect, to a molecular tool, which was precise, active, and manipulable.[28] In their training and early careers, physiologists like Fraenkel, studying hormones and vitamins during the 1920s and 1930s, were driven by the pursuit of chemical compounds as causal agents. Fraenkel used bioassays to interrupt an insect’s normal pattern of circulation, implant an organ from another insect, or surgically attach several live insects. Such attempts to identify the molecular cause of a higher-level biological phenomenon like metamorphosis and to identify its centers of production, with the eventual goal of extracting and purifying it, were part and parcel of the new molecular mindset.

Fraenkel’s vitamin work: Molecules inside the laboratory

In 1935, Fraenkel moved to Imperial College and accepted what was perhaps the first full-time lectureship in insect physiology.[29] World War II again altered the trajectory of his work, however, as it did for many physiologists in Britain. Concerns about the food supply motivated the British Medical Research Council to begin heavy

---

[27] Goodman, "Plants, Cells and Bodies: The Molecular Biography of Colchicine, 1930-1975," 83.
[28] Borell, "Organotherapy, British Physiology, and Discovery of the Internal Secretions," 268.
[29] Prossert,Friedman, and Willis, "Gottfried Samuel Fraenkel," 173.

funding of nutrition and pest-control research, and physiologists were well positioned to contribute to these efforts.[30] Wartime relocation brought Fraenkel to Imperial College's Pest Infestation Laboratory at Slough, Bucks. His research there on the diets of stored-product insects began, he would recall later, because battling such pests was "very important to the war effort."[31]

The research I describe below, however, shows that the relevance of his nutritional work to the development of better human diets became an equally compelling motivation for Fraenkel. His confidence that insect colonies were an underappreciated resource for the study of vertebrate nutrition, far more reliable and cost-effective than rodent populations,[32] grew over the course of the next decade. As in vertebrate nutrition research, he modified elements of the insects' food systematically and gauged the success of the diets based on mortality and growth rates.[33] Gradually, he also became convinced that the components of insect diets and vertebrate diets alike were virtually universal. This insight was critical not only to his efforts to weigh in on the nutrition of the British populace, but it would also become the basis for his later work on the interactions of insects and plants.

---

[30] Chadarevian and Gaudillière, "The Tools of the Discipline: Biochemists and Molecular Biologists," 4.; Kamminga, "Vitamins and the Dynamics of Molecularization: Biochemistry, Policy and Industry in Britain, 1914-1939," 86.
[31] Fraenkel, "80th Birthday Recollections."
[32] Ibid.
[33] Alesia Maltz, "The Role of Language in the Discovery and Acceptance of Vitamins" (Ph.D. diss., University of Illinois at Urbana-Champaign 1990).; Gottfried S. Fraenkel and M. Blewett, "The Basic Food Requirements of Several Insect," *Journal of Experimental Biology* 20 (1943).

While the questions and techniques of this new research were different in many ways from Fraenkel's earlier hormone work, the study of vitamins only reinforced his sense of the deeper molecular mechanisms of physiology and his conviction that insects provided ideal models for biomedical research. Moreover, his increasingly molecular view of food allowed him to acknowledge the importance of sense stimuli in motivating feeding behavior, but seek the "actual forces" that caused feeding below the level of gross morphology and scent. This view of the deeper biological meaning of feeding behavior would be pivotal to his later hypotheses about the evolution of relationships between insects and plants. He would come to see the proximate stimulants or inhibitors of insect feeding, like scent and form, as secondary to an evolutionary locus of causation.

As I emphasized above, the ability to isolate and control the most basic causal elements in biological systems was central to the new molecular paradigm. And with this isolation of "actual causes" came a new sense of power, a "notion of intervention at the level of a specific molecule."[34] Simultaneously natural and technological, molecules promised highly specific biological solutions. Nutrition research, like hormone research, quickly adopted this ideal. But in the first decades of the 20th century, nutrition researchers had trouble finding discrete, isolable nutritional elements. These "[p]roponents of the vitamin hypothesis, primarily biochemists," writes historian Alesia Maltz "had considerable inferential proof for the existence of vitamins—that is, they

---

[34] Chadarevian and Kamminga, "Introduction," 2.

managed to starve and stunt the growth of quite a few rats."[35] But direct proof was not forthcoming, despite their best efforts.

Soon enough, though, successful efforts to ascertain the structure of molecules in the interwar years began to transform the "hypothetical entities" of nutrition into tools that could be manipulated. The ability to control nutritional elements was "used to promote a molecular view of diet, of particular diseases, and of the body."[36] By the time World War II began, renewing fears of malnutrition amongst civilians and the military, new vitamins were regularly being identified, characterized, and touted as solutions to myriad health problems.[37] Though Fraenkel had already completed preliminary studies on the metabolism of carbohydrates in his blowfly colony,[38] it was in this milieu, at the beginning of WWII, that he began his own pursuit of the ideal insect diet—and, by extension, an ideal human diet as well.

With the help and coauthorship of a new research assistant, Marjorie Blewett, as well as the financial support of the Royal Society, Fraenkel began publishing on his nutritional research in the early 1940s.[39] In his early experiments, Fraenkel tested

---

[35] Maltz, "The Role of Language in the Discovery and Acceptance of Vitamins", 6.
[36] Kamminga, "Vitamins and the Dynamics of Molecularization: Biochemistry, Policy and Industry in Britain, 1914-1939," 100.
[37] Madeleine Mayhew, "The 1930s Nutrition Controversy," *Journal of Contemporary History* 23, no. 3 (1988).; Rima D. Apple, *Vitamania: Vitamins in American Culture* (New Brunswick, NJ: Rutgers University Press, 1996).; Sally M. Horrocks, "Nutrition Science and the Food and Pharmaceutical Industries in Inter-War Britain," in *Nutrition in Britain: Science, Scientists and Politics in the Twentieth Century*, ed. David F. Smith (London: Routledge, 1997).
[38] Gottfried S. Fraenkel, "Utilization and Digestion of Carbohydrates by the Adult Blowfly," *Journal of Experimental Biology* 17 (1939).
[39] See, for e.g., Gottfried S. Fraenkel,J.A. Reid, and M. Blewett, "The Sterol Requirements of the Larva of the Beetle, *Dermestes Vulpinus* Fabr.," *The Biochemical*

fourteen different sterols, gauging their nutritional value based on the rate of growth of the beetle larvae.[40] These experiments required precise control of the percentages of known nutritional agents, while varying the quantity and quality of sterols with equal precision. Careful composition of the molecular components of insect diets required a heightened awareness of the kinds of impurities common to different substances, particularly, in this case, commercially available cholesterol. Fraenkel himself was not a chemist, but he engaged two biochemists to refine cholesterol so that he could compare both its pure and impure forms.[41]

Fraenkel's nutrition papers exhibit the resourcefulness required of all researchers who seek isolated, purified chemicals for experimentation. Pharmaceutical companies were an especially good source of refined "molecules," and already, in 1940, Fraenkel credited Glaxo Laboratories with a "gift" of samples for a series of experiments on the sterol requirements of the hide beetle (*Dermestes vulpinus*).[42] Historians of molecularization have emphasized connections like these, made between academic researchers and corporations, uniting research objectives that might otherwise seem at variance.[43] As molecules became tools manipulable for human benefit, the interests of academics, industry, medicine, and the military all converged upon them as objects of

---

Journal 35 (1941).; Gottfried S. Fraenkel and M. Blewett, "The Vitamin B-Complex Requirements of Several Insects," *The Biochemical Journal* 37 (1943).

[40] Fraenkel, Reid, and Blewett, "The Sterol Requirements of the Larva of the Beetle, *Dermestes Vulpinus* Fabr.," 712-714.

[41] Ibid.: 712.

[42] Ibid.: 720.

[43] Shostak, "The Emergence of Toxicogenomics: A Case Study of Molecularization."

research,[44] showing how the technological manipulation implicit in the “molecular vision of life” had broad implications for human social institutions. In fact, it is precisely this integration of basic and applied goals, of research objectives that might otherwise seem at variance, that typifies many historical accounts of molecularization.[45] Molecules do not only circulate and act within the blood stream or between plants and insects, but also “outside the lab walls,”[46] within and amongst human social groups that have different, sometimes conflicting, ideals. This quality of molecules makes them constructive tools for historians, “historical probes” that may be used to trace links built between groups with different basic and applied interests.[47]

Like many nutrition scientists, Fraenkel made use of yeast in constructing and testing his experimental diets, benefitting from its superior nutritive value. In fact, dissecting and analyzing the nutritional qualities of yeast yielded a number of critical biological insights for Fraenkel. His work became increasingly “molecular” as he began to hone in on a mysterious “growth factor” found in yeast, which he suspected to be a new B vitamin. Other researchers at the time had identified at least one other unknown

---

[44] See references cited in note 24, as well as Jordan Goodman, "Can It Ever Be Pure Science? Pharmaceuticals, the Pharmaceutical Industry and Biomedical Research in the Twentieth Century," in *The Invisible Industrialist: Manufactures and the Production of Scientific Knowledge*, ed. Jean-Paul Gaudillière and Ilana Löwy (NY: St. Martin's Press, Inc., 1998).

[45] Shostak, "The Emergence of Toxicogenomics: A Case Study of Molecularization."

[46] Oudshoorn, "On the Making of Sex Hormones: Research Materials and the Production of Knowledge," 24.

[47] Goodman, "Plants, Cells and Bodies: The Molecular Biography of Colchicine, 1930-1975," 18.; see also Soraya de Chadarevian, "Following Molecules: Hemoglobin between the Clinic and the Laboratory," in *Molecularizing Biology and Medicine: New Practices and Alliances, 1910s-1970s*, ed. Soraya de Chadarevian and Harmke Kamminga (Amsterdam: Harwood Academic Publishers, 1998)..

nutritional factor in yeast, and Fraenkel himself had found folic acid to be an important component of yeast extracts.[48] But another unidentified B vitamin remained, which Fraenkel dubbed B_T in 1947, in honor of the yellow mealworm, *Tenebrio molitor*, which could not thrive without it.[49] His first indication of B_T came with the startling realization that *Tenebrio* could no longer survive on a standard diet that had previously sustained it. It was now necessary to supplement the diet with extracts from yeast or liver. Gradually, Fraenkel focused in on the commercially produced casein included in the standard artificial diet. Through a careful process of testing casein samples that he had acquired over the years, he realized that methods for purifying commercial casein had become increasingly sophisticated—gradually eliminating the mysterious "growth factor," B_T, and concomitantly stunting the growth of *Tenebrio*.[50] As before, he enlisted the help of chemists to isolate the compound from both yeast and liver, to purify and analyze it, degrading it and testing it against standard chemical reagents, and then purifying it further with column chromatography, verifying his inference about the purified casein and its missing nutrient.[51]

But it was not Fraenkel's method of zeroing in with great precision on its molecular makeup that made the story of B_T a case study in the history of

---

[48] Gottfried S. Fraenkel, "The Importance of Folic Acid and Unidentified Members of the Vitamin B Complex in the Nutrition of Certain Insects," *The Biochemical Journal* 41 (1947).

[49] Ibid.: 474.

[50] Fraenkel, "80th Birthday Recollections"; ———, "B(T), a New Vitamin of the B-Group and Its Relation to the Folic Acid Group, and Other Anti-Anaemia Factors," *Nature* 161, no. 4103 (1948).

[51] Herbert E. Carter et al., "Chemical Studies on Vitamin B(T). Isolation and Characterization as Carnitine," *Archives of Biochemistry and Biophysics* 38 (1952).

molecularization. Instead, it was the continued elaboration of Fraenkel's scientific supply network, which included such pharmaceutical companies as Lederle Laboratories, Parke Davis, Merck, and Glaxo Laboratories. It was the funding he received from the Medical Research Council and the promising possibility that the vitamin could offer protection against anemia.[52] And it was the bridge that Fraenkel built between agriculture and medicine, the pharmaceutical companies and academic research, using the freshly minted currency of molecules. Finally, and most significantly for my larger project, it was the process by which Fraenkel moved from a biological phenomenon to a specific biological agent, B_T, which he conceptualized as active, isolable, and a useful tool for examining insect physiology, as well as human nutrition.

Fraenkel's contribution to the molecularization of insect-plant relationships was also reflected in the work of his students. With Fraenkel's help, a Canadian studying at Imperial College, A.J. Thorsteinson, took up a recapitulation of Verschaffelt's research as his graduate thesis topic, using far more rigorous experimental techniques. His methods demonstrate the usefulness of the molecular paradigm for a new generation of biologists studying the interactions of insects and plants. Standard protocols for extracting and purifying the components of crucifer leaves had been established and published in the 1920s and 1930s; Thorsteinson merely used and cited these critical papers, acknowledging the chemists who had confirmed the identity and purity of the substances

---

[52] On both pharmaceutical companies and anemia, see Fraenkel, "B(T), a New Vitamin of the B-Group and Its Relation to the Folic Acid Group, and Other Anti-Anaemia Factors," 983.

he had extracted.[53] Thorsteinson employed Verschaffelt's "simple technique" of smearing compounds onto various leaves and fibers, but quickly moved on to more sophisticated methods, building on decades of entomological and physiological research on the formulation of insect diets. After all, Verschaffelt's approach did "not lend itself to quantitative determination of feeding responses to media treated with various mixtures of test substances at different concentrations." Nor did it "provide for experimental control of physical characteristics of the media."[54] Precise control over the variables, both macro- and microscopic, was the standard of the day. The careful calculation of concentrations, the ability to synthesize diets that contained those exact concentrations, and the effort to reliably quantify the insects' responses—these techniques embodied the value of the molecular approach for the study of insect feeding behavior.

Thorsteinson conclusively affirmed the attractive power of chemicals extracted from crucifers for crucifer-feeding insects. He also made an argument for the formidable "gustatory sense of insects," which had previously—and mistakenly—been "compared unfavorably with that of humans."[55] Molecular methods allowed Thorsteinson to look below the threshold of human sensation and observe that insects seemed especially attuned to the substances of plants that they ate. This fact was "most illuminating," he wrote, since "the test substances are of significance in the biology of the insect."[56]

---

[53] A. J. Thorsteinson, "The Chemotactic Responses That Determine Host Specificity in an Oligophagous Insect (*Plutella Maculipennis* (Curt.) Lepidoptera)," *Canadian Journal of Zoology* 31, no. 1 (1953).

[54] Ibid.: 55.

[55] Ibid.: 69-70.

[56] Ibid.: 69.

Though Thorsteinson's work was not published until 1953, it was completed as early as 1947,[57] according to Fraenkel, who was one of his more influential teachers.[58] It was Fraenkel, in fact, who took the initiative in early 1947 to write to Vincent G. Dethier, a renowned insect physiologist, then at Ohio State University. He inquired about Dethier's interesting field of study, still relatively unfamiliar to Fraenkel: the chemistry and physiology of insect food choice. This original letter is lost, but Dethier's formal reply to "Dr. Fraenkel" has an air of tutelage. Dethier directed Fraenkel to the bibliography in his forthcoming book, *Chemical Insect Attractants and Repellents*,[59] which he believed to include "most of the known references to this field of experimentation." He sent two reprints and even enclosed some copied manuscript pages from his book, which would, as Dethier put it, help Fraenkel "gather some idea of the type of work which has been done." Dethier also expressed "great interest" in the "topic of your student's thesis."[60] And, indeed, he would eventually read a full draft of Thorsteinson's thesis.[61] While the degree to which Dethier influenced Fraenkel's thinking is unclear, the connection that the two scientists made here would prove to be important. Both men would come to apply a distinctive combination of molecular methods and evolutionary logic to the study of insect-plant interactions. And in the

---

[57] Fraenkel, "80th Birthday Recollections."

[58] A. J. Thorsteinson, "This Week's Citation Classics," *Citation Classics* 45 (1980).

[59] Vincent G. Dethier, *Chemical Insect Attractants and Repellents* (Philadelphia: The Blakiston Company, 1947).

[60] Dethier to Fraenkel, 6 March 1947, GSF Papers, UIUC Archives.

[61] Thorsteinson, "The Chemotactic Responses That Determine Host Specificity in an Oligophagous Insect (*Plutella Maculipennis* (Curt.) Lepidoptera)," 71.

1950s, they would both become known for their roles in establishing the study of insect-plant interactions as a newly burgeoning field.

The questions and techniques of vitamin research were different in many ways from Fraenkel's earlier hormone work. But they only reinforced his sense of the deeper molecular mechanisms of physiology, and his search for the "actual forces" that functioned below the level of gross morphology and scent. This view of the deeper biological meaning of feeding behavior would be pivotal to Fraenkel's later hypotheses about the evolution of relationships between insects and plants. He would come to see the proximate stimulants or inhibitors of insect feeding, like scent and form, as secondary to an evolutionary locus of causation, which operated at the organismal level.

Molecules outside the laboratory

Fraenkel's use of yeast in his experiments also began to yield insights about higher-level biological phenomena outside the lab: interactive, organismal phenomena occurring in nature. Though the final summary from his paper on the sterol project refers only to the quantity and quality of sterol required by hide beetles,[62] an earlier discussion of the data reveals that he was already thinking beyond the bounds of his laboratory walls. In this discussion, Fraenkel compared a colleague's research on the sterol requirements of *Drosophila* with his own work on *Dermestes*. His colleague's work demonstrated that *Drosophila*'s need for sterol could be fulfilled by ergosterol, the primary sterol found in yeast. This made good biological sense, Fraenkel concluded,

---

[62] Fraenkel,Reid, and Blewett, "The Sterol Requirements of the Larva of the Beetle, *Dermestes Vulpinus* Fabr.," 720.

since “it is generally considered that living yeast is the main food of the *Drosophila* larva.” With equal logic, *Dermestes*, the hide beetle, requires cholesterol—after all, it eats mostly desiccated and smoked meats and hides, “dried-up cadavers and the like in which cholesterol constitutes the only or main sterol present.”[63] Already Fraenkel had employed his increasing insight into the minute particulars of insect diets to a broader biological context.

At the same time, Fraenkel’s research efforts continued to be guided by the needs of British society and the exigencies of war. The “newer science of nutrition,” with its atomistic model of causation and emphasis on the discovery of isolable and marketable molecules, had generated public enthusiasm for the consumption of vitamins. [64] By the 1930s, particularly in Britain, companies selling dietary supplements had employed significant numbers of trained biochemists, scientists who not only performed research but maintained credibility and contacts in the world of academic science and science policy.[65] The work of these scientists, as well as academic scientists, promoted a molecular ideal of health, based on a reductionistic notion of nutrition, to the government and public alike.

Physiologists’ use of molecules to induce higher-level biological phenomena rested on an atomistic model of biological causation, a form of reductionism that scholars

---

[63] Ibid.: 719.

[64] Apple, *Vitamania: Vitamins in American Culture*, 3,6; Mayhew, "The 1930s Nutrition Controversy," 447-449.

[65] Horrocks, "Nutrition Science and the Food and Pharmaceutical Industries in Inter-War Britain," 56.

have heavily emphasized in their accounts of molecularization.[66] Implicitly and explicitly, science-studies scholars like Lily Kay insist that the molecular program "distanced its concerns from interactive processes occurring within higher organisms, between organisms (e.g. symbiosis), and between organisms and their environments." Furthermore, this reductionistic approach "negated historical explanations in biology, [as well as] developmental and evolutionary accounts of life processes – the arrow of time."[67]

And yet, even as Fraenkel pursued these molecular agents of causation in his research, he maintained a more holistic view of the place of nutritional knowledge in society. He did not suggest, for instance, that a broad program of vitamin distribution, based on cutting-edge scientific calculations of nutritional requirements, would repair the deficiencies that most nutrition scientists saw running rampant in British and American society. Instead, he contended—at a time when dietary supplements were only gaining in popularity[68]—that whole foods were of far higher nutritional quality than any amount of dietary supplementation or fortification.

In a 1941 paper written with Marjorie Blewett, he recounted how one of his favorite research organisms, the confused flour beetle (*Tribolium confusum*), had confirmed that refined white flour was seriously deficient in nutrients. His "hitherto little

---

[66] Robert Olby, "The Molecular Revolution in Biology," in *Companion to the History of Modern Science*, ed. R.C. Olby et al. (London: Routledge, 1990).
[67] Kay, "Life as Technology: Representing, Intervening, and Molecularizing," 89.
[68] Apple, *Vitamania: Vitamins in American Culture*.

used method,"[69] of employing an insect as a test subject, proved an effective model, comparable even to similar experiments on white rats.[70] By adding varying amounts of riboflavin to samples of white flour, he gauged the mixtures' nutritional value based on the number of days it took flour beetle larvae to reach pupation, verifying what was already suspected: riboflavin was the critical element missing from white flour. The paper was a rebuttal of the Ministry of Food's efforts to "fortify" white flour with the addition of vitamin B_1, which, in light of Fraenkel's evidence of the missing riboflavin, was an entirely misguided effort.

Five years later, in a 1946 Fabian Society tract, *Towards a Socialist Agriculture*, Fraenkel disputed the wisdom of fortification in any form. In his chapter, "Britain's Nutritional Requirements," he presented the "'white bread versus brown bread' controversy," which was apparently "in full swing" as early as 1937. He came down firmly on the side of whole wheat or "brown" bread.[71] It was widely known that white flour was nutritionally worthless, he wrote, but its enrichment was hardly a solution. In fact, the process "has been condemned on nutritional grounds by most experts on both side of the Atlantic, and is widely regarded as capitulation to the business interests of the millers and the vitamin manufacturers."[72]

---

[69] i.e., "little used" by other nutrition researchers. Gottfried S. Fraenkel and M. Blewett, "Deficiency of Riboflavin in White Flour," *Nature* 147, no. 3736 (1941): 716.
[70] Ibid.: 717.
[71] Gottfried S. Fraenkel, "Britain's Nutritional Requirements," in *Towards a Socialist Agriculture: Studies by a Group of Fabians*, ed. F.W. Bateson (London: Victor Gollancz LTD, 1946), 52.
[72] Ibid., 52-53.

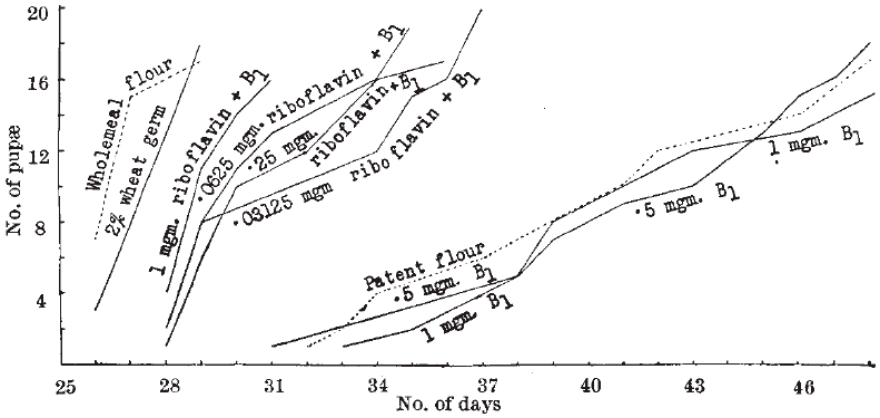

Fig. 2.

LARVAL GROWTH OF *Tribolium confusum* ON PATENT FLOUR SUPPLEMENTED BY VITAMIN B_1 AND RIBOFLAVIN. QUANTITIES PER 2 GM. OF FOOD.

Figure 2. This graph, from Fraenkel and Blewett's 1941 paper, reports that the number of days till pupation (i.e., rate of larval development) was highest with whole-wheat flour and lowest with white, processed flour. Processed flour with riboflavin added still delayed development, but not as much as white flour alone.[73] [Image reprinted by permission from Macmillan Publishers Ltd: *Nature* 147 (3736): 716-717, 1941.]

Rejecting a molecular ideal that he himself employed in experimentation, which historians of biology describe as "intervention at the level of a specific molecule,"[74] Fraenkel asserted that the nutritional needs of society could only be addressed as a whole. True to the socialist ideals of the Fabian Society,[75] Fraenkel focused not on per capita quantification of calories or nutrients consumed, but on the patterns of distribution of

---

[73] Fraenkel and Blewett, "Deficiency of Riboflavin in White Flour," 716.

[74] Chadarevian and Kamminga, "Introduction," 2.

[75] Gordon Brown, "Foreword," in *Radicals and Reformers: A Century of Fabian Thought*, ed. Mark Thomas and Guy Lodge (London: Fabian Society, 2000).; Subrata Mukherjee, "Fabian Socialism: One Hundred Years in the Life of a Doctrine," in *Essays on Fabian Socialism*, ed. M.M. Sankhdher and Subrata Mukherjee (New Delhi: Deep and Deep Publications, 1991).;Patricia Pugh, *Educate, Agitate, Organize: 100 Years of Fabian Socialism* (Lodon: Methuen, 1984).

these, which he believed to reflect social stratification.[76] In essence, he argued that the agricultural system and the nutritional needs of all individuals should not be subject to molecularization, but should be considered and guided holistically. Fraenkel endorsed the "marriage of agriculture and nutrition," even if it must be "arranged"; market forces alone could never guarantee that British farmers, food manufacturers, and importers provide the populace with sufficient food and sufficiently nutritious food.[77] In other words, though Fraenkel worked within a molecular framework behind the laboratory bench, his view of the movement of molecules in the broader biological context and in society was more organismic and more holistic. This interplay of values within Fraenkel's work reaffirms the experimental power of the analytic molecular approach even as it belies the claim that molecularization was solely a reductionist trend.

Moreover, Fraenkel would sustain this balance between organisms and molecules throughout his career, applying it to the study of evolutionary adaptation between insects and plants, precisely those "interactive processes occurring within higher organisms" that Kay and other science-studies scholars claim to have been neglected in the development of molecularization. The use of molecules to study evolution—the *co*evolution of insects and plants—brought "the arrow of time" to the forefront of Fraenkel's research and located the primary levels of causation at the organismic level and in the evolutionary past. In other words, the work of Fraenkel and his colleagues, which formed the basis for coevolutionary studies in the mid-20th century, examined biological causation at multiple loci that are often otherwise considered to be in conflict. It was this very juxtaposition of

---

[76] Fraenkel, "Britain's Nutritional Requirements," 51.
[77] Ibid., 43.

molecular and evolutionary causal loci that made the question of chemical specificity between plants and insects such a compelling area of investigation.

The skills that Fraenkel developed over the course of his hormone and nutrition work, of transforming "hypothetical explanatory devices"[78] into both causes and tools, would guide how he came to see the compounds of plants and how he investigated them. Attempts to get a grasp on molecules, both practically and conceptually, would provide useful skills in the reinterpretation of the "secondary" compounds of plants.[79] These compounds, whose utility to the plant had long been denied,[80] were transformed into natural "chemical defenses" and "weapons," highly specific "mediators" of biological interactions. Thus, while Fraenkel and his colleagues launched a new program of study that exploited this reductionistic molecular approach, they also began to see the immediate action of molecules as secondary to broader biological—and in the case of Fraenkel's wartime nutrition research, social—functioning. This interplay between the study of molecules and higher-level biological and social phenomena may be further understood in light of Garland Allen's recent taxonomy of dialectical interactions in late-19th-century and 20th-century biology. Allen asserts that the life sciences have been characterized by a dialectical interplay between higher-level synthetic thought and reductionist analytic thought.[81] As Richard Levins and Richard Lewontin define it,

---

[78] Goodman, "Plants, Cells and Bodies: The Molecular Biography of Colchicine, 1930-1975," 83.

[79] Called "secondary" because they are ancillary to plants' *primary* metabolic processes.

[80] Karl Paech, *Biochemie Und Physiologie Der Sekundären Pflanzenstoffe* (Berlin: Springer, 1950).

[81] Garland E. Allen, "A Century of Evo-Devo: The Dialectics of Analysis and Synthesis in Twentieth-Century Life Science," in *From Embryology to Evo-Devo: A History of*

"These are the properties of things we call dialectic: that one cannot exist without the other, that one acquires its properties from its relation to the other, that the properties of both evolve as a consequence of their interpenetration."[82] Seeing biological causation at the molecular level does not necessarily negate causation at a higher level; instead, the tension between the two perspectives is often mutually productive. In a sense, then, this chapter is not only a history of the early foundations of coevolutionary studies, but it is also a case study of the dialectical interplay between analysis and synthesis in the 20th-century life sciences.

A venue for insect-feeding research: Fraenkel moves to the U.S.

By 1947, Fraenkel's work at Imperial College London had solidly established him as a leading researcher in insect physiology and nutrition. Yet, he faced two central challenges in his research. He had begun to draw general biological conclusions about the natural feeding behaviors of insects, based on his research on stored-product insects. But the proliferation of data on the nutrition of stored-product insects, stimulated by the

---

Developmental Evolution, ed. Manfred D. Laublicher and Jane Maienschein (Cambridge: The MIT Press, 2007), 125-127. The synthetic end of the spectrum includes "speculation," seeking historical causation for phenomena, and viewing organisms holistically; the analytic end includes experimental methods, seeking mechanical and proximate causation for phenomena, and viewing organisms as mechanical assemblages of atomistic biological components.

[82] Richard Levins and Richard C. Lewontin, "Introduction," in *The Dialectical Biologist*, ed. Richard Levins and Richard Lewontin (Cambridge: Harvard University Press, 1985), 3.

war, was not met by a similar proliferation of data on plant-eating insects in nature.[83] Moreover, his conviction that insects were ideal biomedical model organisms gained no purchase with his British patrons. His attempts to convince Edward Mellanby of the Medical Research Council of the "general significance" of such work, which he believed to merit a "separate unit of the Medical Research Council," were not met enthusiastically.[84] Standard mammalian models for nutrition research, thanks in part to their more obvious analogy with human bodies, remained the model organisms of choice for biomedical research.[85]

His correspondence with Mellanby suggests that these frustrations alone may have been enough to motivate him to look for research opportunities in the United States. In 1947, he traveled to the U.S. for the first time, taking a visiting professorship at the University of Minnesota's Entomology and Economic Zoology department, teaching a course on insect nutrition from March though June of 1947.[86] "One of the world's half-dozen top scientists in insect physiology has arrived at the University Farm campus school," announced *The Minneapolis Star*. "Fraenkel's subject is one of great importance to an agricultural area such as the Upper Midwest," the paper reported. Fraenkel confirmed the usefulness of his research to agriculture, claiming that it was important to know "why one insect feeds on cabbage and another on cereal crops, because then you

---

[83] The food plants of many plant-eating insects (especially butterflies) were known, but their *nutritional requirements* had not been studied in the same way that Fraenkel studied the requirements of stored-product insects.

[84] Fraenkel to Mellanby, 10 February 1948, GSF Papers, UIUC Archives.

[85] Fraenkel, "80th Birthday Recollections."

[86] University of Minnesota, "Notice of Appointment," 18 February 1947, GSF Papers, UIUC Archives.

can discover how to control them."[87] The thirteen-page bibliography that he assembled for his course cites a wide array of literature; from papers on specific types of nutrients, to books on plant biochemistry, and at least seven full pages of references on the nutrition of insects feeding on the leaves, wood, sap, or nectar of plants.[88]

Apparently, Fraenkel used his visit to the U.S. as an opportunity to network with American colleagues and prospective employers.[89] It was not long after his return to London that he was offered a full professorship at the University of Illinois. Writing to Mellanby, Fraenkel lamented that it was "deplorable and not in the best interest of science in Britain that this work, which began in this country under very difficult circumstances and has been developed with the aid of the Royal Society and the Medical Research Council, should now be transferred to the United States."[90] Mellanby, for his part, was remorseless, replying, "I am sorry to hear that you have decided to go to the United States, but under the circumstances I felt that this was inevitable when you told me of the offer that the University of Illinois made to you, and I therefore did not feel

---

[87] *The Minneapolis Star*, "One of 'Top Six': German Insect Expert to Aid 'U' Research," 26 March 1947, GSF Papers, UIUC Archives.

[88] Gottfried S. Fraenkel, "Bibliography on Insect Nutrition, Course of Lectures given by G. Fraenkel," undated, GSF Papers, UIUC Archives.

[89] The Minneapolis Star piece cited in note 72 refers to Fraenkel giving a lecture given in Iowa. There is also correspondence with an entomologist from UW-Madison. Correspondence between Fraenkel and University of Minnesota entomology professor Glenn Richards shows that Fraenkel initiated the appointment by inquiring whether such an opportunity existed and suggesting that, if so, he "should very much appreciate if [Richards] would perhaps propose me as a candidate" (Fraenkel to Richards, 10 October 1946, Division of Entomology and Economic Zoology Papers, University of Minnesota Archives). The head of the department subsequently wrote to the Rockefeller Foundation requesting funds for Fraenkel's visit (Clarence E. Mickel to H.M. Miller, 2 November 1946, Division of Entomology and Economic Zoology Papers, University of Minnesota Archives).

[90] Fraenkel to Mellanby, 10 Feb 1948, GSF Papers, UIUC Archives.

able to persuade you to alter your views." Mellanby continued more encouragingly, however, writing that he was "quite sure from what I have seen of American research that you will get good backing."[91]

And, indeed, it seems that Mellanby was correct. Though his first appeals to the Rockefeller Foundation were futile,[92] Fraenkel almost immediately started garnering funds from the U.S. Public Health Service and the Office of Naval Research.[93] By 1951, his frequent correspondence with Warren Weaver had yielded his first Rockefeller Foundation grant, of $8,000, an amount that would grow considerably over the next decade.[94] Part of his funding success in the early years of the 1950s was undoubtedly due to the high profile of his discovery of vitamin B_T, which went to press first in a 1948 paper in *Nature*.[95] The vitamin received increasing attention in 1951 and 1952 with the publication of more detailed chemical studies.[96] In many local and national newspapers, Fraenkel's "New 'B' Vitamin"[97] was touted for its practical and scientific value.[98]

---

[91] Mellanby to Fraenkel, 18 Oct 1948, GSF Papers, UIUC Archives.

[92] Warren Weaver to Fraenkel, 17 March 1949, GSF Papers, UIUC Archives.

[93] For example, one of Fraenkel's Public Health Service grant applications, dated 24 January 1957, shows Public Health Service grants dating back to 1949 and Office of Naval Research grants dating back to at least 1956, all listed in the previous and current support section of the proposal (GSF Papers, UIUC Archives).

[94] Fraenkel to Weaver, 19 March 1953, GSF Papers, UIUC Archives.

[95] Fraenkel, "B(T), a New Vitamin of the B-Group and Its Relation to the Folic Acid Group, and Other Anti-Anaemia Factors."

[96] Gottfried S. Fraenkel, "Isolation Procedures and Certain Properties of Vitamin B(T)," *Archives of Biochemistry* 34, no. 2 (1951).; ———, "Effect and Distribution of Vitamin B(T)," *Archives of Biochemistry and Biophysics* 34, no. 2 (1951).; Carter et al., "Chemical Studies on Vitamin B(T). Isolation and Characterization as Carnitine."

[97] Waldemar Kaempffert, "New 'B' Vitamin Tested on a Worm," *New York Times*, 6 May 1951.

[98] See, for e.g.: Science Service press release, "Pampered Cockroaches May Give Clue to Better Health," 14 April 1950; *New York Times*, "New 'B' Vitamin Tested on a Worm,"

This mix of basic and applied emphases was undoubtedly appealing to Fraenkel's supporters, and can also be seen in the language of his grant applications.[99] His practical emphases shifted away from potential biomedical applications, toward the agricultural applications that would be highly valued at a Land Grant institution like Urbana-Champaign. Simultaneously, his interests in nutrition shifted slightly also. Originally, Fraenkel's interest in nutrition focused primarily on the animal, the insect consuming nutrients, making the grain or plant simply a substrate on which the animal subsisted. Gradually, however, for Fraenkel—and others interested in insect food choice—the plant began to assume a more important role. In fact, it was the *interaction between* the plant and insect that gradually became the focus of much of this research.

Moreover, the skills that Fraenkel developed over the course of his hormone and nutrition work, of transforming "hypothetical explanatory devices" [100] into both causes and tools, would guide how he came to see the compounds of plants as he began to investigate these interactions. Attempts to get a grasp on molecules, both practically and conceptually, would provide useful skills in the reinterpretation of the "secondary" compounds of plants.[101] These compounds, whose utility to the plant had long been ignored, despite the eary-20th-century arguments of Verschaffelt, were transformed into

---

6 May 1951; *St. Louis Post Dispatch*, "Discovery," 7 December 1951; *Daily Illini*, "Entomological Mystery Solved!" 15 December 1951; *Newsweek*, "Insect Impresario," 29 December 1952.

[99] The series of grant applications found in the GSF papers (UIUC Archives) merge appeals to the ideals of basic biology to the goals of applied, economic entomology and agriculture.

[100] Goodman, "Plants, Cells and Bodies: The Molecular Biography of Colchicine, 1930-1975," 83.

[101] Called "secondary" because they are ancillary to plants' *primary* metabolic processes, such as respiration.

natural “chemical defenses” and “weapons,” highly specific “mediators” of biological interactions. Thus, applying the molecular framework to plant secondary compounds gave Verschaffelt’s research new significance. Simultaneously, modern evolutionary theory became increasingly pervasive and began to influence the work even of biologists like Fraenkel, who had spent the early years of their careers focused primarily on proximate physiological phenomena. Below, I show how this growing emphasis on the importance of evolutionary history worked in conjunction with molecularization, transforming the immense variety of plant compounds, and their role in insect feeding behavior, into a compelling biological problem.

The evolution of plant compounds: Molecules moving on “the arrow of time”

By the mid-1940s, many insect physiologists and entomologists had become more interested in the dynamics of insect food choice. Molecular knowledge had given them unprecedented insight into the microscopic mechanisms of insect biology and the sense that they were accessing the “actual forces”[102] that caused biological phenomena. Most recognized the truth of Verschaffelt’s observations, that plants’ secondary compounds could attract or repel insects seeking food. But beneath this simple observation, there were scientific problems to be solved. How did these compounds evolve? And why did insects make the choices that they made?

Most insect biologists had long believed that insect choice was based on nutritional value, a view that Fraenkel also held for the first decade of his career. But

---

[102] Fraenkel, "Pupation of Flies Initiated by a Hormone," 1.

near the end of the 1940s, Fraenkel's opinion of insect food choice underwent a sea change, which he documented in a letter to Dutch entomologist Jan de Wilde in early 1951. De Wilde was organizing a session for the 9th International Congress of Entomology, to be held in Amsterdam in August 1951. He requested that Fraenkel lecture alongside other insect-feeding luminaries of the time, like Johns Hopkins insect physiologist Vincent Dethier[103] and Kansas State University economic entomologist Reginald H. Painter. This shared session, "The Physiological Relations between Insects and their Food Plants," would later be recognized as a landmark in the study of plant-insect interactions.[104] At Fraenkel's suggestion, de Wilde gave him the topic, "The Nutritional Value of Green Plants for Insects."[105] Fraenkel's assertions on this theme would likely come as a surprise to many of his colleagues. "I have been working in this field for over 11 years," Fraenkel wrote to de Wilde, "and have come to the conclusion that all insects require basically the same chemical substances for growth and development." Furthermore, he continued, "plant materials nearly always contain these substances in adequate amounts, and [therefore] the question of host plant selection is more one of sensore perseption [*sic*], i.e., attraction and repulsion."[106] In other words,

---

[103] Dethier and Fraenkel shared earlier correspondence and the former's influence on the latter is clear (Dethier to Fraenkel, 6 March 1947, GSF Papers, UIUC Archives.).

[104] L. M. Schoonhoven, "After the Verschaffelt-Dethier Era: The Insect-Plant Field Comes of Age," *Entomologia Experimentalis et Applicata* 80 (1996): 1.

[105] de Wilde to Fraenkel, 31 Jan 1951, GSF Papers, UIUC Archives.

[106] Fraenkel to de Wilde, 22 Jan 1951, GSF Papers, UIUC Archives.

Fraenkel had completely reversed his earlier conviction that nutrition determined host plant selection.[107]

This reversal began with the molecular paradigm and was foundational to a new evolutionary interpretation of plant-insect relationships. Seeing the similarities of animal diets from the molecular level taught Fraenkel and other insect physiologists to look below the surface of sensory stimuli that most biologists noticed most immediately, to interrogate feeding behaviors on multiple biological levels: The biological significance of feeding behaviors might be located at both the molecular level *and* at the organismal level. Similarly, the emerging modern evolutionary synthesis would induce them to look beyond the ecological present, into the evolutionary past. In the remaining pages of this chapter, I argue that insect physiologists combined their molecular understanding of insect feeding behavior with 20th-century evolutionary theory, initiating a new research program on the evolution of plant compounds in the 1940s and 1950s. I contend that the development of a new research program on plant-insect interactions, which was the precursor for coevolutionary studies, was dialectical, following the path of molecules as they moved and acted through evolutionary time.

I focus less tightly on Fraenkel here, placing him in the context of the pivotal conference mentioned above. That “The Physiological Relations between Insects and their Food Plants,” was cutting-edge demonstrates that Fraenkel himself was extremely influential in the development of this new field of study. At the same time, the harmony

---

[107] Fraenkel and Blewett, "The Basic Food Requirements of Several Insect."; Gottfried S. Fraenkel, “Application to the Royal Society for a Government Grant in Aid of Scientific Investigation,” 22 March 1943, GSF Papers, UIUC Archives.

between the themes of the three lectures outlined below also demonstrates that Fraenkel was no renegade; the molecular and evolutionary study of plant-insect interactions was taking shape in the 1950s, and Fraenkel was only part of a larger scientific movement.

The landmark symposium

Fraenkel's interest in insects' eating habits had grown over the course of the 1940s, and he was certainly not alone in this. In the United States, Dethier had already dedicated most of the previous decade to studying the sensory physiology of insect food choices.[108] Economic entomologist Painter had built his career on the study of plants' chemical *resistance* to insect feeding, breeding crop plants in order to enhance their naturally occurring repellant compounds.[109] All three approached the question of insect feeding from different angles, yet their work, in concert, would help to further "evolutionize" insect-plant relationships.

Dethier's decade of research on the sensory physiology of insect feeding had already motivated him to hypothesize confidently about the biological significance of the chemicals produced by plants. Like Verschaffelt before him, Dethier had conducted simple feeding experiments, smearing plant extracts on various substrates. Like Thorsteinson after him, Dethier was able to exploit molecular techniques to maintain precise control over the substances he administered and their concentrations. Like his

---

[108] See, for e.g., Vincent G. Dethier, "Gustation and Olfaction in Lepidopterous Larvae," *Biological Bulletin* 72 (1937). and ———, "Chemical Factors Determining the Choice of Food Plants by Papilio Larvae," *The American Naturalist* 75, no. 756 (1941).

[109] See, for e.g., Reginald H. Painter and J.H. Parker, *Resistance of Plants to Insects: A Bibliography* (Manhattan, KS: Kansas State College of Agriculture, 1932). and Reginald H. Painter, *Insect Resistance in Crop Plants* (NY: Macmillan, 1951).

colleague Fraenkel, Dethier was able to exploit commercial contacts for his chemical supplies, which were “put up” by Eastman Kodak and drug company Dodge & Olcott.[110] And finally, to a far greater extent than any of the above scientists, Dethier extended his experimental results to an analysis of their broader biological significance, explaining the geographical range of various insect groups based upon the range of their host plants. He posited transitions, in which one insect group moved between different groups of plants, based upon the plants’ chemical affinity. Dethier’s attention to the molecular structure of the compounds he analyzed was meticulous. The relations between structure and odor, and between different compounds with subtly overlapping or conflicting types of odors, were all brought to bear on the choices that insect larvae made in his experiments. Natural ecological ranges of both plants and insects were correlated with feeding patterns and with plant chemistry. In other words, by 1941, Dethier had already begun to employ molecular knowledge and methods to better understand the history of interactions between insects and plants.[111]

Dethier also contributed to changing ideas about the significance of insect nutrition by demonstrating that feeding habits had more to do with secondary compounds—by definition, non-nutritious molecules—than with the nutritional needs of insects. Nutrition constitutes a proximate explanation, tied directly to the immediate needs of the insect, rather than its evolutionary history. “[T]he problem of plant selection [by insects],” he wrote in his 1947 monograph, has been “frequently confused with that

---

[110] Dethier, "Chemical Factors Determining the Choice of Food Plants by Papilio Larvae," 64.
[111] Ibid.: 70-73.

of nutrition. [However, since] the nutritive value of various angiosperm leaves is not markedly dissimilar, as evidence by the fact that a given monophagous larva may by various experimental artifices be fed on a variety of plants, factors governing choice may be largely divorced from nutritional requirements."[112] This passage, in particular, seems to have impressed Fraenkel when he read Dethier's book. In a set of undated notes, typed by Fraenkel while reading up on insect food preferences, it was this passage alone that he transcribed from Dethier's book, without comment.[113] Its importance, apparently, was self-evident.

In August 1951, many of the world's most accomplished insect biologists gathered in Amsterdam for the 9th International Congress of Entomology. The symposium on "Physiological Relations between Insects and their Host Plants" was a highlight of the congress, and would still be remembered decades later as "state-of-the-art."[114] It included presentations by Dethier, Fraenkel, and Painter,[115] each of whom had

---

[112] ———, *Chemical Insect Attractants and Repellents*, 39. "Monophagous" insects generally eat only one species of plant; "Oligophagous" insects eat a restricted number of plant species; and "polyphagous" insects eat many different species. "Phytophagous" simply refers to all plant-eating insects.

[113] Gottfried S. Fraenkel, undated notes from a folder entitled "Green Leaves: Basis of Specificity," GSF Papers, UIUC Archives. These notes were typed on letterhead from the Marine Biological Laboratory in Woods Hole, MA. It appears that Fraenkel worked at Woods Hole a number of times in the 1950s and 1960s, however, so it is difficult to date it thus. Most likely, these notes date from 1953 or 1959, based upon the dates of Woods Hole folders in the collection (see finding aid at http://www.library.uiuc.edu/archives/archon/index.php?p=collections/controlcard&id=3178&q=fraenkel). Even more likely is that these notes are from 1959, from Fraenkel's preparation of his well-known 1959 paper, which I will discuss in the next chapter, "The Raison d'Etre of Plant Secondary Compounds."

[114] Schoonhoven, "After the Verschaffelt-Dethier Era: The Insect-Plant Field Comes of Age," 1.

a slightly different perspective on the problem of insect-plant relationships. Yet, all converged upon important central themes, emphasizing detailed molecular knowledge of insect-plant relationships and the historical basis of those relationships.

Remarkable as it may have been in 1951, readers of coevolution literature from the 1960s will find Dethier's opening trope quite familiar: "Of all organisms," he stated, "the insects show the greatest diversity of diets, the most outstanding of plasticity on the one hand and the most rigid of restrictions on the other."[116] The completion of this trope—its botanical reciprocal—does not emerge until a few pages later, when Dethier concludes, "The remaining link in the chain of events consummated by feeding lies in the realm of plant physiology and biochemistry." Here Dethier contradicted the assumptions of so many zoologists who saw the plant world as an endless, uniformly green, and "homogeneous" food source for insects. "The plant," he challenged his entomological colleagues, "which is the source of the chemical stimuli, is by no means a standard repository of specific compounds. It is an extremely complex organism in its own right."[117] Increasing knowledge about the complexity of molecular interactions—the motion, action, and causal agency occurring constantly below the threshold of human sensory experience—had given Dethier a new sense of the invisible chemical geography that shaped the life histories of his study organisms. And this new awareness had

---

[115] The fourth presentation in the symposium was by and Fraenkel's former student, behaviorist John S. Kennedy (John Brady, "J.S. Kennedy (192-1993): A Clear Thinker in Behavior's Confused World," *Annual Review of Entomology* 42 (1997).). Because his talk is not directly relevant to my aims, I am not going to discuss it here.

[116] Dethier, "Host Plant Perception in Phytophagous Insects," 81.

[117] Ibid., 86.

naturally spread beyond the bounds of those organisms, the insects, to the plants with which they interacted.

To extend their molecular awareness, attempting to see chemical interactions from the perspective of the plant, multiplied the apparent complexity of biological interactions for insect physiologists. And the picture was about to become even more complex, as the broad relevance of evolutionary history became increasingly apparent. In fact, in the first "fundamental" issue that Dethier raised, he asked, "What is the genetic basis and evolutionary history of specific diet preferences?"[118] As Dethier saw it, the restrictions imposed and opportunities presented by the contingencies of history—the results of geographical and ecological isolation, for instance—had consequences not only for basic biological knowledge, but also for pest control. The importance of understanding the origin and maintenance of insect food preferences could not be overemphasized, considering "the behavior of introduced pests which in various parts of the world have tasted and found to their liking plants not formerly available."[119] The shared evolutionary history of plants and insects had relevance also, then, to the needs of human society: How could we understand and control invasive pests without this basic knowledge?

Fraenkel spoke next, opening with a claim about the great "amount of economical damage done by leaf eaters," which he considered to be "one of the most important

---

[118] Ibid., 81.
[119] Ibid., 82.

problems which confront the entomologist."[120] Fraenkel approached the problem from the perspective of a nutritionist, seeking the ideal synthetic diet for leaf-feeding insects. After all, little was known about the nutritional needs of insects beyond studies of stored-product pests. What little *was* known, however, suggested that all insects shared "essentially similar" nutritional requirements. For most of this presentation, Fraenkel focused on reviewing data about the nutritional components of various leaves, knowledge that was "entirely confined to a few species of the forage plants, and to a small number of vegetables…most, if not all [of which] are cultivated varieties." [121] He compared data on the detailed molecular composition of various cabbages, lettuce, barley, oats, and other crops, likely collected for agricultural and nutritional purposes.[122] Where Dethier had used inference, observing that a monophagous insect could often survive on a non-preferred plant if necessary, Fraenkel presented direct molecular evidence: "The chemical composition of leaves, as far as it is of importance in the nutrition of insects, seems to be very similar in different plants. There is no evidence of differences in different species, genera, families, or orders which might be responsible for the specificity of host plants for their insects." His conclusion? An "admittedly extreme and one-sided" explanation based upon chemical cues from secondary compounds, those plant substances, like alkaloids and tannins, which had been demonstrated time and again to attract or repel

---

[120] Gottfried S. Fraenkel, "The Nutritional Value of Green Plants for Insects," in *Symposia of the Ixth International Congress of Entomology (Amsterdam)* (Amsterdam: DR W. Junk, Publishers, 1953), 90.

[121] Ibid., 91.

[122] Ibid., 92-97.

insects in the laboratory. These “token stimuli,” he argued, were *wholly* responsible for the specificity of insect-plant relationships.[123]

Painter, like Fraenkel, excelled at “emphasizing the biological conclusions that can be drawn from some aspects of applied entomology.”[124] He was also interested in the same plant molecules as Fraenkel, those “[i]nsecticidal materials [that] have been extracted from many different plants.” Painter’s experience artificially selecting plants with higher levels of such “insecticides” had given him insight into the processes of natural selection that might have produced specific chemical relationships between insects and plants. Moreover, he knew that such naturally derived insecticides were not uniformly effective. “Such toxic materials differ greatly in their specificity, [and] the plants that bear them often carry insect pests that are immune to, or avoid the insecticide.”[125]

The most striking aspect of Painter’s talk was his broad evolutionary hypothesis about plants and insects, made possible, in part, by his own direct experience with such evolution in an agricultural context. Citing evolutionary relationships between flowering plants and their insect pollinators as an example, Painter proposed a “similar parallel evolution between host plants and the behavior patterns and physiologic potentialities of

---

[123] Ibid., 99. The language of “token stimuli” is interesting. While Fraenkel claims these “token stimuli” to be “*wholly* responsible,” the word “token” suggests contrarily that they are not in and of themselves biologically significant—they are mere tokens, representative of a more profound biological (in this case evolutionary) process.

[124] Reginald H. Painter, "The Role of Nutritional Factors in Host Plant Selection," in *Symposia of the Ixth International Congress of Entomology (Amsterdam)* (Amsterdam: DR W. Junk, Publishers, 1953), 101.

[125] Ibid.

insect."[126] He then sketched out the skeleton of reciprocal coevolutionary theory, which would not be fleshed out for more than a decade: The "genetic changes in plants in the direction of resistance may be paralleled by changes in the phytophagous insects." His field experience with crop pests was invaluable here, for he was able to cite, with certainty, the existence in nature of strains of insects already able to feed on resistant plants. Such strains, in other words, were the basis for the evolution, by natural selection, of an insect that could feed, exclusively, on an otherwise toxic plant.[127] In this hypothetical scenario of "parallel evolution" Painter masterfully synthesized his knowledge of evolution, gleaned from his own direct experience with applied entomology, with the growing body of knowledge about plants' natural "insecticides." Central to his hypothesis was the power of natural selection to explain the evolution of both insecticides and insects' resistance to insecticides.

Conclusion

The three symposium papers highlighted above were the manifestations of converging strands of research from insect physiology and economic entomology. The arguments formulated therein rested on increasingly sophisticated knowledge of molecules, a view of molecules as natural tools, and a belief in the important role that molecules, like insecticides or vitamins, played in society. Their arguments also promoted an increasingly interactive and historical interpretation of the ecological

---

[126] Ibid., 103.
[127] Ibid., 104.

relationships between insects and plants: Plants were biochemically complex organisms, not homogeneous substrates for insect life, and insects selected plants based on highly sensitive sensory systems that had evolved over time, as a result of complexly interacting geographical and biological factors. It was this awareness of molecules moving through both time and space, as integrated parts of organisms that shared intimate interactions with other organisms, that made Verschaffelt's research of a half-century earlier compelling to a new generation of biologists, and provided a basis for the development of early coevolutionary theory.

This developing research program provides a historical case study for Allen's conception of dialectical biology; it was analytic and synthetic, atomistic and—perhaps, rather than holistic—interactive.[128] But it also provides an opportunity to significantly extend Allen's cautious conclusions about the importance of social goals in the development of experimentalism in the early 20th century. As part of his dissection of dialectical biology, Allen tentatively suggests that a "broader economic and social context…gave an increasing interest in, and even urgency to, the experimental ethos,"[129] citing the "engineering ideal," a concept developed by Philip Pauly in his study of Jacques Loeb. According to Pauly, in the early 20th century, experimental biology was

---

[128] Describing this developing research program as holistic could be taken to mean (inaccurately) that the emerging coevolutionary perspective saw plants and insects functioning together as a "superorganism." Interactive, suggests, more accurately, that while insects and plants are considered "atomistic" individuals, they are adapted to and are constantly responding to (and even, in some cases, relying upon) individuals of other species with which they coexist in close proximity.

[129] Allen, "A Century of Evo-Devo: The Dialectics of Analysis and Synthesis in Twentieth-Century Life Science," 136.

no longer seen as “a natural science, but as an engineering science.”[130] Loeb’s Progressive-Era social context put him in contact with colleagues “deeply concerned about the broad transformative potential of science in the modern world.”[131] Thus, the engineering ideal embodied both a model of “pure science” and the motive power of practical challenges. While evolutionary theory about relationships between insects and plants was certainly grounded in the ideals of basic biology, there is no doubt that it also received attention and funding thanks to its promise of applications that could benefit society. Even more to the point, insect physiologists and entomologists came to see plant compounds as active, isolable tools—“natural insecticides” that could be extracted and manipulated. The process of molecularization allowed, as Kay writes, the “conceptualization of life as a technology.”[132] Thus, just as synthetic insecticides were a technology engineered by humans, natural insecticides were a technology engineered by natural selection to thwart the advances of hungry insects. And the potential of this natural technology for future evolutionary engineering, by humans, became as much a part of coevolutionary theory and practice as insect-feeding experiments and biochemical analyses.

---

[130] Philip J. Pauly, *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology* (New York: Oxford University Press, 1987), 199.

[131] Ibid., 7.

[132] Kay, "Life as Technology: Representing, Intervening, and Molecularizing," 85. It’s important to note, also, that we are not necessarily talking about the origin of “molecular biology,” which even in its broadest conception usually has to do with the origin of molecular genetics (see, for e.g., Olby, "The Molecular Revolution in Biology.") This, instead, is about “molecularizing” a far broader array of biological processes (see Chadarevian and Kamminga, "Introduction.").

Chapter Two

Selection, Natural or Unnatural: The evolution of insecticide resistance and the emergence of coevolutionary theory in the 1960s.

In 1958, the epic war that humans waged against insect pests seemed all but lost to many people. "Through all the centuries of man's existence on earth, insects have buzzed and darted and crawled around him, chewing up his food and houses and clothes, lacerating his skin and infecting him with dreadful diseases," lamented journalist Albert Rosenfeld in *Life* magazine. "Man has fought back with all his resources and ingenuity," he continued, and "swatted, sprayed, burned, bombed, and gassed bugs." Despite all of this, "he has never been able to wipe out even one of the more than 10,000 varieties of insects that harass him."[1] The advent of synthetic organic insecticides little more than a decade earlier had appeared to signal the defeat of the insects decimating crops and spreading disease. But these new weapons had proven not only toxic to many other organisms, but also increasingly ineffective. Astonishingly, insects had shown themselves capable of developing a resistance to even the deadliest poisons. However, according to Rosenfeld, this litany of human losses was about to give way to a new "Ultimate Weapon": "Now at last there is every reason to believe that man will win this ancient war. The promise of victory is based on an entirely new kind of insecticide, one that makes use of the insect's own body chemistry rather than poison."[2] An American insect physiologist, Carroll M. Williams, had stumbled upon this potent insecticide, and

---

[1] Albert Rosenfeld, "The Ultimate Weapon in an Ancient War," *Life* 45, no. 14 (1958): 105.
[2] Ibid.

in a most unexpected place: ordinary paper toweling. When isolated, this insect hormone mimic, synthesized by a number of trees species, had successfully stunted the development of a model laboratory insect.

Williams' discovery heralded the birth of third-generation pesticides. These compounds targeted specific pests via their own physiological peculiarities, interfering with mating or metamorphosis, as an alternative to dumping broad-spectrum poisons into the environment. For Williams, however, his discovery would come to represent something quite different from "an entirely new kind of insecticide." Insecticide it certainly was, but *new* it was not. In fact, as he would write a decade later, its derivation from a plant suggested that the hormone mimic had acted as an insecticide for millennia, persisting as one of the plant kingdom's evolutionary solutions to its own war against insects.[3]

In this chapter, I demonstrate that the "insecticide crisis," brought on in part by the evolution of insecticide resistance in pest populations, provided motivating energy and an intellectual milieu for the development of coevolutionary studies in the 1960s. Coevolutionary theory emerged as an explanation for the origin of plants' and insects' otherwise inexplicable biochemical characters—in terms of their shared evolutionary history. Formally, this meant a primary research focus on interactions between insects and plants. But the implications for human relationships with both insects and plants

---

[3] Carroll M. Williams, "Hormonal Interactions between Plants and Insects," in *Chemical Ecology*, ed. Ernest Sondheimer and John B. Simeone (New York: Academic Press, 1970), 104. Curiously, Williams does not cite coevolutionary research in this account, though it is obvious that he refers to coevolution. His papers offer few clues as to when and where he first read about coevolutionary theory (Carroll M. Williams Papers, Accession 12265, Harvard University Archives).

were manifold. Most obviously, it became apparent that the “ancient war” between humans and insects was only an extension of what evolutionary biologists came to see as an even older war between insects and plants. And I argue that the “weaponry” of this older war, as coevolutionists phrased it, the “natural insecticides” of plants, provided the material and intellectual resources for the development not only of our own synthetic insecticides, but also for the development of coevolutionary theory.

Two research schools converged upon the study of coevolution between insects and plants. The first, introduced in Chapter One, were insect physiologists, whose work studying molecules as agents of causation in insect bodies in the mid-20th century led them to hypothesize about the shared evolutionary history of insects and plants. Inversely, the second school, composed of a new generation of evolutionary biologists, whose work studying the shared evolutionary history of insects and plants in the 1960s led them to a molecular explanation of that history. These two groups, approaching insect-plant relationships from opposite directions, with contrasting approaches to studying insects and plants, together developed the new field of coevolutionary studies in the midst of the insecticide crisis. Simultaneously molecular, evolutionary, and militaristic, coevolutionary studies represented not only a dialectic between the study of upper- and lower-level biological phenomena, as I described in Chapter 1, but also a synthesis of purportedly “pure” science ideals and practical goals and experience.

First, I elaborate upon my earlier account of insect physiologists, like Gottfried Fraenkel, who sought out and characterized the molecular agents at work in insect bodies. The intellectual habits and experimental methods that allowed them to look below the level of the organism, tracing the activity of molecules through physiological space, led them to follow the same molecules through evolutionary time. In the context of growing agricultural, pharmacological, and industrial interest in these molecules, the interactive model of reciprocal insect-plant evolution developed by Fraenkel and his colleagues was simultaneously a theory of evolutionary history and of the evolutionary present.

At the same time, a new generation of evolutionary biologists and evolutionary ecologists were coming of age. They were highly attuned not only to the new molecular paradigm and the modern evolutionary synthesis, but they were also motivated, to an unprecedented degree, by the imperative of understanding human interactions with other organisms. The environment appeared to be in crisis, primarily as a result of human activity, and they felt a responsibility to intervene. In the second part of this chapter, I introduce some of these young evolutionary biologists. In particular, I focus on entomologist Paul Ehrlich and botanist Peter Raven, who collaborated in 1964 to write a seminal paper that would incite the first wave of explicitly coevolutionary research.[4] Both trained as taxonomists, Ehrlich and Raven brought the evolutionary histories of their respective groups to bear on the antagonistic relationships of herbivory. Beginning with their own ecological insight into relationships between butterflies and their food plants, they developed a biochemical hypothesis about the evolution of those relationships, drawing on the work of phytochemists, insect physiologists like Gottfried Fraenkel, and real-time observations of populations of agricultural pests, which were constantly evolving in response to the insecticides applied by humans.

---

[4] Paul R. Ehrlich and Peter H. Raven, "Butterflies and Plants: A Study in Coevolution," *Evolution* 18, no. 4 (1964).

The intersection of the biological sciences and insecticide research in this period has already captured the attention of science-studies scholars like Joshua Blu Buhs, John Ceccati, and Edmund Russell.[5] Buhs and Russell, in particular, describe some of the fascinating ways in which our understanding of nature and our attempts to control it became enmeshed in the practices and ideologies of insecticide research and application. They posit a reciprocal relationship between attempts to understand nature through science and attempts to control nature through the application of chemicals. Yet, in both historians' accounts, the fully reciprocal character of this relationship is lost: Buhs and Russell address how biological knowledge provided material and intellectual resources for the use of synthetic chemicals, but overlook how the application of synthetic insecticides changed the way that biologists understood nature. In contrast, I trace specific ways that ideas, materials, and methods from insecticide research and application made direct contributions to the development of coevolutionary theory, which became one of the most broadly relevant bodies of evolutionary theory and research in the last half of the 20th century.

---

[5] Joshua Blu Buhs, "The Fire Ant Wars: Nature and Science in the Pesticide Controversies of the Late Twentieth Century," *Isis* 93 (2002); ———, *The Fire Ant Wars: Nature, Science, and Public Policy in Twentieth-Century America* (Chicago: The Chicago University Press, 2004); John S. Ceccatti, "Resisting Insects: Shifting Strategies in Chemical Control," *Endeavour* 28, no. 1 (2004); ———, "Biology in the Chemical Industry: Scientific Approaches to the Problem of Insecticide Resistance, 1920s-1960s," *AMBIX* 51, no. 2 (2004); Edmund P. Russell, *War and Nature: Fighting Humans and Insects with Chemicals from World War I to Silent Spring* (Cambridge: Cambridge University Press, 2001); ———, "'Speaking of Annihilation': Mobilizing for War against Human and Insect Enemies, 1914-1945," *The Journal of American History* 82, no. 4 (1996).

My argument also builds upon the work of historians of biology who have claimed an important role for practical agriculture knowledge in the generation of basic biological knowledge. As Jonathan Harwood, Barbara Kimmelman, and William Provine have amply demonstrated, agricultural interests and experience with animal breeding supported and shaped the emerging discipline of genetics.[6] More recently, though, Harwood has decried historians’ neglect of agricultural research beyond genetics.[7] Though historical scholarship has demonstrated that agriculture may “prompt biologists to study particular basic phenomena,” according to Harwood, the conduit of exchange

---

[6] Lloyd T. Ackert, "The Role of Microbes in Agriculture: Sergei Vinogradskii’s Discovery and Investigation of Chemosynthesis, 1880–1910," *Journal of the History of Biology* 39 (2006); Jonathan Harwood, "Geneticists and the Evolutionary Synthesis in Interwar Germany," *Annals of Science* 42 (1985); ———, "National Styles in Science: Genetics in Germany and the United States between the World Wars," *Isis* 78, no. 3 (1987); ———, *Styles of Scientific Thought: The German Genetics Community, 1900-1933* (Chicago: The University of Chicago Press, 1993); ———, "Metaphysical Foundations of the Evolutionary Synthesis: A Historiographic Note," *Journal of the History of Biology* 27, no. 1 (1994); Barbara A. Kimmelman, "The American Breeders' Association: Genetics and Eugenics in an Agricultural Context, 1903-13," *Social Studies of Science* 13, no. 2 (1983); ———, *A Progressive Era Discipline: Genetics at American Agricultural Colleges and Experiment Stations, 1900-1920. Dissertation, University of Pennsylvania* (1987); ———, "Organisms and Interests in Scientific Research: R.A. Emerson's Claims for the Unique Contribution of Agricultural Genetics," in *The Right Tools for the Job: At Work in Twentieth-Century Life Sciences*, ed. Adele E. and Joan H. Fujimura Clarke (Princeton: Princeton University Press, 1992); William B. Provine, "The Development of Wright's Theory of Evolution: Systematics, Adaptation, and Drift," in *Dimensions of Darwinism: Themes and Counterthemes in Twentieth-Century Evolutionary Theory*, ed. Marjorie Grene (Cambridge: Cambridge University Press, 1983); Thomas Wieland, "Scientific Theory and Agricultural Practice: Plant Breeding in Germany from the Late 19th to the Early 20th Century," *Journal of the History of Biology* 39 (2006).

[7] Jonathan Harwood, "Introduction to the Special Issue on Biology and Agriculture," *Journal of the History of Biology* 39 (2006); ———, "Biology in the Universities," in *Life and Earth Sciences since 1800*, ed. Peter and John V. Pickstone Bowler, *The Cambridge History of Science* (Cambridge: Cambridge University Press, forthcoming).

between agricultural and biological knowledge remains poorly understood.[8] Rather than merely claiming that applied research may generate basic knowledge, then, I explore the substance of this relationship, the way that applied goals have penetrated and influenced fundamental areas of basic biology.

As I mentioned in Chapter 1, the infiltration of applied biological data and methods into scientific conceptions of insects and plants reflected, in particular, the ideas and practices of control embodied by Pauly's early formulation of the "engineering ideal."[9] This ideal, which used experimental methods to hybridize the pursuit of pure scientific knowledge and the effort to control biological entities, can be seen clearly in the way that insecticide application and burgeoning evolutionary theory intersected. And at this point of intersection the two schools described above came together and generated a new notion of *co*evolution. More than just a fresh conception of how insects and plants related to each other, coevolutionary theory had deep implications for how humans related to other organisms in nature, embodying the "engineering ideal" thanks to its relevance to human attempts to control insect pests. In the final section of this chapter, I suggest that the interrelationship between pest control and coevolutionary began to reconstruct how scientists saw humans' biological place in nature. Through an account of insect physiologist Carroll Williams' discovery of a new plant-derived toxin, I will show

---

[8] Harwood, "Introduction to the Special Issue on Biology and Agriculture," 239. See, for example, Ackert, "The Role of Microbes in Agriculture: Sergei Vinogradskii's Discovery and Investigation of Chemosynthesis, 1880–1910."; Kim Kleinman, "His Own Synthesis: Corn, Edgar Anderson, and Evolutionary Theory in the 1940s," *Journal of the History of Biology* 32 (1999); Wieland, "Scientific Theory and Agricultural Practice: Plant Breeding in Germany from the Late 19th to the Early 20th Century."

[9] See Chapter One and Philip J. Pauly, *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology* (New York: Oxford University Press, 1987).

how the notion of "natural insecticides" nourished a new sense of human interactions with other species: Even as the damage wrought by insecticides suggested that society was destructively separating from some unsullied notion of "nature," a more interactive, historical view of nature, in which "biochemical warfare" might be considered an evolutionary adaptation, was also taking root.

Insect physiologists: From molecules to evolution

In the previous chapter, I described how insect physiologists like Gottfried Fraenkel, upon examining insect feeding from a molecular perspective, found the nutritional theory of insect choice lacking. It was this failure of the theory of nutrition, as well as the strength of physiological methods, that allowed biologists like Fraenkel to follow molecular agents of causation into the evolutionary past. Moreover, my analysis of the 1951 symposium on "The Physiological Relations Between Insects and their Foodplants,"[10] also revealed how the question of insect feeding united the interests of physiologists, like Fraenkel and Dethier, with those of agricultural entomologists, like Painter. The evolution of biochemical interactions between insects and plants clearly had a wide relevance, beyond the laboratory, to the interests of human society, which appeared to face an increasingly invincible army of pest insects. However, despite the insights that scientists like Fraenkel, Dethier, and Painter all appeared to bring to subject of insect and plant evolution, the growing ranks of evolutionary biologists in the mid-

---

[10] Vincent G Dethier,Gottfried S. Fraenkel, and Reginald S. Painter, "The Physiological Relations between Insects and Their Foodplants," in *Symposia of the Ixth International Congress of Entomology (Amsterdam)* (Amsterdam: DR W. Junk, Publishers, 1953).

century looked with derision upon the disciplines of both physiology and applied biology (particularly applied entomology), claiming that these studies led to a narrow understanding of biology and a neglect of ultimate, evolutionary causation of phenomena.[11] In part, this antagonistic attitude originated in a sense of unease over the growing power of molecules to solve both practical and theoretical problems in biology. Molecular biology gained disciplinary ground rapidly, challenged the preeminence of the newly achieved evolutionary synthesis just as it seemed to be gaining a foothold in the discipline of biology.[12] But the fact that Fraenkel led the charge in the 1950s to synthesize molecular causation with evolutionary causation demonstrates how misleading the claims of these evolutionary biologists could be. Fraenkel's dynamic, interactive view of the "interdependence"[13] of insects and plants would become a fundamental constituent of coevolutionary theory in the 1960s. And the relationship between coevolutionary studies and traditions of molecular, physiological, and applied biology, would continue to be a mutually fruitful, reciprocal exchange even in the 1960s, after the field of coevolutionary studies was established as a part of evolutionary ecology.

---

[11] David Lack, "Evolutionary Ecology," *Journal of Animal Ecology* 34 (1965); Ernst Mayr, "Cause and Effect in Biology," *Science* 134 (1961); Gordon H. Orians, "Natural Selection and Ecological Theory," *The American Naturalist* 96 (1962).

[12] Vassiliki Betty Smocovitis, "Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology," *Journal of the History of Biology* 25 (1992).

[13] These quotations are from a paper given in 1953, published in 1956: Gottfried S. Fraenkel, "Insects and Plant Biochemistry: The Specificity of Food Plants for Insects," *Proceedings of the XIV International Congress of Zoology, Copenhagen* (1956).

After the 1951 symposium, Fraenkel became increasingly confident about what he had once qualified as his “admittedly extreme and one-sided view”[14] on insect-plant relationships. Presenting on the topic again in 1953, at the 14th International Congress of Zoology in Copenhagen, he made the role of plants more central. Where the insect’s-eye view was implicit in his 1951 paper, “The Role of Nutritional Factors in Host Plant Selection,” the title of his 1953 paper reflected a new appreciation for plants: “Insects and Plant Biochemistry: The Specificity of Food Plants for Insects.” Fraenkel’s goals in the paper were both methodological and theoretical. He proposed a series of investigative steps that would “establish the interdependence between insects and secondary plant substances.”[15] While primarily molecular and experimental, these steps also entailed a basic knowledge of evolutionary relationships in the plant kingdom, requiring the investigator to seek out phylogenetically unrelated but chemically similar plants, in order to independently verify the effects of specific compounds on the feeding habits of insects.

Already, Fraenkel was engaging in the discourse of *interaction* that would come to distinguish coevolutionary research. Two years earlier, Painter had tentatively described what he saw as the “parallel” evolution of insect and host plant;[16] by 1953, Fraenkel was prepared to define the same evolutionary dynamics as “reciprocal adaptive evolution,” a restatement that clearly indicated an intimate, responsive relationship

---

[14] ———, "The Nutritional Value of Green Plants for Insects," in *Symposia of the Ixth International Congress of Entomology (Amsterdam)* (Amsterdam: DR W. Junk, Publishers, 1953), 99.

[15] Fraenkel, "Insects and Plant Biochemistry: The Specificity of Food Plants for Insects," 384.

[16] Reginald H. Painter, "The Role of Nutritional Factors in Host Plant Selection," in *Symposia of the Ixth International Congress of Entomology (Amsterdam)* (Amsterdam: DR W. Junk, Publishers, 1953), 103.

between insects and plants. Moreover, Fraenkel also began to invoke the ancient evolutionary history that lay behind these intimate relationships, beginning with the plants, which had “developed early in their evolution the means by which they became unpalatable to the rising multitude of insects. This was accomplished by the introduction of the various chemical substances which now characterize the different plant families.”[17] Describing how insects may have adapted to feeding on these “unpalatable” plants, he proposed that “[i]nsects, in turn, may then have developed specific predilections for certain substances, with the result that the former repellant became an attractant.” “This reciprocal adaptive evolution,” he continued, “occurred in the feeding habits of insects and the biochemical characteristics of plants,” a convincing account of evolutionary history, he pointed out, to anyone familiar with flowering plants and their insect pollinators.[18] This latter case of “coadaptation,” while known as such since Darwin’s time, had yet to stimulate its own body of coevolutionary theory. And it would not do so until after “coevolutionary studies” had cohered around the more antagonistic feeding relationships studied by Fraenkel and his peers.

In 1959, Frankel crystallized his ideas on “reciprocal adaptive evolution” in a paper published in *Science*, “The Raison d’Être of Secondary Plant Substances.” An early indicator of how the field of coevolution would bridge disciplinary divides, this paper was an adaptation of a talk that Fraenkel had given at the 4th International Congress of Biochemistry in Vienna a year earlier. He reiterated his account of early plant

---

[17] Fraenkel, "Insects and Plant Biochemistry: The Specificity of Food Plants for Insects," 384-385.

[18] Ibid.: 385.

evolutionary history, and elaborated upon his method for testing the chemical specificity of insect-plant relationships.[19]

The body of evidence marshaled by Fraenkel for this paper far exceeded the few suggestive studies he had cited in 1953. Already, interest in chemical specificity was growing, and his profile of recent research hit a number of plant families. In particular, Fraenkel presented data on the alkaloids[20] found in the Solanaceae (the family of potatoes, tomatoes, and tobacco). It was no coincidence that Fraenkel could cite seven sources on the Solanaceae, all published since 1955: The economic importance of solanaceous crops, as well as the ferocity of their pests, like the potato beetle and tobacco hornworm, provided an attractive system of research subjects. More importantly, the glycoalkaloids of these plants, while repellant and even toxic to many insects, were attractive to the plants' specific pests—a case in point for the evolution of specificity.[21] Fraenkel's use of this data demonstrated that the reams of agricultural research on relations between crops and pest insects were more than just a repository of data that a physiologist or evolutionist could mine for his own more biologically significant ends. In the evocative story that they told about relations between insects and plants, this data influenced the very shape of coevolutionary theory. The industrialization of agriculture

---

[19] Gottfried S. Fraenkel, "The Raison D'être of Secondary Plant Substances," *Science* 129 (1959).

[20] The alkaloids are a particularly important class of secondary compound. Others include tannins, terpenoids, phenols, glycosides, and more.

[21] The Solanaceae was not the only economically important family cited by Fraenkel. The other families included the Crucifereae (the family of cabbage and broccoli), the Umbellifereae (a family containing spices such as caraway and coriander), the Leguminosae (the family of the soybean), the Moraceae (the family containing the mulberry, interesting here because of its food value for silkworms), and the Gramineae (critically, the family of rice, corn, and wheat).

in the early 20th century concentrated single food crops in high numbers over large continuous areas, stimulating increasingly severe pest outbreaks.[22] The application of more potent insecticides, in larger quantities, as well as the resistance that insects began to develop against insecticides, made agriculture seem increasingly like a perpetual war that humans could not win. Advancing armies of insects appeared to be only strengthened by the chemical weapons farmers threw at them. And the moral of the story was evolutionary: "Had the plants been entirely successful in developing their chemical protection against insects," Fraenkel wrote in 1959, "there would be no insect problem in agriculture. In fact, however, insects on their part responded to the chemical control of the plant."[23] Here, then, was a point of intersection, where the sense of warfare that infused farmers' battles with insect pests entered the nascent coevolutionary discourse. Further, Fraenkel's suggestion that plants could use a form of "chemical control" against insects reflected the connections that were already being built between human attempts to control nature and scientific ideas about natural ideas—connections that acted, like Pauly's "engineering ideal," to fuse practical and pure scientific goals.

Fraenkel's evolutionary reasoning was hardly original. After the first documented cases of insecticide resistance near the end of the 19th century, the phenomenon had only grown in prevalence.[24] Explanations for resistance were quite divergent, however. The agrochemical industry at first blamed farmers' improper application of pesticides. Even when it became clear that farmers were not to blame, the industry remained entrenched in

---

[22] John Perkins, "Insects, Food, and Hunger: The Paradox of Plenty for U.S. Entomology, 1920-1970," *Environmental Review* 7, no. 1 (1983).
[23] Fraenkel, "The Raison D'être of Secondary Plant Substances," 1466.
[24] Ceccatti, "Resisting Insects: Shifting Strategies in Chemical Control," 14.

its strategy of developing newer and always more potent insecticides in an attempt to outrun the insects.[25] The industry also heavily patronized the discipline of entomology, deeply influencing its research objectives and skewing its numbers toward the economic end of the entomology spectrum. As historian of science Paolo Palladino writes, in the first half of the 20th century, increasing numbers of entomologists could be defined more accurately by the appellation "economic," and had "by the mid-1950s took the chemist rather than the ecologist or biologist as the paragon of professional excellence."[26] Even in insect physiology, where an idealized notion of an "untainted vintage of pure research" persisted, interest in the development and study of insecticides—and the financial profit that could be expected therein—grew.[27]

In contrast to the pesticide industry's response to insecticide resistance, the evolutionary luminary Theodosius Dobzhansky claimed insecticide resistance for the field of evolutionary biology in 1937, writing in his landmark *Genetics and the Origin of Species* that the phenomenon was "probably the best proof of the effectiveness of natural selection yet obtained."[28] The implications of Dobzhansky's assertion for the strategies of the agrochemical industry may seem clear in retrospect: Attempts to chemically "outrun" insects are likely futile; insects may always evolve to "run faster." Yet,

---

[25] Ibid; ———, "Biology in the Chemical Industry: Scientific Approaches to the Problem of Insecticide Resistance, 1920s-1960s."
[26] Paolo Palladino, *Entomology, Ecology, and Agriculture: The Making of Scientific Careers in North America, 1885-1985* (Amsterdam: Harwood Academic Publishers, 1996), 21.
[27] Williams, "Hormonal Interactions between Plants and Insects," 104. Williams also refers here to the research that led to the discovery of the first 3rd-generation pesticide as "sufficiently pure and impractical to scandalize any Congressional Committee."
[28] Theodosius Dobzhansky, *Genetics and the Origin of Species* (New York: Columbia University Press, 1937), 161.

according to science historian John Ceccatti, the claims of this eminent biologist held no sway in the industry.[29] Twenty-two years later, when Fraenkel made his own claims about the relevance of evolution to agriculture, evolutionary biologists were celebrating the pervasive explanatory power of natural selection on the centenary of Darwin's *On the Origin of Species*. Nevertheless, as Paul Ehrlich would write four decades later, the insecticide industry "proceeded largely as if Darwin had never lived."[30]

For some entomologists, however, as well as military and international health officials, the lack of basic biological data about the development of insecticide resistance by the early 1950s seemed a serious impediment to understanding the problem. The use of dichloro-diphenyl-trichloroethane (DDT, a potent and highly toxic synthetic insecticides) in during World War II had resulted in the development of resistance in European fly populations.[31] And the Korean War, begun in 1950, generated new concerns, as it became apparent that many Korean populations of houseflies, mosquitoes, and body lice had quickly developed resistance to a variety of insecticides.[32] In early November 1951, the National Research Council (NRC), at the behest of the U.S. Army, called an emergency "Conference on Insect Physiology," to be held in Cincinnati only a month later, in conjunction with a joint meeting of the Entomological Association of

---

[29] Ceccatti, "Resisting Insects: Shifting Strategies in Chemical Control."; ———, "Biology in the Chemical Industry: Scientific Approaches to the Problem of Insecticide Resistance, 1920s-1960s."

[30] Paul R. Ehrlich, *Human Natures: Genes, Cultures, and the Human Prospect* (Washington, DC: Island Press, 2000), 281.

[31] Ceccatti, "Resisting Insects: Shifting Strategies in Chemical Control," 17.

[32] M.C. Winternitz to Fraenkel, 6 November 1951, Gottfried S. Fraenkel (GSF) Papers, University of Illinois Urbana-Champaign (UIUC) Archives.

America and the American Association of Economic Entomologists.[33] The NRC wrote to entomologists and insect physiologists all over North America, appealing to them for help with this urgent matter. In a letter of invitation to Fraenkel, Milton C. Winternitz, a medical doctor specializing in pathologies of chemical warfare and pest control agents, and chairman of the NRC's Division of Medical Sciences,[34] admitted that it finally "seems clear that greater emphasis should be given now to the more fundamental aspects of insect physiology—including biochemical, genetic, ecological and others—than has occurred in recent years."[35]

The conference's attendees were a mix of economic entomologists, basic entomologists, and insect physiologists. Like Fraenkel (who did not, in the end, attend the meeting), Dethier and Williams were both invited. The economic entomologists were employed by a variety of institutions, such as the U.S. Public Health Service, the USDA, many branches of the military, as well as laboratories of insect pathology and experimental stations from California to eastern Canada.[36] Many of the entomologists invited had been trained in basic research fields, such as systematics, and had become involved in pest research in the mid-1940s, when the U.S. Army's Sanitary Corps recruited many entomologists to contribute to the war effort.[37] Professor Charles D. Michener of the University of Kansas Department of Entomology is a prime example of

---

[33] Ibid.
[34] Robert E. Mellors, "Obituary, M.C. Winternitz, M.D. (1885-1959)," *Cancer* 13, no. 1 (1960).
[35] M.C. Winternitz to Fraenkel, 6 November 1951, GSF Papers, UIUC Archives.
[36] "National Research Council, Division of Medical Sciences, Ad Hoc Conference on Insect Physiology," agenda and list of invitees, GSF Papers, UIUC Archives.
[37] H.B. Hungerford, "Relation of Entomology to the War Effort," *Transactions of the Kansas Academy of Science* 46 (1943).

this phenomenon. Michener's career began with a lifelong love of bees, graduate training in systematics, and a position as a lepidopterist at the American Museum of Natural History (AMNH). But in 1943, he volunteered for the Army Sanitary Corps and began mosquito control work in Mississippi.[38] Later he would also develop a method for raising chigger larvae, after chiggers became a significant vector for typhus in the Pacific.[39] After the war, he returned to his job at the AMNH, and soon moved to the University of Kansas, where he was finally able to concentrate his attention on the systematics of bees.[40]

But Michener's attendance at the NRC's emergency conference on insecticide resistance reflected more than his past involvement in the Army's entomological war efforts. After one presentation on the genetics of insecticide resistance, Michener spoke up, contributing to the extensive discussion, which was printed in the wake of the conference. "For some time I have been interested in some work on resistance, simply because I am interested in it as a problem in selection, essentially natural selection." Michener was, in fact, already pursuing this interest in concert with his colleague Robert Sokal. "We have spent a good many months getting techniques perfected, and we are just starting what we speak of as a main selection experiment, using Drosophila."[41] Their experiment would, by 1954, be part of a larger effort organized by the Office of the

---

[38] Charles D. Michener, "The Professional Development of an Entomologist," *Annual Review of Entomology* 52 (2007).
[39] Ibid; ———, "A Method of Rearing Chigger Mites (Acarina, Trombiculinae)," *American Journal of Tropical Medicine* 26 (1946).
[40]Michener, "The Professional Development of an Entomologist," 8.
[41] Charles D. Michener, "Comments," in *Conference on Insecticide Resistance and Insect Physiology* (Washington, DC: National Academy of Sciences, National Research Council, 1952), 77.

Surgeon General on the "Ecology and Control of Disease Vectors and Reservoirs." A 1956 Department of Defense progress report describes the rationale for the project, arguing that diseases carried by insect vectors "presented a greater threat of military disaster than enemy action."[42] The twenty-four entomological research projects included therein were conducted all over the United States, including a University of Illinois component coordinated by Fraenkel, studying the nutrition of houseflies, and two insecticide resistance studies coordinated by Sokal at the University of Kansas.[43]

Michener was one of only a handful of conference attendees who spoke of evolution of insecticide resistance; most focused on proximate, physiological mechanisms for insecticide resistance, living up to the criticisms that evolutionary biologists often wielded against applied scientists. Among the other attendees that addressed evolution was Milislav Demerec, head of the Department of Genetics at Cold Spring Harbor, who presented the "Development of Bacterial Resistance to Chemicals," discussing his research on the now well-known phenomenon of antibiotic resistance. While Demerec described the selection of resistant strains of bacteria from genetically varied populations in the laboratory as the study of a "genetic mechanism," never once using the word "evolution," it is clear that he referred to evolution.[44] Demerec's fellow *Drosophila* geneticist Dobzhansky was slightly less circumspect, taking the conference as

---

[42] Report on "Ecology and Control of Disease Vectors and Reservoirs," Research and Development Division, Office of the Surgeon General, 31 December 1956, GSF Papers, UIUC Archives, page 543.
[43] Ibid., 547-548.
[44] Milislav Demerec, "Development of Bacterial Resistance to Chemicals," in *Conference on Insecticide Resistance and Insect Physiology* (Washington, DC: National Academy of Sciences, National Research Council, 1952).

an opportunity to lambast what his fellow modern synthesizer Ernst Mayr called the "typological species concept," writing in his remarks (presented in his absence) that "Biologists should abandon the habit of thought, inherited from the pre-evolutionary era, which regards each species, race, or population as an embodiment of a certain 'type' or 'norm'."[45] Like Demerec before him, Dobzhansky emphasized the significance of the genetic variation that already exists in pest populations, the raw material for a highly resistant population, given a strong enough selecting force in the form of high-dosage, extremely potent pesticides. And, as in 1937, Dobzhanksy asserted that anthropogenically generated evolution was, nonetheless, real evolution, resulting from natural selection. His use of the words *natural* and *artificial* in the passage below seems, in its formulation, to actually diminish the difference between the two ideas: "If the environment, either a 'natural' or 'artificial' one, favors a certain group of these genotypes more than the others, the former increase in frequency and tend to supplant the latter. The insecticides are, then, merely selecting agents which eliminate the relatively susceptible, and encourage the spread of the relatively resistant genotypes."[46] In this simple fashion, Dobzhansky used the mechanism of evolution by natural selection to synonymize all forces acting as "selecting agents," employing quotation marks to demonstrate how little he thought of the distinction between natural and artificial, and acknowledging humans and their actions as part of the evolutionary environment.

---

[45] Theodosius Dobzhansky, "Summary of Remarks of Th. Dobzhansky," in *Conference on Insecticide Resistance and Insect Physiology* (Washington, DC: National Academy of Sciences, National Research Council, 1952), 86.

[46] Ibid.

Like Dobzhansky or Demerec, many of the scientists participating in these efforts to combat insecticide resistance were located at academic institutions, reflecting the collusion between basic and applied research interests characteristic to the scientific response to the insecticide crisis.[47] But as contemporary biologists would be quick to point out, neither the use of economically important insect-plant systems in research, nor the study of insect responses to insecticides, transformed scientists like Sokal or Fraenkel into economic entomologists. Coevolutionary biologists and head of the University of Illinois, Urbana-Champaign entomology department rejected just such a claim when I interviewed her, speaking of the historical reasons that her department hired Fraenkel back in 1947. “I don’t think anybody would ever call Gottfried Fraenkel an applied entomologist,” Berenbaum told me. “I mean, he worked on silkworms, it doesn’t necessarily mean he was a sericultural entomologist. That goes back to Forbes, our first department head…[his paper], “The Lake as Microcosm,” [represents] a basic ecological insight that he had, yet, read his papers over and over again, his argument is that if you can study a basic phenomenon in an economically important insect, that’s the way to go if you’re an entomologist because that's the sort of justification for the discipline.”[48] Indeed, as Berenbaum’s comment about Forbes’ philosophy suggests, the dual economic

---

[47] Ceccatti, "Biology in the Chemical Industry: Scientific Approaches to the Problem of Insecticide Resistance, 1920s-1960s."; Palladino, *Entomology, Ecology, and Agriculture: The Making of Scientific Careers in North America, 1885-1985*.

[48] May Berenbaum. Interview by author. Digital audio recording. Champaign-Urbana, IL, 19 April 2007.

Ehrlich said the same of Sokal when I interviewed him (Paul Ehrlich. Interview by author. Digital audio recording. Palo Alto, CA, March 2007.).

and biological significance of research on insecticide resistance demonstrates something critical about these particular researchers and about the field of entomology in general.

As I described in the previous chapter, Fraenkel had already established a pattern of merging basic and applied research goals, just as he merged molecular approaches with broad biological and social theorizing. But his ability to achieve these syntheses within entomology and the developing field of insect physiology also reflects what historians have long known about entomology. According to historians of entomology, American economic entomology, in particular, thrived thanks to a healthy "symbiosis" between basic and applied research, in which practical interests often supported—not stifled—the pursuit of fundamental biological knowledge. Since the mid-nineteenth century, the growing need for entomological expertise in American agriculture had created professional positions at universities, agricultural experiment stations, government agencies, and, beginning in the early 20th century, the chemical industry.[49] But by no means was basic biological research abandoned, and debates over the origin of mimicry reveal that many prominent entomologists sustained a motivating interest in the evolution of insects.[50] The insecticide crisis proved no exception in this respect. As

---

[49] Ceccatti, "Resisting Insects: Shifting Strategies in Chemical Control."; Palladino, *Entomology, Ecology, and Agriculture: The Making of Scientific Careers in North America, 1885-1985*; Russell, *War and Nature: Fighting Humans and Insects with Chemicals from World War I to Silent Spring*; Richard C. Sawyer, *To Make a Spotless Orange: Biological Control in California* (Ames: Iowa State University Press, 1996); Willis Conner Sorensen, *Brethren of the Net: American Entomology, 1840-1880, 2nd Ed* (Tuscaloosa: University of Alabama Press, 1995).

[50] William C. Kimler, "Mimicry: Views of Naturalists and Ecologists before the Modern Synthesis," in *Dimensions of Darwinism*, ed. Marjorie Grene (Cambridge: Cambridge University Press, 1983); Edward B. Poulton, "Insect Adaptation as Evidence of Natural Selection," in *Evolution, Essays on Aspects of Evolutionary Biology*, ed. G.R. de Beer

Dethier wrote decades later in *Man's Plague? Insects and Agriculture*, the support generated by interest in defeating insect enemies "was a tremendous boon to the study of basic insect physiology."[51] More than just material support, it became clear to many familiar with the problem of insecticide resistance and with evolutionary biology that insect adaptation to the onslaught of synthetic chemicals was also, in substance, deeply relevant to the evolutionary history of insects and plants.

Nonetheless, for a number of years, Fraenkel's insights of 1959 went unnoticed outside of the field of entomology, where the boundary between practical and basic insights was so fluid. In retrospect, today's coevolutionary researchers acknowledge Fraenkel's work as the initiation of coevolutionary theory.[52] In fact, Fraenkel himself claimed as much in 1980, when his paper was deemed a "Citation Classic," commenting that his ideas were the "basis for the entire field" of coevolutionary studies.[53]

But the citation data preserves the record clearly: Little general attention was paid to "The Raison d'Être of Secondary Plant Substances" when it was first published.[54]

(London: Oxford University Press, 1938); Sorensen, *Brethren of the Net: American Entomology, 1840-1880, 2nd Ed*; William Morton Wheeler, *Ants: Their Structure, Development and Behavior* (New York: Columbia University Press, 1910).

[51] Vincent G Dethier, *Man's Plague? Insects and Agriculture* (Princeton, NJ: The Darwin Press, Inc., 1976), 118.

[52] May R. Berenbaum and Arthur Z. Zangerl, "Facing the Future of Plant-Insect Interaction Research: Le Retour À La ''Raison D'être''," *Plant Physiology* 146 (2008).

[53] Fraenkel to Eugene Garfield [Institute for Scientific Information (ISI)], 12 June 1981, GSF Papers, UIUC Archives.

[54] In fact, throughout the following decades, Fraenkel would even describe the early reception of his ideas as "hostile." There are few different sources for this claim. It especially irked him that some of his fellow entomologists persisted in their apparent commitment to the nutrition hypothesis. Fraenkel felt particularly betrayed when his former student, A.J. Thorsteinson suggested in a 1960 paper that common plant nutrients were enough to stimulate feeding in Colorado potato beetle larvae [A. J. Thorsteinson,

Throughout the first half of the 1960s, the paper was cited only once or twice each year. Then, in 1966, the number of citations jumped to 7, and to 10 in the following year, remaining strong until a decade later, when it peaked at 20 citations in 1978.[55]

Fraenkel and the colleagues that would follow in his footsteps generally explained this pattern quite simply: It was not until 1964, when Paul Ehrlich and Peter Raven published "Butterflies and Plants: A Study in Coevolution" in *Evolution*, that Fraenkel's notion of "reciprocal adaptive evolution" between insects and their food plants gained a wider audience.[56] Though they cited Fraenkel's work, as well as Dethier's and many of the same agricultural and horticultural sources that these insect physiologists drew upon, Ehrlich and Raven approached the problem of insect-plant relationships from the entirely opposite direction. From their background in evolutionary biology, they came to see the importance of molecules first in terms of evolutionary adaptation. Yet, even from their viewpoint, the importance of the "artificial" systems of agriculture loomed large. Like Fraenkel's 1959 paper, Ehrlich and Raven's 1964 paper was underpinned by the previous decades' experience struggling to manage pest insects. Moreover, they made use of direct experience with the evolution of insecticide resistance to formulate a theory of

---

"Host Selection in Phytophagous Insects," *Annual Review of Entomology* 5 (1960).]. Fraenkel referred specifically to this paper of his former student when he characterized the response to his 1959 paper as "crticism, almost bordering on animosity" [Gottfried S. Fraenkel, "Evaluation of Our Thoughts on Secondary Plant Substances," *Entomologia Experimentalis et Applicata* 12, no. 5 (1969): 473.] Thorsteinson, for his part, seemed to be disturbed that Fraenkel viewed it as such [A. J. Thorsteinson, "This Week's Citation Classic: Host Selection in Phytophagous Insects.," *Citation Classics* 45 (1980).].

[55] Robert Rogers (ISI) to Fraenkel, 13 October 1981, GSF Papers, UIUC Archives.

[56] Berenbaum and Zangerl, "Facing the Future of Plant-Insect Interaction Research: Le Retour À La ''Raison D'être''."; Ehrlich and Raven, "Butterflies and Plants: A Study in Coevolution."; Gottfried S. Fraenkel, "This Week's Citation Classic: The Raison D'être of Secondary Plant Substances," *Citation Classics* 11 (1984).

coevolution that explained both "natural" and anthropogenic evolution in pest populations.

Evolutionary biologists: From evolution to molecules

Paul R. Ehrlich's decision to attend graduate school might be considered unexpected, considering his lackluster performance as an undergraduate at Penn and self-professed prioritization of "skirt-chasing." But in 1952, after finishing his bachelor's degree, as he considered his future profession, a connection he had made with bee-specialist Michener much earlier in life proved invaluable. Like many of the scientists whom I interviewed for this project, Ehrlich's early life experiences in nature were formative. More strikingly, however, as early as their teenage years, many of these scientists also made direct connections with working scientists, whose intellectual interests and professional influence would directly benefit them later in life. Perhaps not surprisingly, then, "serendipity" was cited as one of the primary explanations for the success and unique trajectory of each scientist's career. And Ehrlich is no exception in any of these regards. As a child, he became interested in butterflies. In exchange for cherished tropical butterfly specimens, the young Ehrlich volunteered at the AMNH, mounting butterflies for Michener himself. Drawing on this history in 1952, when the Entomological Society of America met in Philadelphia, Ehrlich made his case to Michener, showing him reprints of some taxonomic papers from his undergraduate years, charging, “You started me in this direction, give me a chance to show what I can do.”[57] Michener agreed and took Ehrlich on as a graduate student the very next year.

Ehrlich’s arrival at the University of Kansas was fortuitous, thanks to the influence of both Michener and Sokal in his graduate education. The “combination of Michener and Sokal, in those days, was unsurpassed if you wanted to move over taxonomy, ecology, [and] evolution, in general,” Ehrlich told me in 2007.[58] And indeed, it was this very combination that garnered Ehrlich his first graduate assistantship, in Sokal’s military-funded study of insecticide resistance, mentioned above. In his book *Human Natures: Genes, Cultures, and the Human Prospect*, Ehrlich writes of this “hands-on introduction to selection”[59] and the *Drosophila* populations that soon “could almost use the DDT solution as an apertif.”[60] “Unnatural selection, so to speak, was at work,” he writes. “We had stood in for nature and used selection to cause the evolution of a strain of DDT-resistant fruit flies to take place right before our eyes, in a matter of months. ‘Unnatural’ our engineering may have been, but the microcosmic process we were observing was simply the laboratory equivalent of natural processes that have changed the characteristics of checkerspot butterflies, daisy-like plants, bacteria that live in the human gut, and mountain lions—indeed, of all living organism, including humans.”[61] Ehrlich’s designation of the insecticide resistance as a product of “unnatural selection” seems to reject Dobzhansky’s assertion that the phenomenon was a clear-cut

---

[57] Ehrlich (Professor, Biological Sciences, Stanford University), in discussion with the author, March 2007.
[58] Ibid.
[59] Ehrlich, *Human Natures: Genes, Cultures, and the Human Prospect*, 16.
[60] Ibid., 17.
[61] Ibid., 17-18.

case of natural selection. This impression is only reinforced by the endnote, which claims, "More technically, it was artificial selection. If selection is occurring in natural populations, it is called natural selection. If people are deciding which genotypes (genetic endowments) are to reproduce more, as when a pig farmer uses his heaviest hogs as breeders, it is called artificial selection."[62] Even though it is manifest in his pig-breeding example, Ehrlich's definition of artificial selection elides the critical element of *intentionality*, which is typically taken as a defining quality of artificial selection. This strange inconsistency between example and definition highlights the very murkiness of this particular form of selection: Humans exerted the selection pressure—but they did so unknowingly and unintentionally, with results diametrically opposed to the end they pursued. Dobzhansky likely identified insecticide resistance as a case of *natural* selection precisely because human intention had gone so severely awry—like any other "force of nature," humans acted blindly.

While Dobzhansky diminished the distinction between *natural* and *artificial*, Ehrlich seems to have enhanced it, defining anthropogenic evolution as unnatural, patently artificial, setting the actions of humans apart from nature. Yet, elsewhere Ehrlich himself belies this clear delineation between the natural and artificial, particularly when he spoke of the boundary between basic and applied biology in my interview with him, claiming that he's "never been very impressed by that line."[63] "Except for maybe part of the Marianas Trench, there isn't a cubic centimeter of the biosphere that hasn't

---

[62] Ibid., note 9, 336.

[63] Paul R. Ehrlich. Interview by author. Digital audio recording. Palo Alto, CA, 14 March 2007.

been influence by human activities." Hence, humans are a part of every ecosystem. Whether the human influence makes nature inherently unnatural or allows human action to become inherently natural is unclear in Ehrlich's comments here, but he believes strongly that "unless you are trying to expand the knowledge of humans or deal with things that affect human beings your research is probably crap, so I wouldn't denigrate applied research."[64] While as a young scientists he had "ducked being called 'applied' because [he] wanted a job in academia," in recent years he has "been one of the people trying to say there is no difference between pure and…so-called applied problems, [some of which] are much more interesting, difficult, and theoretical, and basic than some of the pure ones."[65] Thus, the actions of human society have written humans into the processes of nature, making them a worthy part of scientific research.

Even though Ehrlich "ducked" association with applied science as a young biologist,[66] his early record already showed his appreciation for the close interdependence between human society and the rest of the natural world, as well as the relevance of purportedly "applied" questions to many basic problems in biology. Ehrlich's name first became a cultural byword in 1968, with the publication of *The Population Bomb*, his warning of an imminent environmental and humanitarian catastrophe due to skyrocketing population growth.[67] But prior to 1968, Ehrlich had already become well known among biologists, most notably for the 1964 publication of "Butterflies and Plants: A Study in

---

[64] Ibid.

[65] Ehrlich. Interview by author. Digital audio recording. Palo Alto, CA, 14 March 2007.

[66] He continues on to note that "outside of the University of Kansas" entomology departments were "mainly controlled by people who were called 'nozzleheads.' The only thing they could think of doing was spraying," an ideology he strove to avoid, Ibid.

[67] Paul R. Ehrlich, *The Population Bomb* (New York: Ballantine Books, 1968).

Coevolution."[68] This paper, the first to use the term "coevolution" to describe feeding relationships between insects and plants,[69] made broad inferences about patterns of evolution, based upon a combined knowledge of taxonomic patterns and butterfly feeding habits.

According to Ehrlich, it was an argument devised over coffee, based upon literature searches and prior field experience, rather than original research.[70] A casual comment about the peculiar eating habits of *Euphydryas* butterflies inspired a series of conversations between Ehrlich and Raven, in which Ehrlich "would describe patterns of foodplant use in butterflies and [Raven] would see what sort of botanical 'sense' they made."[71] Because butterflies are an attractive subject to amateurs and scientists alike, the foodplants of about half their genera were already known. In studying the existing literature on these foodplants, "[i]t was not long before we realized that the so-called 'secondary compounds' of the plants played a major role in the interactions."[72] The realization, of course, was aided immensely by their reading of insect physiologists Fraenkel, Dethier, and Thorsteinson, all of whom were cited in the 1964 paper. In fact, the literature review that Ehrlich and Raven undertook spanned the breadth of the field of insect-plant interactions, from insect physiology, to chemical taxonomy (classifying

---

[68] Ehrlich and Raven, "Butterflies and Plants: A Study in Coevolution."

[69] An earlier paper from parasitology used the term "co-evolution" to describe relationships between parasites and hosts [Charles J. Mode, "A Mathematical Model for the Co-Evolution of Obligate Parasites and Their Hosts," *Evolution* 12, no. 2 (1958).], and since Darwin's time the word "coadaptation" has been widely used, but this is the first known use of the term "coevolution" that I have found.

[70] Ehrlich. Interview by author. Digital audio recording. Palo Alto, CA, 14 March 2007.

[71] Paul R. Ehrlich, "This Week's Citation Classic: Butterflies and Plants: A Study in Coevolution," *Citation Classics* 37 (1984).

[72] Ibid.

plants based upon their biochemical characteristics), applied entomology, ecology, and agronomy.

The theoretical questions they aimed to address were no less sweeping, most notably their search for “predictive generalities about community evolution,” based upon the coevolution of “ecologically intimate organisms.”[73] Moreover, they extended Fraenkel’s assertions, more than a decade earlier, of “reciprocal adaptive evolution”[74]: “Probably our most important overall conclusion is that the importance of reciprocal selective responses between ecologically closely linked organisms has been vastly underrated in considerations of the origins of organic diversity. Indeed, the plant-herbivore ‘interface’ may be the major zone of interaction responsible for generating terrestrial organic diversity.”[75] To Ehrlich, in retrospect, this aspect of the paper still seems the most important, that plants and insects *interact*. A responsive reciprocal interaction between organisms of entirely different species stretched the limits of what had already been considered “co-evolution” by parasitologists, who “treated human beings or the hosts as a fixed thing.” Conversely, “people who were interested in disease tended to view the pathogens as a fixed thing.” Setting himself apart from this static view of hosts and pathogen, Ehrlich continued, “Of course, I already had the experience in Sokal’s lab,”[76] in which the insects—the “pathogens” in this coevolutionary system—had demonstrated their extensive ability to evolve dynamically in response to the shifting chemical challenges in their environments. “[Y]ou collect all this stuff,” continuing to

---

[73] Ehrlich and Raven, "Butterflies and Plants: A Study in Coevolution," 586.
[74] Fraenkel, "The Nutritional Value of Green Plants for Insects."
[75] Ehrlich and Raven, "Butterflies and Plants: A Study in Coevolution," 606.
[76] Ehrlich, in discussion with the author, March 2007, page 7.

speak of his graduate research experience, but "do you get opportunities to put it together?"[77] In Ehrlich's case, the answer is resoundingly affirmative: The seed of a potent synthetic notion, joining coevolution and insecticide resistance, was built into Ehrlich and Raven's theory. Citing Fraenkel, they reformulated the evolutionary scenario he had outlined in the 1950s. A flowering plant evolves potent chemicals that "serve to reduce or destroy [its] palatability…Such a plant, protected from the attacks of phytophagous animals, would in a sense have entered a new adaptive zone." Their critical insights into evolutionary reciprocity indicated that insects may also evolve "in response to physiological obstacles, as shown by man's recent experience with commercial insecticides. Indeed response to secondary plant substances and extreme nutritional imbalances and the evolution of resistance to insecticides seem to be intimately connected."[78] The connection that Dobzhansky had made between insecticide resistance and natural selection bore scientific fruit in this statement, suggesting that a phenomenon induced by human action could serve as a model for coevolutionary theory.

Ehrlich's synthetic understanding of plant-insect coevolution and the evolution of insecticide resistance would only become more pronounced over the course of the next decade, as he further developed his role as a public scientist, speaking out against the environmental degradation caused by insecticides. In a series of popular-science pieces in the 1970s, published in such venues as *The Mother Earth News* and *The Saturday Review*, Ehrlich wrote of plants' secondary chemicals as "nothing less than sophisticated

---

[77] Ibid., p8.

[78] Ehrlich and Raven, "Butterflies and Plants: A Study in Coevolution," 602.

weapons of chemical warfare," part of an "evolutionary war,"[79] in which humans had become the most recent combatants. "It's not surprising that man has a great deal of difficulty in controlling his insect competitors with man-made poisons. Not only have insect pests been dealing with poisons for millions of years, but they are usually in an excellent position to increase whatever natural resistance to poisons they may have."[80] Just as the evolution of insecticide resistance could serve as a model for coevolutionary theory, so could the coevolutionary history of insects and plants offer explanation for the evolution of insecticide resistance.

Metaphors of warfare have been used in reference to evolution sine Darwin's time.[81] But coevolutionary theory's close association with insecticide research, a field already so heavily freighted with metaphorical and material connections with human warfare,[82] suggests that the military metaphors of coevolution carried their own particular nuance, unique amongst the metaphors of evolutionary biology. The theory and data that framed early coevolutionary theory had a clear provenance in the wheat and tobacco fields of American farmers, who battled increasingly ferocious swarms of hungry insects with ever more potent chemicals created for the purpose. In witnessing real-time evolution in populations of pest insects, the parallel between agricultural warfare with

---

[79] Anne Ehrlich and Paul R. Ehrlich, "Coevolution and Pest Control," *The Mother Earth News* 50 (1978).

[80] Paul R. Ehrlich and John P. Holdren, "The Co-Evolutionary Race," *Saturday Review* (1970).

[81] Gillian Beer, *Darwin's Plots: Evolutionary Narrative in Darwin, George Eliot and Nineteenth-Century Fiction, 2nd Ed.* (Cambridge: Cambridge University Press, 2000), 58, 116.

[82] Russell, *War and Nature: Fighting Humans and Insects with Chemicals from World War I to Silent Spring*.

insects and plants' ancient warfare with insects became more than a parallel—it was the same phenomenon.

In 1967, Ehrlich and Raven again coauthored a paper, "Butterflies and Plants," for *Scientific American*, in which they reiterated their central arguments. Visually illustrated with photographs, sketches, and tables, the piece was also verbally illustrated with the persuasive martial metaphors that would be increasingly associated with the "coevolutionary arms race." Though plants have long suffered devastation by hungry insects, they "have not taken the onslaught lying down….The plant world's main line of defense consists in chemical weapons," many of which humans had extracted and used for their own insecticidal purposes long before the development of synthetic insecticides like DDT. Moreover, the active properties of marijuana, opium, and peyote might be explained using the same principles: "Considering [their] hallucinogenic properties…it is amusing to speculate that the plants bearing them may practice 'chemopsychological warfare' against their enemies!"[83] The less amusing lesson to be learned from "battle-hardened" plants, however, was the futility of common methods of insecticide application. Despite plants' impressive arsenal, herbivorous insects "reply with specializations to cope with the special defenses [of plants], as a hunter uses a high-powered rifle to hit deer or bear, a shotgun to hit birds or a hook to catch fish." For the plants, this ability of insects to evolve specialized responses, creates a new challenge, one "like that of the farmer, who is obliged to defend his crops from attack by a variety of

---

[83] Paul R. Ehrlich and Peter H. Raven, "Butterflies and Plants," *Scientific American* 216, no. 6 (1967): 105.

organisms."[84] The resulting interplay between plants and insects—and farmers and insects—seems endless, and certainly not won by attempting to run an "arms race" against rapidly evolving insect populations.

Much of the language quoted above is drawn from popular periodicals rather than scientific journals. Lest the reader be tempted to dismiss these metaphors as mere mechanisms of popularization, however, it is important to recognize the influence that such language had on later work in the field. The "arms race" became the standard metaphor used to describe coevolution between insects and plants.[85] In Chapter Four, I will more deeply explore the effects of these and other common evolutionary and coevolutionary metaphors on the further development of the field.[86]

Learning from the "ancient war" between plants and insects

Of course, unlike plants, humans had the resources with which to act less blindly, at least as early as 1937. As Ehrlich writes, "Had those who deal with agricultural pests made use of evolutionary knowledge, we human beings would have been much cleverer

---

[84] Ibid.: 109.

[85] See, for example: Berenbaum. Interview by author. Digital audio recording. Champaign-Urbana, IL, 19 April 2007; R. and J.R. Krebs Dawkins, "Arms Races between and within Species," *Proceedings of the Royal Society of London. Series B, Biological Sciences* 205, no. 1161 (1979); Robert H. Whittaker and Paul P. Feeny, "Allelochemics: Chemical Interactions between Species," *Science* 171 (1971).

[86] While the "arms race" metaphor and its closely associated military and competitive tropes, originated in the deep connections between insecticide research and coevolutionary research, there is little doubt that the Cold-War context of emerging coevolutionary theory reinforced the persuasive strength of the analogy (Berenbaum. Interview by author. Digital audio recording. Champaign-Urbana, IL, 19 April 2007; Daniel H. Janzen. Interview by author. Digital Audio Recording. Philadelphia, PA, 4 December 2007.).

in our coevolutionary race with our competitors."[87] And though it seems that the agrochemical industry never put the lessons of coevolution into practice, biologists did make an effort to apply evolutionary knowledge to the management of agricultural pests, combining chemical methods with biological control in an approach dubbed integrated pest management (IPM).[88] The "ultimate weapon" introduced at the beginning of this chapter was the first of the third-generation pesticides, which were important elements of IPM, bringing hope to the ecologically- and environmentally-minded entomologists who sought better ways to target pest insects without harming other organisms. Williams, for his part, was quick to claim that the discovery had emerged out of physiological research "sufficiently pure and impractical to scandalize any Congressional Committee."[89] Nevertheless, he was equally quick to turn the solution of an esoteric scientific mystery into both a lesson for evolutionary biology and a promising new potential insecticide.

Williams' scientific mystery began in 1964, when scientist Karel Sláma left Czechoslovakia for the United States with a six-legged traveling companion. Sláma had already bred hundreds of generations of the seed-eating European fire bug and hoped that his work with Harvard insect physiologist Carroll Williams would delve more deeply into the hormones that control the bug's development. But almost immediately, Sláma's fire bugs began to die. At first, each bug appeared to develop normally, passing through several larval stages, growing larger as it approached sexual maturity. Then, just when

---

[87] Ehrlich, *Human Natures: Genes, Cultures, and the Human Prospect*, 281.
[88] Palladino, *Entomology, Ecology, and Agriculture: The Making of Scientific Careers in North America, 1885-1985*.
[89] Williams, "Hormonal Interactions between Plants and Insects," 104.

they should have completed development, the bugs entered another larval stage instead—grotesquely outsized, and destined soon to die.

Sláma and Williams were stymied. In Prague, Sláma had never witnessed this perplexing pattern. And though the European fire bug was unfamiliar to Williams, his extensive experience with the insect endocrine system suggested—impossibly—that the bugs had been exposed to a potent hormonal factor, one that stimulated growth but stunted development: insect juvenile hormone.

Though the importance of juvenile hormone in insect growth was identified in the 1930s, it was only in the 1950s and 1960s that insect physiologists managed to extract the compound and identify its chemical structure. Carroll Williams himself had led this search by creating strange surgical chimeras: carefully dismembering insects and excising their organs, then reconstructing them as new, exquisitely complex composite organisms. These living amalgams allowed Williams to trace the pathway of a growth stimulant or inhibitor from its origin, through the shared circulation of several insects, to its ultimate effect on development. In one such feat of "parabiosis" in the 1950s, Williams had discovered an almost inexhaustible source of juvenile hormone when he grafted a decapitated male cecropia moth to a pupating cecropia caterpillar.

Since juvenile hormone is produced in a gland in the insect brain, it followed that the decapitated adult moth could not produce any of the development-stunting hormone. Similarly, the pupa was in the midst of metamorphosis, therefore its own production of juvenile hormone *had* to be suppressed, in order for development to proceed. Nevertheless, when the two circulatory systems were united, the pupa's development immediately froze. It grew larger and larger, but never metamorphosed into a mature adult moth. Further examination led Williams to the adult male's abdomen, which contained enough juvenile hormone to be easily extracted. This extracted "cecropia oil" became a powerful experimental tool that Williams used to examine the effects of juvenile hormone on different insect tissues. Thus, in 1964, having studied the experimental effects of cecropia oil for years, Williams quickly recognized the unmistakable signature of juvenile hormone in the lethal life cycles of Sláma's fire bugs.

The origin of the hormone remained a mystery, however. As the Harvard team eliminated sources of contamination and identified suspicious variables, attention turned to the paper toweling that lined the Petri dishes that the fire bugs called home. When the suspect toweling was exchanged for a standard circle of filter paper, the problem disappeared and the fire bug larvae developed into normal, sexually mature adult insects. Naturally, Williams and Sláma immediately inquired into the constiuents of the Scott Brand 150 paper towels. The simple answer they received—paper pulp—seemed, at first, only more mystifying.

Their curiosity piqued, Sláma and Williams sought similar results from a plethora of paper products, from napkins and toilet paper to *Nature* and the *New York Times*. Not only did the team find an active chemical analog of the fire bug's juvenile hormone in many of these sources, but they observed a distinctive pattern of chemical activity that they could correlate with particular taxa of trees. While the paper pulp of European and Japanese trees did not stunt the fire bugs' development, products and publications made of North American paper pulp quickly killed them. Williams soon identified balsam fir as an especially potent source of juvenile hormonal action. The fire bug mystery had been solved with the discovery of a chemical analog of juvenile hormone, a molecular mimic that could be extracted from Scott paper towel and other products made with North American paper pulp.

In contrast with DDT, the juvenile hormone analog that Williams' team had painstakingly eked from paper towels was a highly specific compound that would only poison a single species of insect. While Williams knew that not all juvenile hormones are species-specific, he hoped that a juvenile-hormone-based insecticide could be used to "discriminate between the 0.1% of species that qualify as pests and the 99.9% that are either innocuous or downright helpful." Such a compound could resolve many of the ecological problems of synthetic insecticides and avoid toxicity to animals higher on the food chain. Moreover, the hormone mimic's presence in paper pulp suggested that compound might be inexpensively harvested from multiple tree species.

Williams' confidence in the promise of the juvenile hormone analog as a potent and specific pesticide stemmed directly from the inferences that he made about its evolution. North American tree species "have gone in for an incredibly sophisticated self-defense against insect predation—a method of insect control that we are just beginning to comprehend." While insecticide resistance had evolved in response to human agricultural manipulation, Williams hoped that plants' own "natural insecticides," evolved over millennia, might provide humans with an invincible biochemical solution, one that he believed could evade the evolution of resistance. After all, he wrote, "insects can scarcely evolve a resistance to their own hormone." Evolution had proven to be a formidable foe for farmers and their insecticides, but Williams and other biologists suggested that evolution might also provide the most effective solution to the very problems it had engendered.[90] It was no coincidence that evolutionary theory, built in part on insights gained from agriculture, now suggested a means of control. In fact, in accordance with the engineering ideal, the notion of control was, itself, built into the evolutionary theory.

Conclusion

In this chapter, I establish that insecticide research and application made direct contributions to the development of coevolutionary theory. In particular, applied research on insecticide resistance offered both the material and intellectual resources that allowed insect physiologists and evolutionary biologists to converge, from opposite intellectual directions, on biochemical coevolution as an explanation for specialized relationships between plants and insect herbivores. The repercussions of insecticide research thus became a part of coevolutionary theory, building a sense of "chemical control" into nature and—conversely—of adaptive "natural insecticides" into human efforts to control pest insects. My analysis of this intimate interplay between basic and applied knowledge heeds the call of Harwood, who encouraged historians of science to

---

[90] The irony here is that this discovery didn't change the "moral" of the coevolutionary story—plants rarely "win" the "race," so why would humans expect to win using plants' weapons? And, indeed, mosquitoes did develop resistance to the pesticide that developed out of Williams' idea by the late 1990s [Anthony Cornel et al., "High Level Methoprene Resistance in Hte Mosquito Ochlerotatus Nigromaculis (Ludlow) in Central California," *Pest Management Science* 58, no. 8 (2002).]. Thus, the notion that the coevolutionary race is never-ending was further reinforced: there is no winning.

interrogate the exchange between agriculture and basic biology more deeply. In doing so, I expanded upon the astute observations of Buhs and Russell, who have analyzed the influence of biological knowledge on the practices and ideology or chemical control, to identify specific ways that the practices and ideology of chemical control reciprocally influenced biological knowledge.

More broadly, the repercussions of this reciprocal interchange had the power to change scientists' view of humans' place in nature. Like other tools used in integrated pest management, especially the application of pests' predators in biological control, the intellectual and ideological power of Williams' third-generation insecticide stemmed from the perception that it was a *natural* solution to an unnatural, anthropogenic problem. But the common description of plant toxins as "natural insecticides" gainsaid this simplistic distinction between natural and unnatural by joining plants' evolutionary history with the human artifice implicit in the term "insecticide." Deploying plants' adaptations as new weapons in the human war against pests changed the very character of the war itself. Biologists did more than draw evocative analogies between human interactions with insects and plant interactions with insects. They formulated a new body of theory that could unify both types of evolutionary interactions. In so doing, they initiated reciprocal changes in the ways that human interactions and plant interactions alike were conceptualized: Could human biochemical warfare with insects be seen as definitively *unnatural* when it was united in so many ways with a *natural* process that had been occurring for millennia? In other words, in uniting evolutionary change over millennia with recent evolutionary change in response to human activity, coevolutionary theory made humans full participants in natural selection and in the dynamic changes of global evolutionary history.

Chapter Three

Biochemical interactions as adaptations: Closing the gap between evolution and ecology with coevolutionary research

Coevolutionary research begins with an observation of an ecological interaction between different species. These species are usually members of different kingdoms—often Kingdom Plantae and Kingdom Animalia. Therefore, this research is predicated on the notion that distantly related organisms have interrelationships that are critical to understanding their biological features. These intimate associations are the focus of ecological research on symbiotic relationships, including mutualism, parasitism, and commensalism.[1] But coevolutionary research, true to the form of evolutionary ecology, with which it emerged in close association in the 1960s, does not end with a diagnosis of symbiosis. Because the biological present is seen as an embodiment of evolutionary history, the history of the symbiosis and the selective forces that shaped and maintained it are the true foci of evolutionary ecology and of coevolutionary studies. And it is these selective forces that the evolutionary biologists deems the *ultimate* cause of present-day biological phenomena. By contrast, most ecologists for the first half of the 20th century considered the process of organismal adaptation to be a physiological or behavioral adjustment to immediate environmental circumstances, explanations that stopped with the *proximate* causation of biological phenomena, not asking how the systems enabling physiological adjustment came into being evolutionarily. It was only with the advent of

---

[1] Jan Sapp, *Evolution by Association: A History of Symbiosis* (New York: Oxford University Press, 1994).

evolutionary ecology in the 1960s that the Darwinian sense of adaptation, as both a historical evolutionary process and the product of that evolutionary process was renewed within ecology.[2]

The search for ultimate causation was an explicit precept of the newly developing field of evolutionary ecology,[3] and part of the "adaptationist" logic that increasingly pervaded evolutionary biology after the modern evolutionary synthesis of the 1930s and 1940s. Stephen J. Gould wrote of this tendency to focus on adaptive evolution exclusively, arguing that the modern synthesis had "hardened" in the mid-20th century thanks to evolutionary biologists' focus on natural selection as the primary mechanism of evolutionary change.[4]

---

[2] James P. Collins, "'Evolutionary Ecology' and the Use of Natural Selection in Ecological Theory," *Journal of the History of Biology* 19 (1986): 578; Douglas J. Futuyma, "Reflections on Reflections: Ecology and Evolutionary Biology," *Journal of the History of Biology* 19, no. 2 (1986); William C. Kimler, "Mimicry: Views of Naturalists and Ecologists before the Modern Synthesis," in *Dimensions of Darwinism: Themes and Counterthemes in Twentieth-Century Evolutionary Theory*, ed. Marjorie Grene (Cambridge: Cambridge University Press, 1983); ———, "Advantage, Adaptiveness and Evolutionary Ecology," *Journal of the History of Biology* 19 (1986); James P. Collins,John Beatty, and Jane Maienschein, "Introduction: Between Ecology and Evolutionary Biology," *Journal of the History of Biology* 19, no. 2 (1986); Joel B. Hagen, *An Entangled Bank: The Origins of Ecosystem Ecology* (New Brunswick: Rutgers University Press, 1992), 146-164. Other historians of ecology concur, pointing out the overwhelmingly physiological emphasis of ecology beginning in the early 20th-century: Eugene Cittadino, "Ecology and the Professionalization of Botany in America, 1890-1905," *Studies in the History of BIology* 4 (1980): 192; Sharon E. Kingsland, *Modeling Nature: Episodes in the History of Population Ecology, 2nd Ed.* (Chicago: University of Chicago Press, 1995), 218.

[3] David Lack, "Evolutionary Ecology," *Journal of Animal Ecology* 34 (1965); Ernst Mayr, "Cause and Effect in Biology," *Science* 134 (1961); Gordon H. Orians, "Natural Selection and Ecological Theory," *The American Naturalist* 96 (1962).

[4] Stephen J. Gould, "The Hardening of the Modern Synthesis," in *Dimensions of Darwinism: Themes and Counterthemes in Twentieth-Century Evolutionary Theory*, ed. Marjorie Grene (Cambridge: Cambridge University Press, 1983).

And as in evolutionary biology more generally, evolutionary ecology concentrated upon adaptation as an evolutionary process and as a product, an approach that was applied as well to the new study of coevolution. Ehrlich and Raven worked within such a framework when they sought evolutionary insights from ecological relationships between butterflies and plants. They began with the specialized ability of certain taxa of butterflies to consume certain taxa of plants. To place these specialized ecological relationships in historical context, Ehrlich and Raven correlated them with the phylogenetic relationships, the lines of familial descent that connected the plant taxa they studied; in other words, the historical process of adaptation was reflected in the phylogenetic patterns. Specialized ecological relationships also encouraged them to hypothesize, like Fraenkel in 1959, about the "raison d'être" of present-day biochemical features of plants and insects: The biochemical adaptations that made the specialized relationships possible were the *products* of the adaptive evolutionary process. In plants, the adaptations were the repellant biochemical compounds that prevented non-specialized insects from feeding upon them. In insects, the adaptations were the biochemical mechanisms that allowed them to feed upon particular plants and tolerate their repellant compounds.

Thus, coevolutionary researchers read a history of evolutionary adaptation onto specialized ecological associations by relating three levels of biological investigation and hypothesis, all of which hinged, critically, upon *interaction* between individual insects and plants. Interaction could be correlated with evolutionary history, the record of an adaptive process, read from phylogenetic reconstructions. It could also be translated into the language of natural selection, understood as an adaptive process resulting from selective pressure that plants and insects reciprocally exerted upon each other. Finally, it could be observed between organisms in the ecological present, in the biochemical characters produced by adaptive evolution. In this chapter I argue that in these forms of investigation, which all turned upon interactions between insect and plants, coevolutionary studies injected a form of radical interactionism into the study of evolved ecological relationships. And with their shift of attention to the space between interacting organisms, coevolutionary researchers began to transform the interactions themselves into adaptations.

One critical tool used to study interaction was biochemistry. Drawing upon the path breaking work of Fraenkel and Dethier, the natural compounds of plants came to be regarded as evolved, highly specific causal agents, adaptive molecules that acted as tools or weapons for the plants that produced them. This characterization of plant compounds as active protective agents ran counter to the prevailing attitudes of many other ecologists at the time, who saw these secondary compounds of plants to be passive, mere byproducts of the primary physiological functions of plants. I will examine this latter perspective in greater detail in Chapter 4, but in this chapter I focus first upon the conception of plant compounds as active defenses against insect herbivory, which provided a basis for coevolutionary thinking, a foundation upon which coevolutionary researchers built arguments about the energetic costs and benefits of coevolved interactions. Placing weight upon biochemical interactions as costly evolutionary adaptations allowed coevolutionists to build analogical arguments that linked myriad characteristics of different organisms, a method used in the development of evolutionary theory since the time of Darwin.[5] In the case of coevolutionary theory, analogy allied the evolved defenses of plants, including their "natural insecticides," with the synthetic chemical defenses that humans used against crop pests, enhancing the sense that plant compounds were evolved tools.

The early history of ecologist Daniel Janzen's career is a rich resource for examining how coevolutionary studies took shape. In pursuing molecules as interactive adaptations, Janzen and other young coevolutionary researchers put recent advances in biochemical methods to good use. Both synthesis and analysis proved critical to examining the space between plants and insects: they sought evidence of evolved biochemical adaptations by extracting natural plant-produced chemicals from interactions and by inserting synthetic chemicals into the natural relationships. The transient phenomena of higher-level organismic interactions and their evolutionary history proved amenable to the molecular tools of applied biology—as in Fraenkel's work,[6] molecules provided a handle on organismal- and community-level processes that did not reductionistically diminish their importance.

---

[5] Gillian Beer, *Darwin's Plots: Evolutionary Narrative in Darwin, George Eliot and Nineteenth-Century Fiction, 2nd Ed.* (Cambridge: Cambridge University Press, 2000). Mark Largent, "Darwin's Analogy between Artificial and Natural Selection in the Origin of Species," in *The Cambridge Companion to The "Origin of Species"*, ed. Michael Ruse and Robert J. Richards (Cambridge: Cambridge University Press, 2009).

[6] See Chapter 1.

The strength of selection: Ants as chemical defense, interaction as adaptation

In 1963, Daniel H. Janzen was still a graduate student in search of a dissertation topic. He had already completed his entomological coursework as an undergraduate at the University of Minnesota, and graduate school in Berkeley's entomology department provided him an opportunity to explore interconnections between different biological fields; in fact, over the course of his graduate career, Janzen recalls spending nearly as much time in the botany department as in the entomology department, ending up with majors in both fields.[7] He also made good use of both botanical and entomological expertise in the execution of his dissertation project, which analyzed in detail the interaction between a species of New-World acacia tree and an intimately associated ant species.

Through extensive field experimentation, discussed below, Janzen demonstrated that the relationship between the ants and the acacia was an obligatory mutualism, research that placed him squarely within the discipline of ecology, while suggesting fascinating evolutionary questions that he would soon pursue.[8] He defended his thesis in 1965, within months of the 1964 publication of Ehrlich and Raven's *Evolution* paper, "Butterflies and Plants: A Study in Coevolution."[9] And his own first paper on coevolution, "Coevolution of Mutualism between Ants and Acacias in Central America,"

---

[7] Daniel H. Janzen. Interview by author. Digital Audio Recording. Philadelphia, PA, 4 December 2007.
[8] Daniel H. Janzen, "Interaction of the Bull's-Horn Acacia (Acacia Cornigera L.) with an Ant Inhabitant (Pseudomyrmex Ferruginea F. Smith) in Eastern Mexico," *The University of Kansas Science Bulletin* 47, no. 6 (1967).
[9] Paul R. Ehrlich and Peter H. Raven, "Butterflies and Plants: A Study in Coevolution," *Evolution* 18, no. 4 (1964).

was published in *Evolution* only one year after earning his Ph.D.[10] By this time, he was a new faculty member at the University of Kansas, in the same entomology department from which Paul Ehrlich had graduated almost a decade earlier, in 1957. And like Ehrlich before him, Janzen received guidance from both Michener, whom he had already met a few years earlier in Costa Rica,[11] and Sokal, who encouraged him to publish his paper in the journal *Evolution*. According to Janzen, a dispute ensued within the editorial board over whether the paper better belonged in an ecological journal. But in the end, this paper on the evolution of an ecological relationship was accepted as appropriate to *Evolution*. Thanks to this decision, which placed his paper solidly in the domain of evolutionary biology, Janzen reflects that he "became" an "evolutionary biologist because of that."[12] And when printed, the paper established the ant-acacia system as an emblem of evolutionary ecology and of the power of coevolutionary theory, while establishing Janzen himself as a rising star in both domains, bridging ecology and evolution.

But long before he analyzed the system from an evolutionary standpoint, he began with a simple ecological observation. When I interviewed Janzen for this project in 2007, he recalled how the impetus for his dissertation research struck him in a moment of pure "serendipity." Much to the chagrin of the Berkeley entomology department, he had

---

[10] Daniel H. Janzen, "Coevolution of Mutualism between Ants and Acacias in Central America," *Evolution* 20, no. 3 (1966). Though he was unable to get his thesis project published until 1967, due to some frustrating delays (Janzen. Interview by author. Digital Audio Recording. Philadelphia, PA, 4 December 2007.)

[11] Janzen. Interview by author. Digital Audio Recording. Philadelphia, PA, 4 December 2007.

[12] Ibid.

entered graduate school already determined to perform his Ph.D. research in Mexico. Growing up in chilly Minneapolis, Minnesota, a series of childhood trips to Mexico had him enthralled with tropical nature. And though his graduate advisors favored dissertation research in California, they granted him one field season in Veracruz to unearth a viable research project. If Janzen failed to find such a project in the summer of 1962, he would resign himself to a thesis project in California.[13] The "serendipity" of the moment, then, was primed by both his childhood experience making naturalistic observations in temperate and tropical climes, and the immediate pressure to find "something that could be decent thesis research," a goal that, admittedly, "in those days," he only grasped in "some vague, vague sense."[14]

Nonetheless, walking down a road lined with shrubby trees one morning, his entomologist's eye was caught by red Chrysomelid beetle, which flew over his head and landed on a leaf. Suddenly, "an ant ran up and bit it or attacked it and [the beetle] jumped off. I went on, but I could still see that happening—it obviously penetrated. When I walked back that afternoon, coming up the same trail, my mind said, 'Why was there an ant on that leaf?' So I looked at the actual leaf and there [were] ants running around on it." Janzen also recalls noticing the enlarged "bull's-horn" thorns, and his curiosity was piqued by the sight of ants entering a thorn through a tiny hole in its side.[15]

---

[13] Janzen recalled in conversation that his graduate advisor told him that if he had wanted to do his research in Mexico, he should have enrolled in graduate program at a Mexican university (Janzen. Interview by author. Digital Audio Recording. Philadelphia, PA, 4 December 2007.).

[14] Ibid.

[15] All quotations and recollections recorded in my interview with Janzen, Ibid.

Later, he would identify the tree as *Acacia cornigera* and the ants as *Pseudomyrmex ferruginea*, but for the moment, as he brought home a branch of the tree, to dissect the thorns, he considered only the ant's odd behavior: Could the ants themselves be worthy of a thesis project? The relationship between the ants and the tree was still peripheral to him, an important detail in any entomologist's natural history of the ant species, but not yet the central focus of a major research project. It would take another serendipitous experience for Janzen to refocus his gaze on the relationship *between* the ants and the tree.

> What I can reconstruct is I was walking across a pasture and there were two trees growing maybe two meters apart, two ant-acacias. And I cut both of them down, with the intent of taking them back to the house and then dissecting the ant colonies. In fact, I took one back, left the other one where I cut it. Three weeks later, maybe a month later, I happened to walk across the same pasture on exactly the same trajectory, and there was the stump that I'd removed the top from. [Nearby] was the stump that I'd left the ant-acacia at. And the stump I'd left the ant-acacia top at had this gorgeous green feathery beautiful perfect stump sprout coming out of it like this. And the one that was just two meters away from it was all ratty and chewed up and the leaves were all shot to hell. And the light bulb went off. I saw that and my thesis was just repeat that 5000 times. Just do it over and over and over again in different circumstances. Because there I had accidentally removed the ants from the tree. There are many ways you can remove ants from a tree and so I did that many ways, but the bottom line was—take the ants away and what happens to the tree? And that just blew the world apart.[16]

This story, which Janzen has recounted elsewhere,[17] has acquired the burnish of personal mythology, like many scientists' accounts of their own "Aha!" moments. Historians are duly cautious about the use of interviews, believing personal biases, presentism, and

---

[16] Ibid.

[17] Rob Dunn, *Every Living Thing: Man's Obsessive Quest to Catalog Life, from Nanobacteria to New Monkeys* (Washington, DC: Smithsonian, 2008).

standardized accounts like the one above to be a threat to an objective account of history. But it also true that these very biases can reveal how speakers position themselves in the past and how they address themselves to multiple audiences at different points in time, particularly when placed in the context of a detailed study of primary source documents.[18] Like all other forms of historical evidence, oral testimony can claim no special access to an objective, "true" account of the past.[19] Instead, it can broaden and enrich the historical account that we construct in trying to understand the past.

More specifically, historian Tamara Giles-Vernick argues that oral history is an invaluable resource in understanding "the ways in which people produce, evaluate, and transmit knowledge about the past," as well as "how people understand themselves and interpret their own pasts"—and both are intrinsic to any historical examination of "popular or elite intellectual change."[20] Similarly, science historians recognize the potential of oral history to reveal the nuances of such change by exposing "humanistic and philosophical concepts underlying major intellectual transformations,"[21] as well as revealing what it means to "do science," lending insight into everyday practices

---

[18] Tamara Giles-Vernick, pers. comm.

[19] Elizabeth Tonkin, *Narrating Our Pasts: The Social Construction of Oral History* (Cambridge: Cambridge University Press, 1992); Megan Vaughan, "Reported Speech and Other Kinds of Testimony," in *African Words, African Voices: Critical Practices in Oral History*, ed. Luise White, Stephan F. Miescher, and David William Cohen (Bloomington: Indiana University Press, 2001).

[20] Tamara Giles-Vernick, "Oral Histories as Methods and Sources," in *A Handbook for Social Science Field Research: Essays and Bibliographic Sources on Research Design and Methods*, ed. Ellen Perecman and Sara R. Curran (Thousand Oaks: SAGE Publications, 2006).

[21] Ronald E. Doel, "Oral History of American Science: A Forty-Year Review," *History of Science* 41 (2003).

inaccessible through print materials.[22] In the case of Janzen, it is relevant to recognize that such “generic” accounts may reveal something of the ethos behind his disciplinary identity.[23] In his retelling of his own history, Janzen has standardized his account to emphasize the aspects that call attention to his own scientific values. In particular, Janzen values the notion that the individual scientist directly experiences the natural world, making observations of real ecological phenomena, prior to hypothesis formation. Janzen’s emphasis on “serendipity” also reveals his own sense of the contingency involved in a naturalist’s experience of the world, and in a scientist’s selection of research topics.

In the fall of 1962, when Janzen returned to Berkeley, ready to present his thesis research plan, he had the good fortune to meet Harvard’s E.O. Wilson. Renowned for his own work on ants,[24] Wilson recognized Janzen’s acacia-ant system as the crux of a historical debate dating back to the late 19th century, which had embroiled another famous Harvard entomologist, William Morton Wheeler. Wheeler, also an ant specialist, had little patience for the prevailing notion of the acacia-ant relationship, which posited that the ants defended the acacia tree from predators. Many of Wheeler’s contemporaries had accepted that the ants “form a most efficient standing army for the plant, which prevents not only the mammalia from browsing on the leaves, but delivers it from the attacks of a much more dangerous enemy—the leaf-cutting ants.” This description,

---

[22] Charles Weiner, "Oral History of Science: A Mushrooming Cloud?," *Journal of American History* 75 (1988).
[23] Giles-Vernick, pers. comm.
[24] For example: E.O. Wilson, "Some Ecological Characteristics of Ants in New Guinea Rain Forests," *Ecology* 40, no. 3 (1959).

penned by British mining engineer Thomas Belt while working in Nicaragua in the late 19th century, turned the more typical benign metaphorical language of symbiosis on its head, employing the militaristic imagery more often used to evoke an ecological "struggle for existence."[25] Wheeler countered in metaphorical kind, challenging the plausibility of an ant-plant symbiosis with his own evocative simile, claiming that the tree needs the ants like a dog needs its fleas.[26]

After meeting Wilson, Janzen immersed himself in the literature of this debate. And when he later wrote up the results of his thesis research, he engaged with the debate directly, coming down definitively on the side of Belt and his compatriots, asserting that, indeed, the ants are a powerful defensive force against the enemies of the acacia tree.[27] An *Acacia cornigera* tree thrives when occupied by a colony of *Pseudomyrmex ferruginea*. The ants, which live in the acacia's thorns and feed from specialized tissues and nectar glands on the tree, provide fierce protection against other insects, phytophagous predators like the red Chrysomelid beetle that flew over Janzen's head that first fortuitous morning. And soon enough, Janzen himself began to build upon Belt's metaphorical language of warfare between the ants and other insects, integrating new metaphors from his own knowledge of 20th-century pest control.

Though it sometimes appears that Janzen spent much of his graduate career trying to escape Berkeley for the tropics, the benefits of his association with the campus were

---

[25] Thomas Belt, *The Naturalist in Nicaragua* (London: E. Bumpus, 1888).
[26] William Morton Wheeler, *Ants: Their Structure, Development and Behavior* (New York: Columbia University Press, 1910).
[27] Janzen, "Interaction of the Bull's-Horn Acacia (Acacia Cornigera L.) with an Ant Inhabitant (Pseudomyrmex Ferruginea F. Smith) in Eastern Mexico."

not lost upon him. In his own words, "the most fascinating, interesting aspect of the entire Berkeley academic offering" was the biological control program, in which he took a minor.[28] "[S]uperficially," his now-classic study of the ant-acacia system might appear to have little to do with biological control. But according to Janzen, biological control is the study of "animal-plant interactions writ economic," while his thesis was the study of "animal-plant interactions writ esoteric."[29] And it was the "old-school" experts on biocontrol, like his minor advisor Carl Huffaker, who best understood his research. Because Huffaker studied animal-plant interactions "in the agricultural countryside," he "read [Janzen's thesis] most carefully and made the very best suggestions; intellectual suggestions [and] editorial suggestions." In other words, biological control offered a useful model for approaching coevolutionary phenomena, by shifting the biologist's focus from individual species or lineages, to the evolution of *interactions between* species and lineages. Interactions came, themselves, to be considered evolved adaptations—and coevolutionary theory, particularly with its emphasis on biochemical interactions, offered a way to study these otherwise transitory phenomena. Moreover, over the course of his study of the ant-acacia system, he made use of the economic entomology resources at hand more than once.

When he cut down two ant-acacias and dragged one home in the summer of 1962, Janzen had inadvertently set up what would become the prototypical experiment for his dissertation research: Remove the resident ant colony from an acacia tree and observe

---

[28] Janzen. Interview by author. Digital Audio Recording. Philadelphia, PA, 4 December 2007.

[29] Ibid.

how this affects the tree. A control, to be left with its resident ant colony, was chosen nearby—under the same “disturbance regimen.” Importantly, these experiments were made possible by the degree to which the Mexican landscape had already been disrupted by human activity. Acacia trees thrive in disturbed areas. According to Janzen, prior to human perturbation of the local ecosystem, the number and proximity of acacias that he found in the Veracruz landscape would have been unimaginable.[30] Thus, the environment in which Janzen first studied a coevolved relationship was heavily conditioned by its coexistence with humans. Already, in this first research project, Janzen observed what would later become a common theme in his work: Human activity not only generates new habitats, but it inserts itself into existing organismal interactions, making humans into participants that can alter ecological and evolutionary dynamics, an acknowledgment that makes the study of nature inextricable from human activity, blurring the boundary between the supposedly natural and unnatural. And the use of knowledge and methods gained from interactions between insects and plants in an agricultural context further enhanced this blurring.

In point of fact, Janzen also employed methods developed in an agricultural context to study natural relationships in an environment where human disruption was omnipresent. Of the “many ways you can remove ants from a tree,” one of the most effective Janzen found was spraying the tree with the insecticide parathion.[31] Here the boundary between the “natural” and “unnatural” becomes even more ambiguous. After

---

[30] Janzen, "Interaction of the Bull’s-Horn Acacia (Acacia Cornigera L.) with an Ant Inhabitant (Pseudomyrmex Ferruginea F. Smith) in Eastern Mexico," 353.
[31] Ibid.: 316.

the ants were removed, he gauged the impact of their loss upon the tree, in order to understand the tree's dependence upon them. As an experimental tool, a stand-in for the operation of nature, parathion worked superbly. And it would not be long before Janzen would refer to the chemicals produced by plants as "natural insecticides."

After the ants were removed, the acacia's health was recorded using a variety of measures, including height, condition of the leaves, freedom from choking vines, leaf and thorn production, and biomass.[32] Janzen established fifty subplots and collected data from his experimental treatments and controls at multiple intervals over the course of yearlong study. At the end the of the year, it was abundantly clear that the ants relied upon the acacia for specialized food and living space, while the acacia relied upon them for defense from herbivores. This was an impressive enough conclusion for a doctoral thesis. But within the burgeoning field of evolutionary ecology, the establishment of this ecological interdependency only invited more questions: How did this relationship evolve? What selective pressures had shaped the adaptations that made the relationship valuable to both ants and acacias? And what phylogenetic context could illuminate this history?

In order to pursue these questions, Janzen took advantage of the biochemical expertise in Berkeley's entomology department to analyze the food the acacia produces for the ants' consumption, including nectar and Beltian bodies, which are small tabs of tissue growing at the tip of each acacia leaf.[33] Harold T. Gordon, one self-proclaimed

---

[32] Ibid.: 315.
[33] Named for Thomas Belt. See: Belt, *The Naturalist in Nicaragua*.

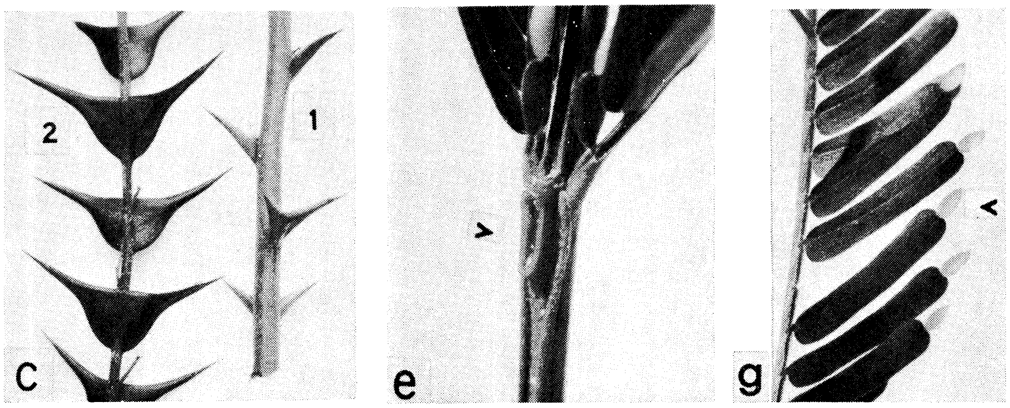

Figure 3. These photographs from Janzen's 1966 paper depict the anatomy of *A. cornigera*'s means for supporting an ant colony. "C" shows the enlarged thorns, in which the ants live. The arrow in "e" points to a foliar nectary. And the arrow in "g" pints to a Beltian body.[34] (Images reproduced by permission of Wiley-Blackwell.)

"biochemically oriented entomologist,"[35] analyzed the nectar exuded by the acacia's foliar nectaries and found that it "consists of about equal parts by weight of sucrose and fructose at an approximate concentration of 40 mg/cc H_20."[36] The Beltian bodies required a slightly different style of analysis, employing the prodigious appetite of German cockroaches. As Janzen wrote in the *University of Kansas Science Bulletin*, "Darwin considered that they were full of oils and proteins. Preliminary experiments to determine the food value of Beltian bodies indicate that they are similar to yeast in quantity and quality of nutrients. This degree of nutritive value of foliar tissue is unusual (H.T. Gordon, personal communication)."[37] Gordon had estimated this value with a typical

---

[34] Janzen, "Coevolution of Mutualism between Ants and Acacias in Central America," 251.
[35] H.T. Gordon, "Citation Classics: Rapid Paper Chromatography of Carbohydrates and Related Compounds.," *Current Contents*, no. 13 (1984).
[36] Janzen, "Interaction of the Bull's-Horn Acacia (Acacia Cornigera L.) with an Ant Inhabitant (Pseudomyrmex Ferruginea F. Smith) in Eastern Mexico," 346.
[37] Ibid.: 345.

insect physiologist's method, raising a colony of cockroaches on a diet of Beltian bodies in the laboratory.[38] As for the ants themselves, there was no laboratory substitute—in the lab they were completely reliant upon Beltian bodies for sustenance.[39] The production of these energetically costly foods continued even throughout the dry season, even when most other plants stop producing new growth.[40] This ecological observation of the constant production of ant-food by the acacia, in combination with Gordon's analyses, allowed Janzen to argue that the acacia tree made a large energetic investment in supporting the life of the ant colony. This argument was critical to its corollary, that the ants, in turn, must provide an equally valuable protective service to the acacia.

Though Janzen acquired no analysis of the secondary compounds present in the leaf tissue of *A. cornigera*, he argued confidently that it would reveal little in the way of repellant or toxic compounds, a claim that he based upon his own sense of taste. Having tasted a number of other New-World acacia species, Janzen could state with authority that the mild flavor of *Acacia cornigera* was unusual among its otherwise bitter-tasting close relatives.[41] And, clearly, phytophagous insects agreed with his assessment of *A. cornigera*'s palatability: When there was no vicious population of *P. ferruginea* to fight them away, herbivores fed heartily on the tree. This comparison of acacia species put the unique biochemical characters of the ant-acacia into a historical, phylogenetic context. The ant-acacia produced costly nutritious foods to support its ant populations. But unlike

---

[38] ———, "Coevolution of Mutualism between Ants and Acacias in Central America," 261.

[39] Ibid.: 269.

[40] ———, "Interaction of the Bull's-Horn Acacia (Acacia Cornigera L.) with an Ant Inhabitant (Pseudomyrmex Ferruginea F. Smith) in Eastern Mexico," 550.

[41] Ibid.: 344.

its close evolutionary relatives, it did not bear the cost of producing toxic secondary compounds. In other words, the ant-acacia had "traded" toxic secondary compounds for a population of attacking ants. Here the notion that toxic secondary compounds played an active causal role in insect-plant interactions came directly into play: Janzen used the evolutionary argument for the production of toxic secondary compounds as a basis for arguing that the ant-acacia's interaction with its ant population was itself an adaptation. In other words, if toxic secondary compounds were plant adaptations used in defense against insects, then, by analogy, the ant-acacia's food production and—more accurately—the ants that subsisted upon that food, were the equivalent evolved defense of the ant-acacia. Thus, Janzen's evolutionary hypothesis for the development of the ant-acacia mutualism was that the ants had, in an evolutionary sense, *replaced* the energetically costly secondary compounds that other acacias maintained to protect themselves from herbivorous insects. The interaction between ant and acacia had become an adaptation.

Janzen's analogy between *Acacia cornigera*'s ants and other acacias' secondary compounds soon became indubitably his own, a signature of his ant-acacia research. But, as he recalls, he was not the first to make this analogy. In fact, it was G. Ledyard Stebbins, the "god in plant biology in California at that time,"[42] who drew an astute connection between the ants and secondary compounds when he attended Janzen's thesis

---

[42] Janzen. Interview by author. Digital Audio Recording. Philadelphia, PA, 4 December 2007.

defense seminar in 1965.[43] By Janzen's own recollection, "I didn't know who [Stebbins] was, [he] didn't mean a thing to me. But this old man came in and sat down at the very back, put his head down and went to sleep…at the end he wakes up, puts his hand up and he said, 'Your ants are like the chemical defenses of plants, aren't they?' And I said, 'Yes, they are, that's exactly what I think.' But I hadn't really thought to—I mean, I am sure my seminar didn't say that, didn't literally say that, didn't analogize them to the chemicals of plants, it just said, 'they *are* protecting the plants.'"[44] But the analogy came naturally to Janzen and other coevolutionary scientists. The activity of ants protecting the acacia tree was obvious; they would physically attack any intruding herbivore. While the defensive activity of chemical was less obvious to the eye, to scientists trained in entomology, the notion of chemicals defending plants was built into the chemical methodology and the rhetoric of their discipline. These chemicals were *natural* insecticides, active protectors of plants thanks to the notion of molecular agency rooted in the practices of economic entomology and the work of insect physiologists like Fraenkel. Regarding the chemicals and the ants as analogous mutually reinforced the sense of

---

[43] Stebbins wrote that as a professor of genetics at Berkeley, he ended up on the oral examination committee of many graduate students. "In this way," he writes, "I became exposed to the first ideas and accomplishments of several biologists who later became nationally known, such as Frank Pitelka and Dan Janzen" [G. Ledyard Stebbins, *The Ladyslipper and I, Autobiography of G. Ledyard Stebbins* (St. Louis: Missouri Botanical Garden Press, 2007), 59.]. In my interview with him, Janzen mentioned nothing about Stebbins serving on his oral examination committee. It is clear, though, from the signatures on Janzen's dissertation, that even if he was present for Janzen's thesis defense, Stebbins did not serve on Janzen's committee during the defense [Daniel H. Janzen, "The Interaction of the Bull's-Horn Acacia (Acacia Cornigera L.) with One of Its Ant Inhabitants (Pseudomyrmex Fulvescens Emery) in Eastern Mexico" (Ph.D. Diss., University of California, 1965).].

[44] Janzen. Interview by author. Digital Audio Recording. Philadelphia, PA, 4 December 2007.

agency that imbued both forms of evolved defense: while the ants were an active “army,” the chemicals suggested a different, but equally powerful, form of warfare against herbivorous insects.

Whether or not he originated it, the analogy would quickly pervade Janzen’s explanatory framework for the coevolution of ants and acacias. In the *University of Kansas Science Bulletin* in 1967, Janzen wrote that *Acacia cornigera* “is unique among plants in that one of its major deterrent characteristics to insect attack can be experimentally removed without directly altering the morphology or physiology of the plant.”[45] Here he pointed out the advantages of the system to the experimenting ecologist; to experimentally test the efficacy of plant secondary compounds in repelling insects was far more difficult than testing the efficacy of the ants, since the former defense cannot be as easily removed from the plant as the latter. To even make such a comparison, Janzen was already actively assuming the analogical relationship between the ants and repellant secondary compounds, and using it to build arguments.

This particular case also illuminates his insistence on using the word “analogy,” rather than “metaphor.” The word “metaphor” implies a resemblance that cannot be literally true. By contrast, to an evolutionary biologist, the word “analogy” implies evolutionary adaptation to a shared selective pressure, a relation that goes beyond a mere resemblance. Writing in 1970 on seed predation, Janzen claimed that “[t]he act of a fox seeking out and eating mice differs in no significant way from a lygaeid bug seeking out

---

[45] Janzen, "Interaction of the Bull’s-Horn Acacia (Acacia Cornigera L.) with an Ant Inhabitant (Pseudomyrmex Ferruginea F. Smith) in Eastern Mexico," 554.

and eating seeds, or a paca seeking out and eating seedlings."[46] In all of these cases, then, whether building an analogy between predatory foxes and predatory insects, or between defensive ants and defensive chemicals,[47] Janzen placed the process and product of evolutionary adaptation first, framing it as the most important explanation, even *the* defining quality, of the biological phenomena under examination—the central approach of the evolutionary ecologist. Distantly related organisms have independently evolved solutions to shared environmental challenges, like the *analogous* fins of whales and sharks. Likewise, different plant species or taxa have independently evolved different solutions to the shared environmental pressure of phytophagy. For Janzen, then, to say that ants and secondary plant compounds were analogous, subject to same strong selective forces, was to render them—evolutionarily, at least—equivalent.

In his 1966 *Evolution* paper, Janzen made a direct claim of the acacia-ants' evolutionary equivalency to defensive toxins, writing that, quite literally, "the obligate acacia ants *are* the secondary plant substances…and they are the means through which the swollen-thorn acacias interact with a large number of the other organisms in the community."[48] Here, Janzen transformed interaction itself into an adaptation, making whatever form it took—ants or toxins—evolutionarily synonymous. In this fashion, then, the analogy served as a hypothesis for the evolution of the ant-acacia mutualism. Janzen

---

[46] Daniel H. Janzen, "Herbivores and the Number of Tree Species in Tropical Forests," *The American Naturalist* 104, no. 940 (1970): 503.

[47] Or even, as Janzen is wont to do, plant defensive compounds and human chemical warfare (Janzen. Interview by author. Digital Audio Recording. Philadelphia, PA, 4 December 2007.).

[48] My italics. Janzen, "Coevolution of Mutualism between Ants and Acacias in Central America," 263.

articulated it as such when he wrote, "The obligate acacia-ant may thus be regarded as a multipurpose characteristic of the acacia, maintained by swollen thorns, Beltian bodies, enlarged foliar nectaries, and year-round leaf production."[49]

In the next chapter, I will explore the language used in the further development of these evolutionary analogies. The scientific identities of plant compounds shifted dramatically through the work of coevolutionary scientists. The causal agency lent to chemical compounds by molecularization would continue to have great power in the field, especially as more sophisticated molecular techniques were applied to coevolutionary problems. And the importance of human chemical interactions with plants and insects and the ideology of pest control would have increasing importance, as I have already implied.

In the remainder of this chapter, I look at ways in which coevolutionists integrated chemical methods into their work. Many of them, like Janzen, were not trained in chemistry, making collaborative ventures the most effective way to access chemical expertise. I also introduce Paul P. Feeny here, another central coevolutionary researcher, and a scientist deeply influenced by the work of Janzen. Trained at Oxford in both chemistry and zoology, Feeny moved to the United States after earning his Ph.D., taking a position at Cornell University, where he would take part in the development of yet another subdiscipline of ecology, *chemical* ecology. Feeny's career reveals the possibilities of integrating chemical and evolutionary methods in the work of one

---

[49] Ibid.: 253.

individual.[50] In either case—collaboration or integration—the fusion of evolutionary ecology and chemistry was crucial to understanding coevolved interactions. Furthermore, this work not only joined evolutionary ecology and chemistry, but it also continued to bring together the ideas and methods of basic biology with those of applied biology.

Scientific collaboration and the "dichotomy" between basic and applied

Janzen began collaborating with chemists early in his career. In 1971, he coauthored a *Nature* paper with E.A. Bell, a phytochemist from the Department of Botany at the University of Texas at Austin. The merger of scientific interests implicit in the collaboration was clearly indicated by its title, "Medical and Ecological Considerations of L-Dopa and 5-HTP in Seeds."[51] L-Dopa was already known as a promising treatment for Parkinson's, thus the authors' "immediate purpose" was "to draw attention to a rich source of L-dopa which may be of use in medicine."[52]

However, this "rich source," the seeds of legumes in the genus *Mucuna*, also raised interesting ecological and evolutionary questions. Why does *Mucuna* produce L-dopa? The authors accounted for the phenomenon evolutionarily, suggesting that an "original mutant strain of *Mucuna*, whose seeds contained a high concentration of L-

---

[50] His transition to the U.S. also offers an opportunity to justify my focus upon scientists employed by American institutions. I do not make causal claims about the emergence of coevolutionary studies in the American context. Nonetheless, Feeny's experiences strongly suggest that the driving energy behind the field's development came, primarily, from within the borders of the United States.

[51] E.A. Bell and Daniel H. Janzen, "Medical and Ecological Considerations of L-Dopa and 5-Htp in Seeds," *Nature* 229 (1971).

[52] Ibid.: 137.

dopa, would only have replaced [other] existing strains…if this trait conferred some net advantage on the individuals displaying it." Moreover, L-dopa was not easy to produce: "A concentration of 6-9% L-dopa in the seed embryo represents a principle commitment both of those metabolic resources available to the parent plant for reproduction, and of the seed's storage potential." The selective advantage that explained this commitment of resources, the authors posited, came from L-dopa's ability to repel a major group of legume seed-predators, bruchid beetles.[53] The exception that proved the rule in this case was *Caryedes brasiliensis*, a bruchid that feeds regularly on *Mucuna*. Bell and Janzen hypothesized that this specialized ecological relationship was a product of coevolution: the legume had evolved a potent toxin that repels most herbivorous insects, while one species of beetle had, in response, evolved the ability to tolerate the toxin.[54] In other words, the present ecological relationship between legume and bruchid, as well as the legume's production of a medically valuable compound, could only be fully understood within the context of the shared evolutionary history of plant and insect.

Bell reported further on the compound in *Phytochemistry*, describing how chromatography, electrophoresis, and mass spectrometry were all used in its extraction and characterization. In this paper, it is critical to note, Bell and his coauthors in the departments of Botany and Chemistry made no mention of the evolutionary or ecological implications of their L-dopa work, which reinforces the sense that Janzen's chemist-

---

[53] That a potential therapeutic agent serves, in other contexts, as a toxin, is hardly a coincidence. Many biologically active plant compounds that are used as pharmaceuticals are thought to be products of this type of coevolution. Below I further discuss the relationship between humans and human culture and plant compounds.
[54] Bell and Janzen, "Medical and Ecological Considerations of L-Dopa and 5-Htp in Seeds," 137.

collaborators continued to pursue their own biochemical research goals, those of phytochemistry and natural products chemistry—isolating, characterizing, and synthesizing biochemical "unknowns"—in parallel to Janzen's biological goals.[55]

In the next few years, Janzen would continue to exploit the evolved relationships between poisonous legumes and bruchid beetles in order to better understand the dynamics of coevolution. These papers perpetuated Janzen's habit of collaboration with researchers cultivating specialized biochemical expertise. One such collaborator, phytochemist and plant physiologist Gerald Rosenthal, focused on the toxic plant-produced amino acid L-canavanine for most of his career.[56] L-canavanine is a potent poison because it is an analog of a critical animal amino acid, L-arginine. When an herbivore ingests L-canavanine, its transfer RNA typically mistakes it for L-arginine, and incorporates L-canavanine into the animal's proteins. "These canavanine-containing proteins, structurally altered, severely disrupt numerous reactions of DNA and RNA metabolism as well as protein synthesis," wrote Rosenthal and Janzen.[57] *Caryedes brasiliensis*, the specialized legume predator, would again prove to be the appropriate

---

[55] E.A. Bell and J.R. Nulu, "L-Dopa and L-3-Carboxy-6,7-Dihydroxy-1,2,3,4-Tetrahydroisoquinoline, a New Imino Acid, from Seeds of *Mucuna Mutisiana*," *Phytochemistry* 10 (1971).

[56] For example: Gerald A. Rosenthal and David Rhodes, "L-Canavanine Transport and Utilization in Developing Jack Bean, Canavalia Ensiformis (L.) Dc. [Leguminosae]," *Plant Physiology* 76, no. 2 (1984). Rosenthal was also the first editor through two editions of a major edited book on plant-insect interactions: Gerald A. Rosenthal and May Berenbaum, eds., *Herbivores: Their Interactions with Secondary Plant Metabolites, 2nd Ed.* (San Diego: Academic Press, Inc., 1991); Gerald A. Rosenthal and Daniel H. Janzen, eds., *Herbivores: The Interactions with Secondary Plant Metabolites* (New York: Academic Press, Inc., 1979).

[57] Gerald A. Rosenthal,D.L. Dahlman, and Daniel H. Janzen, "A Novel Means for Dealing with L-Canavanine, a Toxic Metabolite," *Science* 192 (1972): 256.

experimental subject. First, they confirmed that the larvae of the bruchid *C. brasiliensis* were capable of tolerating L-canavanine. By contrast, L-canavanine had already proven toxic to tobacco hornworm, southern armyworm, and a number of other crop pests.[58] But they sought not only to confirm the bruchid's tolerance of L-canavanine, but also to understand the mechanism of tolerance, so they devised an experiment to test whether *C. brasiliensis* could distinguish between L-canavanine and L-arginine during protein synthesis. Radioactively labeled L-canavanine was injected into both tobacco hornworms and *C. brasiliensis* larvae for comparison. The larvae were then freeze-dried and ground to a powder. After a series of chemical reactions and centrifugations, they confirmed their suspicions: While tobacco hornworm had incorporated the destructive L-canavanine into its protein structure, *C. brasiliensis* had not. They concluded that *C. brasiliensis* larvae "avoid canavanine toxicity by converting it to an innocuous compound."[59] Rosenthal would continue, in his collaboration with Janzen and individually, to examine the ability of the bruchid to break down canavanine and the ability of plants to produce it.[60]

This study, with its use of a crop pest like tobacco hornworm, also shows Janzen's further incorporation of the methods and theoretical stances of economic entomology and attests to the relevance of agricultural ecology to the study of coevolution. This not only furthers my own argument that coevolutionary research drew heavily upon these resources, but it also better clarifies Janzen's attitude toward the practices of pest control

---

[58] Ibid.
[59] Ibid.: 257.
[60] See footnote 55, for example.

and its relationship to basic science. Until now, I have portrayed this attitude as uncomplicated, as if Janzen easily acknowledged the importance of practical goals and methods to biological research. But an examination of book reviews written by Janzen at the time reveals that he shared reservations about applied biology with his contemporary evolutionary ecologists.[61] In a 1973 review of a symposium volume entitled *Insect/Plant Relationships*, Janzen critiqued "[t]he embryonic field devoted to animal-plant interactions," which he found "cripplingly cluttered with data and attitudes from a multitude of reductionist, descriptive, and nonevolutionary studies by the past three generations of physiologists, biochemists, agriculturalists, entomologists, behaviorists, and others."[62] As a solution, he proposed the "evolutionary-ecological approach," in essence, searching for adaptive explanations for ecological phenomena, positing the selective advantages and disadvantages of traits and placing them in the context of evolutionary history.[63]

In an earlier review of a similar symposium volume, Janzen notes approvingly that the publication "alludes to selective processes and evolutionary strategies more than is usual among economically oriented population biologists." He goes on to observe a "dichotomy" between "those who see the study of insect populations from a resource-management viewpoint and those who investigate population density for more esoteric reasons." Obviously, "esoteric" is Janzen's code word for basic biology and, as

---

[61] See footnote 3.
[62] Daniel H. Janzen, "Embryonic Field of Ecology, Review: Insect/Plant Relationships," *Science* 182, no. 4117 (1973): 1125.
[63] Ibid.: 1126.

evidenced by a quotation earlier in this chapter, it is how he identifies his own work.[64] According to Janzen, the very real repercussions of the cited dichotomy play out when it "must be decided whether investigations of pests or of biologically more interesting species chosen for their potential in elucidating population theory should receive the limited research resources."[65] Here it appears that Janzen is taking a stand against organizing research around human utility.

However, it is quite clear from other papers that I profile here that Janzen did not regard all such data as "crippling," nor could he have denied the contributions that research on pest insects, and funds for such research, made to his own work. To the contrary, the study of L-dopa was partially funded by and undertaken at the Kentucky Agricultural Experimentation Station in Lexington. And in point of fact, the project was explicitly framed in terms of the parallels between synthetic and natural insect poisons, as well as the importance of the research to the above-maligned practice of resource management: "While our understanding of insect detoxification of certain synthetic insecticides is often quite detailed, a comparable appreciation for naturally occurring defensive compounds is lacking. This deficiency will become increasingly important as humans continue to intensify their management of agricultural systems."[66] After all, in many cases, the evolved physiological mechanisms that insects used to detoxify the

---

[64] I am referring to a quotation from my interview with Janzen, where he describes his dissertation as "animal-plant interactions writ esoteric," while biological control is "animal-plant interactions writ economic" (Daniel H. Janzen. Interview by author. Digital Audio Recording. Philadelphia, PA, 4 December 2007.).
[65] Daniel H. Janzen, "Review: Insect Abundance. Fourth Synmposium of the Royal Entomological Society of London," *Science* 162, no. 3853 (1968).
[66] Gerald A. Rosenthal,D.L. Dahlman, and Daniel H. Janzen, "A Novel Means for Dealing with L-Canavanine, a Toxic Metabolite," *Science* 192, no. 4236 (1976): 256.

“natural insecticides” of plants were already thought to be the same mechanisms they used to detoxify human-synthesized insecticides. To coevolutionary biologists, insects’ evolutionary history, their millennia of evolution in response to plant defenses had prepared them for the new battle that they fought with humans who tried to protect their agricultural crops by applying their own biochemical weapons.[67] Coevolutionary biologist May Berenbaum would write of the parallels between supposedly natural and unnatural molecular toxins in 1999, asserting that a toxin's "origin, whether on a laboratory bench or in a plant stem, is in some ways irrelevant."[68] What the “natural” world of a tropical ecosystem had produced given great spans of time for evolution, the “artificial” world of agriculture was able to produce in a shorter time, given, instead, populations of organisms and doses of chemicals highly concentrated in both space and time.

It is clear that Janzen did not necessarily see research on agricultural pests to be a waste of scientific resources. Instead, the critiques quoted above indicate more about Janzen’s view of evolutionary ecology. The depiction here of “physiologists, biochemists, agriculturalists, entomologists, behaviorists, and others” as “reductionist,

---

[67] See, for example, L.C. Terriere, "The Oxidation of Pesticides: The Comparative Approach," in *Enzymatic Oxidation of Toxicants*, ed. Ernest Hodgson (Raleigh: North Caroline State University, 1968), 182. Terriere writes, "Species which have not experienced the right kind of evolutionary pressures [i.e., those exerted by plant toxins] may be highly susceptible to the man-made poisons now being discharged into their environment." By contrast, insects that have experience " the right kind of evolutionary pressures" have resulted in the phenomenon of insecticide resistance. "There seems little doubt that resistance is due to the selection of populations of insects with highly active detoxicating enzymes."

[68] May Berenbaum, "Genetic Variation in Cytochrome P450-Based Resistance to Plant Allelochemicals and Insecticides," in *Herbivores: Between Plants and Predators*, ed. H. Olff, V.K. Brown, and R.H. Drent (Oxford: Blackwell, 1999), 57.

descriptive, and nonevolutionary" is the construction of a straw man, useful in order to promote the merits of the "evolutionary-ecological approach." The "reductionist, descriptive, and nonevolutionary studies" were the work of scientists seeking *proximate* explanations for biological phenomena, physiological mechanisms or triggers. Evolutionary ecologists, in contrast, sought *ultimate* explanations, seeing causation of biological phenomena to be located in evolutionary past. Ehrlich took up the same subject in 1969, in a conference volume that I will discuss in greater depth in Chapter 4, *Biochemical Coevolution*.[69] Proximate explanations hinged upon the role that "physical tolerance limits" play in determining the distribution of species, he claimed, which is "the preoccupation of a branch of 'physiological ecology.'"[70] In comparison to coevolutionary studies, the conclusions of physiological studies seemed like sterile dead-ends to Ehrlich, since "the usual conclusion of a study in this field is the determination that the organism can indeed live where it lives."[71] Instead, the search for ultimate causation motivated evolutionary ecologists to take data on such physical limits and ask *why* they exist, and to answer that in many "cases the answers probably lie in the area of coevolutionary interaction."[72] In the instance described above, L-canavanine was a potent "natural insecticide" produced by legumes, capable of killing even the southern armyworm, with its generally high tolerance of toxins. The ability of *C. brasiliensis* to tolerate L-canavanine was an ecologically interesting feature, with an even more

---

[69] Paul R. Ehrlich, "Coevolution and the Biology of Communities," in *Biochemical Coevolution: Proceedings of the Twenty-Ninth Annual Biology Colloquium, April 26-27, 1968*, ed. Kenton L. Chambers (Corvallis: Oregon State University Press, 1970).
[70] Ibid., 9-10.
[71] Ibid., 10.
[72] Ibid.

interesting physiological back-story, since it seemed that the bruchid could avoid incorporating the amino acid analog into its proteins. But an evolutionary perspective induced Janzen and his colleagues to step beyond the ecological relationship and physiological mechanism and ask *why* these exist, in other words, how they came to be. In this case, the selective pressure exerted by the legume upon *C. brasiliensis*, via the toxin L-canavanine, provided an evolutionary explanation for the specialized relationship between the plant and insect. That this type of explanation could be placed in phylogenetic context and examined further, opening new questions and generating knowledge about coevolution that could be applied to other such specialized relationships, confirmed the conviction of biologists like Janzen and Ehrlich that an ecological observation, without evolutionary comprehension, was a scientific dead-end.

While it's clear that the selective pressure of herbivory shaped the evolution of plants by selecting for more toxic or repellant secondary compounds, it is equally clear, particularly from the example of *C. brasiliensis* above, that plants exerted a selective pressure on insects. The successful feeding strategy of *C. brasiliensis*, after all, resulted from a long history of evolutionary adaptation in response to plant toxins—studying reciprocal adaptation required accepting the notion that both plants and insects played critical roles, exerting selective pressure and, thus, evolutionarily altering each other. In the next chapter I will explore more fully the repercussions of this reciprocal model, in which both plants and insects have ecological and evolutionary agency. Suffice it to say here, though, that the study of toxic compounds as "natural insecticides" or "chemical weapons," molecular causal agents in plant-insect interactions, did not diminish the role of plants. Instead, just as humans wielded chemical weapons against insects, so did plants—their chemical adaptations to fend off pests were much like our own.

Recruiting chemists for collaboration

In order to expand critical biochemical analyses like those described above, Janzen also encouraged chemists to take on the challenges of secondary plant compounds themselves. One paper, published in *Pure and Applied Chemistry* in 1973, stands out as a plea to chemists to look more closely at the "Community Structure of Secondary Compounds in Plants."[73] To make the best use of the growing bodies of ecological and biochemical information requires "the chemist and ecologist working together," "uniting these two bodies of information.[74] More specifically, Janzen asked chemists for help gauging degrees of chemical similarity and dissimilarity between different species and taxa of plants. This knowledge was essential to decoding patterns of host-specificity in insects—the patterns of ecological distribution in insects, like the bruchids he knew so well, that had evolved the ability to tolerate the toxins of specific plants.[75] In a theoretical construction that would become increasingly familiar, Janzen described the

---

[73] Daniel H. Janzen, "Community Structure of Secondary Compounds in Plants," *Pure and Applied Chemistry* 34 (1973).

[74] Ibid.: 530.

[75] Ibid.: 535. Much that was already known about secondary compounds at the time came from the efforts of chemotaxonomists, who attempted to use the chemical diversity of the plant world to classify plants [For example: Tony Swain, *Chemical Plant Taxonomy* (London: Academic Press, 1963).]. But as coevolutionists mounted increasingly sophisticated arguments that these chemicals were adaptations, they became "no more useful in chemotaxonomy than are such traits in animals as fur colour, tooth length, pupil diameter, etc." (Janzen, "Community Structure of Secondary Compounds in Plants," 529.).

effort to map ecological relationships onto molecules and vice versa. This was an effort, in other words, to plot the "community structure of secondary compounds." In this community, "individuals are molecules" and "the processes that generate patterns in secondary compound community structure are the same as those that generate patterns in communities of whole organisms."[76] This "molecularization" of individual organisms helped to bridge a potential divide between chemists and biologists and between different levels of biological causation. However, lest the notion that "individuals are molecules" suggests a reductionistic view of community interactions, it's important to reemphasize that coevolutionary research, in considering interactions from both the plant's perspective and the insect's perspective, worked intently on broadening and enriching the biological view of community interactions—not simplifying it. For Janzen, molecular analysis of interspecific relationships was a tool, a handle with which the transitory nature of interactions could be, for one moment at least, grasped. In the effort to consider these interactions as evolved adaptations, such a handle was critically important. Rather than a replacement for natural history and ecology, Janzen encouraged "the biochemist and pharmacologist" to "bolster" the "intuition" of the field biologist, who saw present-day ecological relationships and their biochemical complexities as the products of ultimate causes operating throughout evolutionary history.[77]

This paper also reveals Janzen's hopes "for the development of *chemical ecologists* who are effectively 'general practitioners' of secondary compounds,"[78] a type

---

[76] Janzen, "Community Structure of Secondary Compounds in Plants," 529.
[77] Ibid.: 536.
[78] My italics. Ibid.: 538.

of chemist quite different from the specialized biochemists and organic chemists with whom ecologists attempted to collaborate. But, despite his hopes, Janzen admitted that it was not easy to be a generalist, based upon his "own experience as an ecologist ('jack-of-all-trades, master of none')" who attempted to bridge many disciplines at once in his own work. He knew that the idealized general practitioner of chemical ecology might not be the most attractive career route for most chemists, since "such a scientist will initially be faced with the huge problem of lack of respect by his more specialized peers."[79] Just as specialization in insect-plant communities could give insects an ecological advantage, specialization in the human community could give scientists a professional advantage.

In the final section of this chapter, I examine the early career of chemist-zoologist Feeny. Feeny undertook to embody the ideal of the "chemical ecologist" as early as his first days in graduate school.[80] In fusing disparate scientific approaches he forged new methods, with which he attempted to see coevolved relationships even more clearly. But just as Janzen feared, Feeny faced hurdles in attempting to bridge two very different disciplines. As he told me in an interview, "It took a long time for chemistry to become visible to the average ecologist, in terms of something that needs to be financed by the [NSF] Ecology Program." In fact, he claimed,

> I don't think NSF had the faintest idea what it costs to run a chemistry lab. And they say, "Well, you should collaborate." Well, you try and collaborate with the chemistry department. What they want is: you take them a relatively pure compound and they will identify it for you. Most of the hard work is the bioassays to find out what compound to purify—it's a needle in a haystack to start with. And secondly, it's all the fractionation and separation by, you know, we

---

[79] Ibid.

[80] Paul P. Feeny. Interview by author. Digital Audio Recording. Ithaca, NY, 12 November 2007.

> used to used everything from thin-layer chromatography, paper, mostly just column chromatography, which is very slow. And then you've got to purify it and then you've got to bioassay it.[81]

In other words, efforts to collaborate and efforts to unite chemical and ecological techniques alike were dogged by technical and social challenges. "[H]ampered by not having enough grant money to buy the right equipment" and by the difficulty of collaborating with chemists, Feeny feels that he has "wasted a lot of time over the years using old-fashioned techniques."[82] However, as I describe below, despite this feeling, Feeny actively and successfully applied the techniques of ecology and chemistry to the study of coevolution from the beginning of his career onward.

A fusion of zoology and chemistry: Paul Feeny and chemical ecology

When Paul Feeny was hired by Cornell University in 1967, he had not yet visited the United States. But over the course of his graduate career, he had met a number of American scientists who fed his growing awareness, as he puts it, "of the world outside of Oxford."[83] Lincoln Brower, visiting Oxford on sabbatical in the early 1960s, had already planted the seeds of coevolutionary theory in Feeny's mind. By 1967, Brower would publish his paper on the tripartite relationship between milkweed, monarchs, and blue jays.[84] Tom Eisner of Cornell also visited while Feeny was a graduate student. Though Eisner became best known for his work on chemical defense among insects, his

---

[81] Ibid.
[82] Ibid.
[83] Ibid.
[84] Lincoln P. Brower,Jane Van Zandt Brower, and Joseph M. Corvino, "Plant Poisons in a Terrestrial Food Chain," *Proceedings of the National Academy of Science* 57, no. 4 (1967).

1964 *Science* paper, “Catnip: It’s Raison d’Être,” was a clear nod to Fraenkel’s 1959 paper, “The Raison d’Être of Secondary Plant Substances.”[85] Feeny also met Lawrence E. Gilbert, who visited Oxford before he began graduate work at Stanford. Feeny’s talks with Gilbert about the state of American ecology were intellectually fruitful, particularly since it appears that Gilbert first introduced Feeny to the work of Ehrlich and Raven.[86]

Feeny’s fusion of zoology and chemistry was well supported when he was a graduate student at Cambridge. His dissertation project, which was funded by Britain’s Agricultural Research Council,[87] analyzed the biochemical contents of oak leaves and correlated them with the feeding adaptations of winter moth larvae. It arose from a tricky ecological scenario—one with evolutionary implications. Every May, winter moth larvae would hatch, sometimes so early in spring that they would often miss the opening of oak leaf buds, which can vary in timing by as many as two weeks. The larvae were incapable of gnawing through the tough buds to get at the tender leaf shoots inside and would consequently die. An ecological perspective on a single season of winter moth larval growth would have little to conclude about this nonsensical pattern. But the burgeoning *evolutionary* ecological perspective, to which Feeny had gained much exposure at Oxford,[88] suggested that some benefit to early hatching must accrue over longer time scales. Feeny hypothesized that mature oak leaves must verge on complete inedibility, a factor so consistent over evolutionary time and detrimental to larval growth that natural

---

[85] Thomas Eisner, "Catnip: Its Raison D'être," *Science* 146, no. 369 (1964).

[86] Paul P. Feeny. Interview by author. Digital Audio Recording. Ithaca, NY, 12 November 2007.

[87] Ibid.

[88] Ibid., more on this topic later.

selection had generated early hatching, even if that meant occasionally missing the larval food source altogether. His first experiment verified that larvae did not thrive either on leaves sampled from oaks in June or on dried leaf powder incorporated into an artificial diet. Feeny then undertook a series of laboratory feeding experiments, leaf-toughness tests, and chemical isolation and analysis of the nutritional elements and secondary compounds of mature oak leaves. Finally, he concluded that their inedibility stemmed from both their toughness and their increasing levels of tannins, which "appear to act as a 'broad spectrum' defensive mechanism against herbivores and pathogens and may exert their effect by three different mean: as repellants affecting palatability, as growth inhibitors affecting protein availability, and as direct toxic agents."[89] He reported the effects of the tannins on winter moth larvae in the *Journal of Insect Physiology* in 1968.[90] And in 1969, he published on the indigestible complexes that oak-leaf tannins form with protein in *Phytochemistry*.[91] It was not until 1970 that he published the complete study—critically—in the journal *Ecology*.[92] He recalls his own worry that his research would be relegated to a behavior journal along with biochemical studies of insect pheromones, rather than being acknowledged as a genuine ecological study. Instead, according to

---

[89] Paul P. Feeny, "Seasonal Changes in Oak Leaf Tannins and Nutrients as a Cause of Spring Feeding by Winter Moth Caterpillars," *Ecology* 51 (1970): 579.

[90] ———, "Effect of Oak Leaf Tannins on Larval Growth of the Winter Moth *Operophtera Brumata*," *Journal of Insect Physiology* 14 (1968).

[91] ———, "Inhibitory Effect of Oak Leaf Tannins on the Hydrolysis of Proteins by Trypsin," *Phytochemistry* 8 (1969).

[92] ———, "Seasonal Changes in Oak Leaf Tannins and Nutrients as a Cause of Spring Feeding by Winter Moth Caterpillars," *Ecology* 51 (1970).

Feeny, it became the first paper with chromatograms to be published in *Ecology*.[93] The worry arose from his own concern as a biologist straddling two disciplines: Could he be taken seriously as both a chemist and as an ecologist? His chemical expertise was self-evident and verged on the heroic when, as graduate student, he built his own gas-liquid chromatograph from scratch, since the expense of the first Perkin Elmer models, newly on the market, was too great.[94] And in biology, he had already studied "behavior, genetics, ecology, evolution, and a bit of physiology," even as an undergraduate. While earning his degrees in chemistry, he had already managed to attend all of Niko Tinbergen's lectures and would, thus, have already been well acquainted with the difference between ultimate (evolutionary) and proximate (often physiological) explanations for biological phenomenon,[95] a distinction that was quickly becoming central to the development of evolutionary ecology.[96] In fact, as Feeny told me, even prior to beginning his graduate studies in zoology, he already felt reassured that "now, thank God, I won't feel a second-class biologist all the time. At least I got a qualification in biology as well as in chemistry."[97] Thus, his own credentials argued that he *could* be taken seriously as both a chemist and biologist. And by his own recollection, and the evidence of his 1970 paper, he already considered himself in those terms, as "chemical

---

[93] Feeny. Interview by author. Digital Audio Recording. Ithaca, NY, 12 November 2007.
[94] Ibid.
[95] Niko Tinbergen, "On Aims and Methods of Ethology," *Zeitschrift fur Tierpsychologie* 20 (1963).
[96] Lack, "Evolutionary Ecology."
[97] Feeny. Interview by author. Digital Audio Recording. Ithaca, NY, 12 November 2007.

ecology."[98] But it still remained to him to face the challenges of balancing and merging these two pursuits in a full-fledged career.

More than just chemistry and ecology, though, Feeny was also learning to straddle the disciplines of evolutionary biology and ecology during his time at Oxford. He had already completed both of his two undergraduate degrees (in chemistry and zoology) and his master's degree in chemistry at Oxford, so he considered attending Cambridge in order to earn his Ph.D. in zoology. But Cambridge seemed "too physiological," and the joint evolutionary and ecological knowledge represented by Niko Tinbergen, David Lack, Charles Elton, and E.B. Ford drew him back to Oxford. At the time, Feeny recalls, the different time scales of ecology and evolution still seemed very distinct, but Ford provided exciting examples of "natural selection happening before your very eyes" in natural populations of butterflies.[99] David Lack, whose work synthesized ecological and evolutionary approaches to bird populations,[100] attracted Feeny's admiration in particular. He was fortunate enough to witness the clash between Lack and group-selection proponent V.C. Wynne-Edwards,[101] a formative event in the development of evolutionary ecology, and a debate that bolstered the increasingly dogmatic adherence to adaptation by

---

[98] As Feeny told me, "I think I called it chemical ecology informally at the time" (Ibid.). Also, he refers to a "precept of modern chemical ecology" soon after finishing graduate school [Feeny, "Seasonal Changes in Oak Leaf Tannins and Nutrients as a Cause of Spring Feeding by Winter Moth Caterpillars."]

[99] Feeny. Interview by author. Digital Audio Recording. Ithaca, NY, 12 November 2007.

[100] See, for example: David Lack, *Darwin's Finches* (Cambridge: The University Press, 1947).

[101] Feeny. Interview by author. Digital Audio Recording. Ithaca, NY, 12 November 2007.

individual-level natural selection amongst many evolutionary biologists.[102] Feeny's hope was to work with Lack on a project studying the chemistry of bird food plants and their effect on dispersal, but Lack was not interested in his research plan and offered Feeny an unappealing position tracking birds by radar.[103] Feeny soon found a home, however, with George Varley, the head of the entomology department, who had been working on the pests of oak trees for 15 or 20 years prior to Feeny's arrival.[104] Varley was himself a population ecologist,[105] but his work provided the jumping off point for Feeny's dissertation project and his growing interest in coevolution between plants and insect herbivores. Thus, even as it is clear that Feeny's intellectual milieu at Oxford represented the mainstream of neo-Darwinian evolutionary theory, his path also provides one more case of an influential coevolutionary researcher who began his career with the support and insight of an entomologist studying insects as pests and the financial backing of agricultural interests.[106]

Despite Feeny's extensive training at Oxford, as he completed his Ph.D. and began to "shop" his research around the U.K., he met mostly disinterest. As a result, he

---

[102] See footnote 3, as well as: Mark E. Borrello, "Synthesis and Selection: Wynne-Edwards' Challenge to David Lack," *Journal of the History of Biology* 36 (2003); Gould, "The Hardening of the Modern Synthesis."
[103] Feeny. Interview by author. Digital Audio Recording. Ithaca, NY, 12 November 2007.
[104] Ibid.
[105] G.C. Varley,G.R. Gradwell, and M.P. Hassell, *Insect Population Ecology: An Analytical Approach* (Berkeley: University of California Press, 1973).
[106] It is interesting to note that Feeny reported in my interview with him that Elton was dubious about his project because of the degree to which he manipulated the environment and food of the winter moth larvae within the lab. While Feeny espouses the importance of observational natural history in suggesting and framing research questions, he also emphasizes the importance of laboratory experimentation in order to test hypotheses (Feeny. Interview by author. Digital Audio Recording. Ithaca, NY, 12 November 2007.).

looked to opportunities across the Atlantic. The connection he had already made with Eisner proved advantageous, and an interview at Cornell led to a faculty position in the entomology department. Like Fraenkel decades before, Feeny's move from Britain to the United States was the result of a search for institutions supportive of an innovative use of chemical and entomological methods. And, like Fraenkel, Feeny found fertile ground for his burgeoning career in the United States.

Chemical ecology and coevolutionary research in the United States

Soon after Feeny's arrival in the States, David Pimentel, head of the Cornell entomology department, gave him the Greyhound fare to take a naturalistic and scientific trip across the U.S. before his teaching duties began. The trip was inspired at least in part by the need to see some of the landscape about which he would soon lecture in his general ecology course.[107] But like his decision to move to the United States, this trip was also motivated in large part by his interest in the work of American scientists, and in particular those studying coevolution between insects and plants. In the course of his Greyhound travels, he visited one of his "all-time heroes," insect physiologist Dethier, then at Princeton. He also travelled to Stanford to meet with Ehrlich and Raven. And he even bussed up into Canada, to Winnipeg, to visit Fraenkel's former student, Thorsteinson. But perhaps most importantly, he travelled to Lawrence, Kansas, where he

---

[107] Feeny. Interview by author. Digital Audio Recording. Ithaca, NY, 12 November 2007.

stayed with Janzen on his farm. And it was “Janzen’s influence,” he recalled, decades later, that “had a huge effect on me.”[108]

With his background in chemistry and dissertation research on the defensive properties of tannins in oak leaves, it’s no surprise that Janzen quickly enlisted Feeny as a collaborator for his work on L-dopa. In 1973, they outlined the results of feeding experiments in “L-Dopa in Legume Seeds: A Chemical Barrier to Insect Attack,” published in *Science*.[109] A similar paper, “Insecticidal Amino Acids in Legume Seeds,” quickly followed in *Biochemical Systematics*, emphasizing the careful chemical identification of the compounds found in the toxic seeds tested. Here, again, phytochemist Bell was a collaborator.[110] Their bioassay organism of choice was the southern armyworm, a notoriously polyphagous feeder and pest insect extraordinaire. The southern armyworm can eat almost anything, thus, “[d]emonstration of any repellent or toxic effects to an insect with such generalized feeding habits should be of broader interest than similar results with a more specialized insect.”[111] In other words, the quality that made the southern armyworm such a uniquely troublesome pest was precisely the quality that also made it such an excellent experimental model. L-dopa was proven a potent toxin indeed, overcoming even the formidable detoxification mechanisms of the

---

[108] All recollections from interview (Ibid.). Note that Dethier and Thorsteinson both come up multiple times in Chapters One and Two.

[109] The first author on all three 1973 publications discussed here was Sherry S. Rehr, a graduate student of Feeny’s who earned her M.S. in 1972, and about whom little else can be found. S.S. Rehr,Daniel H. Janzen, and Paul P. Feeny, "L-Dopa in Legume Seeds: A Chemical Barrier to Insect Attack," *Science* 181, no. 4094 (1973).

[110] S.S. Rehr et al., "Insecticidal Amino Acids in Legume Seeds," *Biochemical Systematics* 1 (1973).

[111] Rehr,Janzen, and Feeny, "L-Dopa in Legume Seeds: A Chemical Barrier to Insect Attack," 81.

southern armyworm. The very lack of specificity in the armyworm's eating habits, so well known to economic entomologists and farmers, helped Feeny and Janzen confirm the highly specialized relationship that toxin-tolerant bruchid beetles maintained with L-dopa-producing legumes.

The same year, Feeny and Janzen again employed the southern armyworm to investigate the chemical defenses of *non*-ant-acacias.[112] Recall that Janzen's argument for the adaptive value of *Pseudormyrmex ferruginea* ant colonies to *Acacia cornigera* hinged, in part, on the hypothesis that non-ant-acacias consumed equal or greater amounts of metabolic energy producing toxic or repellent phytochemicals.[113] Ant-acacias could "afford" to support ant colonies for the same reason that non-ant-acacias could "afford" to produce toxic secondary compounds: The benefits of fending off damage by herbivores outweighed the energetic expense—*especially* over an evolutionary time scale, where small differences in energy consumption could affect patterns of natural selection. This hypothesis had begun with Janzen's own judgment that while *A. cornigera* tasted bland, the non-ant-acacias tended toward an unpalatable bitterness, thus one expensive adaptation (toxins) had been traded, over the course of evolution, for another (ants). And tracking down the source of the bitter flavor, the hypothetical toxins produced by non-ant-acacias, was precisely the type of biochemical

---

[112] Also in collaboration with graduate student Rehr, who was, again, listed as first author. S.S. Rehr,Paul P. Feeny, and Daniel H. Janzen, "Chemical Defence in Central American Non-Ant-Acacais," *The Journal of Animal Ecology* 42, no. 2 (1973).

[113] Janzen, "Coevolution of Mutualism between Ants and Acacias in Central America."

mystery that had drawn Feeny into chemistry in the first place.[114] In “Chemical Defence in Central American Non-Ant-Acacias,” published in *The Journal of Animal Ecology*, they reported their finding that non-ant-acacias did, indeed, produce a compound toxic to all vertebrates and a good many insects: cyanide.

The paper details a series of extractions, purifications, and the concoction of various artificial diets; the molecular methods developed and perfected by a previous generation of insect physiologists and chemists, and used extensively by Feeny in his dissertation research. Notably, some of the specific extraction methods cited were also attributed to agronomical journals, yet another signal of the overlapping scientific approaches that this research drew upon. In this project, however, these molecular methods, while shown to be very powerful, were not up to the task of identifying a critical toxin found in the leaves of non-ant-acacias. While whole acacia leaves, freeze-dried and incorporated into a standardized artificial diet, were toxic to that great generalist feeder, the southern armyworm, isolated cyanide was *not* toxic. Further feeding tests confirmed this result, particularly when leaves “depleted of [cyanide] proved only slightly less toxic.”[115] They could only surmise that another compound must work synergistically with the cyanide, but their efforts to identify it were to no avail. In this case, then, causation for the plant’s chemical defenses remained embodied by the leaf in its entirety, and could not be attributed to a single, isolable, well-honed molecular “weapon.” Despite this lack of specificity, however, Janzen and Feeny had combined

---

[114] Feeny. Interview by author. Digital Audio Recording. Ithaca, NY, 12 November 2007.

[115] Rehr, Feeny, and Janzen, "Chemical Defence in Central American Non-Ant-Acacais," 412.

their expertise and used molecular and entomological methods to verify Janzen's original hypothesis: "The presence of cyanogenic glycosides and of the additional toxic chemical appears to confer protection on non-ant-acacias against a broad spectrum of phytophagous insects, and possible also against fungi and bacteria. Such chemical defence is not present in the ant-acacias, in which symbiosis with ants serves as an alternative means of protection." [116] Even if the specific "chemical defence" was beyond their current means of molecular investigation, the evidence of a costly adaptation, equivalent in function to the ant-acacia's "standing army" had been demonstrated. The interaction had been demonstrated to be an adaptation, based upon the analogy with non-ant-acacia's costly chemical defenses. And, reciprocally, the adaptive value of ants and chemicals alike were reinforced.

Feeny's collaborations with Janzen represented what he saw chemical ecology to be: detailed study of secondary chemicals to understand the evolution of interactions between organisms. In 1968, as he outlined a lecture on chemical ecology for Cornell's General Ecology course, in his first point he described the "Scope of the Subject" as "[t]he ecological significance of secondary chemical interactions between living organism which result in a selective advantage to one or more species."[117] It is clear, then, that from the beginning Feeny saw the practice of chemical ecology as an explicitly evolutionary study. As he would describe it more than three decades later in an essay on "The Evolution of Chemical Ecology," "interest exploded in the 1960s as ecologists

---

[116] Ibid.

[117] Fall 1968, Bio. Sci. 361, General Ecology course, Cornell University, lecture outline on chemical ecology. Feeny, pers. comm..

chemists, behaviorists, and others came to the realization that they were all studying different aspects of the same phenomena. This was, perhaps not coincidentally, a time of rebirth for the field of evolutionary ecology." And beginning in 1970, he took part in presenting "what seems to have been the first college-level course entitled Chemical Ecology."[118] Indeed, a confluence of burgeoning interest in ecology and the rapid proliferation of ecological subfields in the 1960s,[119] in combination with relatively recent technological advances in the molecular methods used to analyze the chemicals of in interspecific interactions, provided momentum to growing enthusiasm for chemical ecology.

For Feeny and many others, an understanding of evolution—of coevolution, more specifically—was one of the driving forces behind the development of the field. But the early proponents of chemical ecology were not always focused on the evolutionary question raised by chemical interactions. In the preface to the first volume of papers to be entitled *Chemical Ecology*, published in 1970, Ernest Sondheimer and John Simeone described multiple scientific rivers with "independent courses," coming together to form

---

[118] Paul P. Feeny, "The Evolution of Chemical Ecology: Contributions from the Study of Herbivorous Insects," in *Herbivores: Their Interactions with Secondary Plant Metabolites, Second Edition* (San Diego: Academic Press, 1992), 2. In his essay for *Herbivores*, Feeny writes that this course was first presented in 1968. Though it is clear that Feeny was giving lectures on chemical ecology to general ecology classrooms as early as 1968, this course was not taught until 1970, as evidenced by the course proposal and budget, found in the R.H. Whittaker Papers (Robert Harding Whittaker Papers, Cornell University Library, Division of Rare and Manuscript Collections, Ithaca, NY.).

[119] Hagen, *An Entangled Bank: The Origins of Ecosystem Ecology*; Sharon E. Kingsland, *The Evolution of American Ecology, 1890-2000* (Baltimore: Johns Hopkins University Press, 2005).

a “mighty new stream” of chemical ecology.[120] These rivers were the “spectacularly successful methods…for the purification and characterization of natural products” and “interest in solving some difficult ecological problems…due no doubt to social pressures,” [121] but not the influence of evolutionary theory or the development of evolutionary ecology. The papers contained therein were the product of series of talks given at Syracuse University in 1968 and coordinated by none other than insect physiologist Carroll M. Williams.[122] In Chapter Two I recounted Williams’ unexpected discovery of a potent insecticide in paper toweling. In his paper for *Chemical Ecology*, “Hormonal Interactions Between Plants and Insect,” Williams reported on this incident and made his case, which I have already described, that the “selective control of insects” with the use of highly specialized insecticides is “an ancient art invented by certain plants and practiced by them for tens of millions of years.”[123] Williams was not along in drawing evolutionary conclusions from his research. Plant ecologist Robert H. Whittaker also addressed the evolution of such “chemical defenses” in plants[124] and John Tyler Bonner drew conclusion about the evolution of multicellularity from the chemical

---

[120] Ernest Sondheimer and John B. Simeone, "Preface," in *Chemical Ecology*, ed. Ernest Sondheimer and John B. Simeone (New York: Academic Press, 1970), ix.

[121] Ibid.

[122] Ibid., x.

[123] Carroll M. Williams, "Hormonal Interactions between Plants and Insects," in *Chemical Ecology*, ed. Ernest Sondheimer and John B. Simeone (New York: Academic Press, 1970), 104.

[124] Robert H. Whittaker, "The Biochemical Ecology of Higher Plants," in *Chemical Ecology*, ed. Ernest Sondheimer and John B. Simeone (New York: Academic Press, 1970). Whittaker’s involvement in the development of coevolutionary theory will be discussed in far greater detail in Chapter Four.

ecology of soil-dwelling microorganisms.[125] Dethier argued that understanding "botanical chemical innovation" could shed light on the evolution of biological diversity in general,[126] and E.O. Wilson wrote of the evolution of "Chemical Communication within Animal Species."[127]

But in the remainder of the eleven papers, when evolution was mentioned at all it was a token acknowledgement of the existence of evolutionary history, rather than an attempt to draw evolutionary implications from an ecological phenomenon—a pattern that would continue, in fact, when the *Journal of Chemical Ecology* was launched in 1975.[128]

Despite this lack of uniform interest in the evolution of chemical interactions between organisms, chemical ecology did continue to gain momentum thanks, undoubtedly, to the factors that Sondheimer and Simeone cited in their preface. In particular, the concept of "natural products" united chemical ecologists interested in coevolution with the rest of their colleagues. The notion that the very "natural insecticides" that plants employed to repulse their predators had become *products* that

---

[125] John Tyler Bonner, "The Chemical Ecologyof Cells in the Soil," in *Chemical Ecology*, ed. Ernest Sondheimer and John B. Simeone (New York: Academic Press, 1970).

[126] Vincent Dethier, "Chemical Interactions between Plants and Insects," in *Chemical Ecology*, ed. Ernest Sondheimer and John B. Simeone (New York: Academic Press, 1970).

[127] E.O. Wilson, "Chemical Communication within Animal Species," in *Chemical Ecology*, ed. Ernest Sondheimer and John B. Simeone (New York: Academic Press, 1970).

[128] See, for example: F.W. Went, "Plants and the Chemical Environment," in *Chemical Ecology*, ed. Ernest Sondheimer and John B. Simeone (New York: Academic Press, 1970). Paul Feeny claims that this volume of talks, as well as the early *Journal of Chemical Ecology*, contained very little that looked like actual ecology—that it was too lab-focused, and that the questions could have been taken out into the field and made ecological but they weren't (Feeny, pers. comm.).

humans could use for their own benefits united the thinking of both evolutionary and non-evolutionary chemical ecologists. As already mentioned in previous chapters, the pharmaceutical industry and the insecticide industry had long regarded plants as natural factories for biochemically active agents for human use. And historical accounts of chemical ecology agree that human uses of plant compounds, whether as traditional medicines or the modern pharmaceuticals of "natural products chemistry," played a critical role in interesting ecologists in the ecological function of chemicals.[129] Moreover, many of the coevolutionary scientists that I have studied for this project shared the perspective that humans, as Feeny put it, are constantly "falling into a trap of being poisoned by a plant defense" in their various uses of naturally-derived drugs, in particular their addictions to caffeine and nicotine.[130] I have already argued that the contributions of economic entomology, biological control, and insecticide research to the development of coevolutionary studies blurred the boundary between the natural world and the artificial, anthropogenic world. In this case, the close interconnection between human cultural uses of chemicals and the evolution of chemical adaptations by natural selection served to further blur this boundary. The notion that molecules were *products*, to be used as tools or weapons in both the human sphere and the natural sphere, generated the

---

[129] Thomas Hartmann, "The Lost Origin of Chemical Ecology in the Late 19th Century," *Proceedings of the National Academy of Science* 105, no. 12 (2008). Timothy Johns, *With Bitter Herbs They Shall Eat It: Chemical Ecology and the Origins of Human Diet and Medicine* (Tucson: University of Arizona Press, 1990).

[130] Feeny. Interview by author. Digital Audio Recording. Ithaca, NY, 12 November 2007. Ehrlich and Janzen both said similar things, and Whittaker was enraged by the drug culture of the 1960s, to the extent that he attempted to incorporate moral lessons about drug use into papers on the evolution of plant chemistry. This topic is discussed further in Chapter Five.

distinctive sense that plant's chemical adaptations, like human chemical innovations, were forms of evolved *technology*.

In coming to the United States, Feeny found opportunities for scientific collaboration and teaching that allowed him to pursue the central questions of coevolution. While chemical ecologists were not agreed upon the importance of studying evolutionary aspects of chemical interactions, this developing area of ecology was broad enough to accommodate many different perspectives and approaches, most of which were centered around the characterization of "natural products." Though Feeny, by his own account, faced challenges, particularly financial, in pursuing his own form of chemical ecology to the fullest extent, he created a niche for the development of new methods that exploited the insights of both chemistry and evolutionary ecology.

Conclusion

In this chapter I examined how two major figures in the early development of coevolutionary studies used molecular methods and evolutionary inference to study interactions between insects and plants. Janzen collaborated with chemists who pursued their own research goals, while Feeny worked within the new rubric of chemical ecology, simultaneously using his training in both biology and chemistry. Both focused on molecules; not as ultimate causes for complex biological interactions, but as handles with which they could grasps the dynamics of those interactions and understand the ultimate causation of their evolutionary history. Through this work, the very interactions between insects and plants transformed interactions themselves in evolutionary adaptations.

The relevant molecular methods were in large part derived from economic entomology and agronomy. But these were not the only theoretical and practical insights obtained from applied biology. Since 1937, when Dobzhansky asserted that natural selection acted in the evolution of insecticide resistance, the interactions between agricultural crops and populations of pest insects had continued to provide examples of real-time biochemical evolution. Witnessing evolution occurring in response to present-day ecological interactions presented a bridge between the disciplines of ecology and evolution by narrowing the apparent gap between ecological and evolutionary time scales. Today it is common to hear academic biologists repeat the adage that ecology and evolution are so interdependent that studying one necessitates understanding the other. Insecticide resistance could not be understood without the insights of evolutionary biology; not just because it was a product of natural selection, but also because the evolutionary history of insects foreshadowed, paralleled, and even preconditioned contemporary insect evolution in response to synthetic chemicals. The overarching perspective offered by coevolutionary theory made this clear: it was possible to study evolution—whether real-time evolution or evolutionary history—in a way that was ecologically meaningful, and vice versa. Furthermore, it became increasingly apparent that the connection between the evolution of insecticide resistance and the evolution of resistance to toxic chemicals in plants was more than just a useful analogy. Humans had inadvertently written themselves into a process of natural selection for biochemical resistance in insects. Theoretically and practically, then, the notion of biochemical *interaction as adaptation* bridged the disparate realms of the insect kingdom and the plant kingdom, the disciplines of botany and entomology, the world of applied biology and pure biology, the time scales of ecology and evolution and, more broadly, the human-modified environment and the unsullied “nature” that supposedly existed apart from human society.

Chapter Four

Collaboration and Conflict Where Plants and Insects Meet: Professional meetings and persuasive metaphors bring together botany and entomology

In late April 1968, biologists interested in the emerging study of coevolution convened in Corvallis for Oregon State University's 29th Annual Biology Colloquium. The proceedings were published two years later as *Biochemical Coevolution*, edited by the conference organizer, botanist Kenton L. Chambers. The conference brought together a diverse group of researchers, all interested, in the words of keynote speaker Paul Ehrlich, in a "new way of looking at the properties of communities."[1] All speakers on biochemical interactions between organisms of different species and—often—different kingdoms, taking part in what Ehrlich deemed a "renaissance of what we used to call 'synecology,'"[2] the ecological study of groups of organisms.[3] As the insights of the modern evolutionary synthesis penetrated 20th-century ecology in the 1950s and 1960s, it came to seem that a focus on individual organisms, as in autecology, or even on populations of only one species, was tantamount, in ecologist Gordon Orians' words, to claiming that "evolutionary concepts have no place in ecological theory."[4] And it was in the late 1950s that ecologist G.E. Hutchinson proposed that the evolution of more complex interrelationships between organisms sharing multi-species communities could

---

[1] Paul R. Ehrlich, "Coevolution and the Biology of Communities," in *Biochemical Coevolution: Proceedings of the Twenty-Ninth Annual Biology Colloquium, April 26-27, 1968*, ed. Kenton L. Chambers (Corvallis: Oregon State University Press, 1970), 87.

[2] Ibid., 1.

[3] Defined according to: Eugene Odum, *Fundamentals of Ecology, 3rd Edition* (London: Saunders, 1971), 7.

[4] Gordon H. Orians, "Natural Selection and Ecological Theory," *The American Naturalist* 96 (1962).

account for the diversity of organisms in the natural world.[5] In other words, greater specialization into narrower ecological roles, driven primarily by interaction with other species, could explain the evolution of diverse, stable communities of organisms.[6] Soon afterwards, animal ecologist Robert Paine hypothesized, more specifically, that the dynamics of predator-prey interactions could explain the species-richness of ecological communities.[7] Community interactions were the evolutionary generators of diversity.

Coevolutionists concurred with Orians, and Ehrlich and Raven criticized past "[s]tudies of community evolution," which had, in their view, "tended to be narrow in scope and to ignore the reciprocal aspects of these interactions. Indeed one group of organisms is all too often viewed as a kind of physical constant." In contrast, coevolutionists attempted to invoke the concerns of both botanists and zoologists and aspired to treat plants and animals alike as active community participants. In so doing, the study of coevolution might serve as a corrective, a new way of approaching community evolution, "[o]ne of the least understood aspects of population biology." Ehrlich and Raven went so far as to reframe Hutchinson's claim in terms of coevolution, positing, "the plant-herbivore 'interface' may be the major zone of interaction responsible for generating terrestrial organic diversity."[8] Writing in 1971 with Feeny, renowned

---

[5] G. Evelyn Hutchinson, "Concluding Remarks," *Cold Spring Harbor Symposia on Quantitative Biology* 22 (1958); ———, "Homage to Santa Rosalia or Why Are There So Many Kinds of Animals?," *The American Naturalist* 93 (1959).

[6] Robert T. Paine, "Food Web Complexity and Species Diversity," *The American Naturalist* 100 (1966).

[7] Ibid.

[8] Paul R. Ehrlich and Peter H. Raven, "Butterflies and Plants: A Study in Coevolution," *Evolution* 18, no. 4 (1964).

ecologist R.H. Whittaker, whose work redefined the concept of "niche" in ecology,[9] claimed, likewise, that "chemical interactions may be essential aspects of niche differentiation."[10]

This new acknowledgement of the biological importance of *interaction* was easy to appreciate in terms of predator-prey interactions. In the chase of predator and prey, both participants were animals and both could display active, purposive efforts to hunt or evade. But extending what seemed true of predator-prey interactions to the interactions of insects and plant was not intuitive for all biologists. As Whittaker wrote, in many biologists' conceptions of nature, "[a]nimals are active, aggressive, and tissue-eating," while "[p]lants, in contrast, are passive and benign."[11] Plants cannot evade their predators in the same immediate, active way that a field mouse can hide from a fox, leading to the misapprehension, in Janzen's words, that "the world is green" for herbivores, an all-you-can-eat banquet of defenseless dinner.[12]

Despite their image as the voracious enemies of human food and health, even insects faced such public relations challenges. One ecological assertion held that insect feeding could not exert an appreciable pressure on plants,[13] the idea, in Janzen's phrasing

---

[9] Robert H. and Simon A. Levin Whittaker, ed., *Niche: Theory and Application* (Stroudsberg, Pennsylvania: Dowden, Hutchinson & Ross, Inc., 1975).
[10] Robert H. Whittaker and Paul P. Feeny, "Allelochemics: Chemical Interactions between Species," *Science* 171 (1971): 767.
[11] Robert H. Whittaker, "The Biochemical Ecology of Higher Plants," in *Chemical Ecology*, ed. Ernest Sondheimer and John B. Simeone (New York: Academic Press, 1970).
[12] Daniel H. Janzen, "Promising Directions of Study in Tropical Animal-Plant Interactions," *Annals of the Missouri Botanical Garden* 64 (1977).
[13] H.G. Andrewartha and L.C. Birch, *The Distribution and Abundance of Animals* (Chicago: University of Chicago Press, 1954); Nelson G. Hairston,Frederick E. Smith,

that insects were “just decorations on the vegetation.”[14] While the power of agricultural pests to decimate crops would appear to clearly invalidate this claim, its proponents felt justified in ignoring agricultural communities because they were *artificial* and unrepresentative of *natural* ecological phenomena.[15] Thus, if one assumed that phytophagous insects were not limited by food supply and could eat a nearly endless supply of plants indiscriminately, it followed that plants could not exert much selective pressure on insects and could not, therefore, shape insect evolution. Likewise, if insect feeding could not seriously impact the well being of plants, it followed that insects could not shape plant evolution.

On the contrary, coevolutionists argued, the impact of insect phytophagy was profound—if not always obvious outside the agricultural context—and must be considered a powerful selective force and a source of diversity amongst plants and their predators, just as in animal predator-prey systems.[16] The physiological and entomological research that rooted coevolutionary theory showed, first of all, that insects do not eat plants indiscriminately. In fact, many insects feed upon groups of plants that share distinctive chemical characteristics and, in many cases, correlated familial relations. Similarly, biochemical research on the secondary compounds had revealed complex

---

and Lawrence B. Slobodkin, "Community Structure, Population Control, and Competition," *The American Naturalist* 94 (1960).

[14] Janzen, "Promising Directions of Study in Tropical Animal-Plant Interactions."

[15] Tibor Jermy, "Insect-Host-Plant Relationship--Co-Evolution or Sequential Evolution?," *Symposium Biologica Hungarica* 16 (1976).

[16] D.E. Breedlove and P.R. Ehrlich, "Coevolution: Patterns of Legume Predation by a Lycaenid Butterfly," *Oecologia* 10 (1971); Paul R. Ehrlich and L.C. Birch, "The ‘Balance of Nature’ and ‘Population Control'," *The American Naturalist* 101 (1967); William W. Murdoch, "'Community Structure, Population Control, and Competition’—a Critique," *The American Naturalist* 100 (1966).

patterns of toxin production. The expense of producing toxic and repellant compounds suggested to evolutionary biologists that they must have adaptive value, and entomological experience and experimental evidence had already shown many of them to function as potent "natural insecticides." Thus, coevolutionists came to make two interdependent arguments about biochemical interaction: 1) Insects' herbivory was a strong enough selective force to generate adaptive evolutionary change in plants; and 2) Plants' secondary compounds were costly defensive adaptations against insects, strong enough to generate adaptive evolutionary change in insects. These arguments generated a core of research questions coevolutionists could work on in collaboration. Simultaneously, they provided points of contention for biologists who disagreed with the methods and ideas of the new coevolutionary biologists.

In this chapter I draw out the points of collaboration and contention, beginning with two conferences that rode the wave of enthusiasm for coevolutionary theory and for using chemical and ecological methods in complementary ways. First I introduce a two-pronged International Biological Program conference on plant/plant interactions and insect/plant interactions, held in Santa Barbara in 1968. The second conference, already mentioned above, which resulted in the publication of *Biochemical Coevolution,* was also held in 1968, in Corvallis. These conferences reveal ways that different groups of researchers, with different types of scientific goals, came together and cross-pollinated, sharing methodological and intellectual resources. The International Biological Program conferences show, as in past chapters, that concerns with generating technological applications, particularly for use in agriculture, provided one unifying theme. And the symposium that spawned *Biochemical Coevolution* will allow me to draw out some of the ways that biologists constructed evolutionary arguments, positing reciprocal adaptation between insects and plants.

These conferences, particularly *Biochemical Coevolution*, also offer striking examples of the critical role that language played in the development of coevolutionary theory. In past chapters, I have introduced some of the analogies that came to characterize coevolutionary theory in its early years. Here I examine these at greater length, analyzing how they were used to frame theoretical positions and build consensus the field of coevolutionary studies. This type of analysis is especially useful in my examination of schisms in the study of the evolution and ecology of communities. Just as the late-19th-century debate over acacia-ants was represented by conflicting analogies explaining the role of ants—either a defensive force or a pack of parasitic fleas—biologists used strong imagery and analogies in the 1960s and 1970s in debating relationships between animals and plants. Were plants a *passive* substrate that supported an indiscriminate horde of insects? Or were both plants and insects *active*—ecologically and evolutionarily—the former defending against herbivory and the latter selectively feeding only on palatable plants? Evolutionary ecology and coevolutionary studies generated new ways to talk about organism's adaptations—and with new ways to talk, came new ways to *think*, as well. Both of these were critical to building mutually reinforcing arguments about coadaptation in both plant and insects.

The International Biological Program conferences

In the early 1960s, inspired by the success of the International Geophysical Year, biologists in the U.K. considered the possibility of a similar program organized instead around the study of biological phenomena. The International Biological Program (IBP) soon emerged, and was taken up enthusiastically in Europe and Canada. But it was not until the late 1960s, motivated in part by growing public awareness of worrying environmental problems, that an American sector of the IBP was organized.[17]

As a whole, the IBP focused primarily on ecosystems ecology, thanks to the efforts of British geneticist C.H. Waddington, who saw ecosystems ecology as the most efficient route to serving what would become the IBP's theme, "The Biological Basis of Productivity and Human Welfare."[18] The U.S. program was no different—to the chagrin of most other ecologists, particularly evolutionary ecologists.[19] After all, of the $11 million disbursed to American ecologists under the auspices of the IBP from the late 1960s through mid-70s, the vast majority of the money went to ecosystems researchers, and predominantly to the development of five biome projects.[20] This pattern of funding was particularly galling considering the recent proliferation of ecological subdisciplines; ecology in the 1960s was so "intellectually fragmented," according to historian Joel

---

[17] Joel B. Hagen, *An Entangled Bank: The Origins of Ecosystem Ecology* (New Brunswick: Rutgers University Press, 1992), 170.

[18] Ibid. Ecosystems ecology was founded around the study of the flow of energy and nutrients through ecological systems [Robert E. Kohler, *Landscapes and Labscapes: Exploring the Lab-Field Border in Biology* (Chicago: University of Chicago Press, 2002), 275.].

[19] Hagen, *An Entangled Bank: The Origins of Ecosystem Ecology*, 165.

[20] Ibid., 165 & 175. Sharon E. Kingsland, *The Evolution of American Ecology, 1890-2000* (Baltimore: Johns Hopkins University Press, 2005), 221-222.

Hagen, that there could be "no consensus within the discipline about the importance of studying ecosystems."[21]

Nonetheless, under the rubric of the IBP, other styles of ecological research could be accommodated to some extent. According to a memorandum distributed by the National Research Council to IBP program directors, "Americans, most particularly, seek ways of understanding" the many "by-products of technological developments, avoiding their disadvantages and using their advantages."[22] And biological control of pest plants and insects was a particularly promising domain within which to pursue these goals. In 1967, the Environmental Physiology Subcommittee of the IBP proposed a pair of "work conferences," focused on biochemical means of biological control. The two conferences, held in tandem in Santa Barbara in 1968, focused on, respectively, biochemical interactions among plants and biochemical interactions between plants and insects. The specific goals of these conferences were related to the "highly active substances" produced by plants, which promised "opportunities for developing new classes of biologically active agents that are selective in action [upon] destructive insects, without hazard to man and his environment."[23] Other such agents would be useful in controlling weeds.[24] The proposal for the conference stated, "It will center on chemical interactions between organisms. It will emphasize control of insects by plants and plants by other

---

[21] Hagen, *An Entangled Bank: The Origins of Ecosystem Ecology*, 166.

[22] Letter from National Research Council to Cornelius H. Muller. Cornelius H. Muller Collection, Cheadle Center for Biodiversity and Ecological Restoration (CCBER), University of California, Santa Barbara (UCSB).

[23] Conference Proposal, National Research Council, 51, Cornelius H. Muller Collection, CCBER, UCSB.

[24] Ibid., 54.

plants. The fact that terpenoids are implicated in both of these phenomena suggests that entomologists and botanists might well be brought together to consider mechanisms and applications."[25] Thus, though ecosystems ecologists certainly contributed to the conferences that emerged from this initiative, a mix of chemists, botanists, entomologists, insect physiologists, and non-ecosystems ecologists attended these work conferences, as well as researchers from agriculture and the pesticide industry. Moreover, the schedule shows a concerted effort to integrate the diverse groups of researchers, with joint sessions that featured alternating presentations by plant/plant and insect/plant attendees. Similarly, the content presented, while framed mostly within the utilitarian goals of the conference proposal, also brought together basic and applied conceptions of organismal interactions, particularly in the keynote speeches, which I will discuss below.

Plant ecologist Cornelius H. Muller, longtime faculty member of UC-Santa Barbara, organized the plant/plant section of the conference, which was later published as *Biochemical Interactions Among Plants*.[26] Muller had built his early career specializing on the study and identification of oak trees, but since the 1950s he had focused on allelopathy. Allelopathy was defined as the inhibition of plant growth by chemicals exuded by other plants in the community. Ecological study of allelopathy drew upon some of the same resources as coevolutionary studies for its general phytochemical background, like the school of chemical taxonomy that attempted to classify plants based

---

[25] Ibid., *iii*.

[26] *Biochemical Interactions among Plants*. (Washington, DC: National Academy of Sciences, 1971).

upon their biochemical components.[27] And much of the practical research in the field came from experience in agriculture, where the practice of monoculture meant that concentrated stands of plants could produce equally concentrated toxins, which leached into the soil and caused what agronomists called "soil sickness."[28]

Allelopathic research had generated a very different conception of these plant toxins than coevolutionary studies or biological control. In biological control, plants might actively *control* other plants or insects with the compounds. In coevolutionary studies, they were engaged in *chemical warfare* over many generations. But in allelopathy, plants *inhibited* each other through a *passive* process of *leaching* toxic waste. The toxins themselves were mere "by-products" of other metabolic processes, wastes to be excreted, rather than the costly adaptations that coevolutionists posited.[29]

I explore the conflict that arose between these different conceptions of plant toxins in the second part of this chapter. But for the time being, I will use the keynote speech of the plant/plant interactions conference to illustrate how—despite these very different conceptions of plant toxins—coevolutionary theory and allelopathy need not necessarily have come into conflict. Broad biological thinker Whittaker, who had long been Muller's friend and correspondent, and whom Muller recruited for the plant/plant

---

[27] Tony Swain, *Chemical Plant Taxonomy* (London: Academic Press, 1963).

[28] James Bonner, "The Role of Toxic Substances in the Interactions of Higher Plants," *The Botanical Review* 16 (1950); W.F. Loehwing, "Root Interactions of Plants," *The Botanical Review* 3 (1937); Frank W. Woods, "Biological Antagonisms Due to Phytotoxic Root Exudates," *The Botanical Review* 26 (1960); Solomon Garb, "Differential Growth-Inhibitors Produced by Plants," *The Botanical Review* 27 (1961).

[29] Cornelius H. Muller, "The Role of Chemical Inhibition (Allelopathy) in Vegetational Composition," *Bulletin of Torrey Botanical Club* 93 (1966).

keynote address, “The Chemistry of Communities,” opened this possibility.[30] Though Whittaker is more generally remembered for proposing that fungi be classified within their own kingdom, he made many of his scientific contributions, like this keynote address, to plant community ecology.[31]

In his address, Whittaker took a measured approach, addressing both the insect and plant delegates with many open questions about the origin and function of toxic plant compounds. Moreover, he pondered ultimate causation, not willing to stop at the level of proximate causation. Instead, Whittaker asked whether “these substances in plants [are] primarily wastes, some of which have been secondarily adapted to chemical defense? Or are they primarily chemical defenses, some of which may be related to plant wastes? By what test does one choose, or is there really a choice to be made?” Whittaker came quite close to directly challenging the work of coevolutionary biologists who argued so vehemently for the adaptive value of plant toxins, not granting priority to either explanation for the evolution of plant toxins and suggesting, instead, that, “Selective advantage can thus add a defensive function to excretory necessity or add excretory necessity to a defensive function with equal utility.” With this he sought not to diminish either hypothesis, but instead to assert that they could not be mutually exclusive, citing with approbation “Janzen’s (1967) suggestion that symbiotic ants and bitter alkaloids are alternative means of defense” and Ehrlich and Raven’s hypothesis of “evolutionary coadaptation.” “Most important for our present concern,” he claimed, is “the probability

---

[30] Robert H. Whittaker, "The Chemistry of Communities," (Washington, DC: National Academy of Sciences, 1971).

[31] Walter E. Westman,Robert K. Peet, and Gene E. Likens, "Robert H. Whittaker," *National Academy of Sciences Biographical Memoirs* 59 (1990).

that there is a strong relationship between allelopathic effects of plants on plants on the one hand and biochemical adaptation of plants versus animals and microorganisms on the other."[32] In other words, to Whittaker, as divergent as the language of passive waste and active weapon might seem, both should be taken into consideration in the evolution of community structure. Moreover, both should be considered from an adaptive viewpoint, as direct products of adaptive processes, rather than by-products of other organismal functions.

Most of the remaining plant/plant talks addressed allelopathic interactions from a far more proximate and practical perspective, assessing mechanisms by which substances leach into the soil and laboratory techniques used to analyze those substances. For instance, in "Leaching of Substances from Plants," horticulturalist H.B. Tukey addresses the "Implications of Leaching" near the end of his paper. These implications are not evolutionary, however, and have mostly to do with "the yield, quality, and nutritive value of economic food plants."[33] Similarly, agronomist LeRoy Holm explained how a better understanding of the history of crop plants could be used to agricultural advantage, in the development of highly specific herbicides or more pest-resistant plants.[34] These plant/plant papers clearly attended to the practical goals laid out in the conference proposal, reaching little beyond immediate practical concerns and proximate mechanisms.

---

[32] All quotations above are from: Whittaker, "The Chemistry of Communities," 11.

[33] H.B. Tukey, "Leaching of Substances from Plants," (Washington, DC: National Academy of Sciences, 1971), 29.

[34] LeRoy Holm, "Chemical Interactions between Plants on Agricultural Lands," (Washington, DC: National Academy of Sciences, 1971).

Few of the thirty-two plant/plant conference attendees would be familiar from the pages of this dissertation.[35] By contrast, the insect/plant conference, organized by entomologist Edward Knipling of the USDA, hosted a number of scientists cited in earlier chapters of this dissertation amongst its forty attendees. Insect physiologist Carroll Williams gave the insect/plant keynote address, and Vincent Dethier, Tom Eisner, Reginald Painter, Karel Sláma (Williams' collaborator), A.J. Thorsteinson (Fraenkel's student), and Carl Huffaker (one of Janzen's graduate advisors), all gave papers as well. Tibor Jermy, a postdoctoral fellow of Dethier's,[36] who would become a critic of coevolutionary theory in the next decade,[37] also presented, in addition to Robert Yamamoto, a collaborator of Fraenkel's.

The proceedings of the insect/plant conference were later published as *Insect-Plant Interactions*.[38] Like the general content of the plant/plant conference, the participants were mostly focused on the practical value of plant compounds, and the possibility that they might serve as agricultural insecticides. Williams' isolation of juvenile hormone had inspired a good deal of hope amongst environmentalists.[39] That a

---

[35] Though it is worth noting that Herbert Baker, who served as Janzen's advisor in the UC-Berkeley botany department during his dissertation research, attended the conference. "Acceptances, Plant-Plant Chemical Interactions Working Group Conference," Cornelius H. Muller Collection, CCBER, UCSB.

[36] Alan Gelperin,John G. Hildebrand, and Thomas Eisner, "Vincent Gaston Dethier," *National Academy of Sciencece Biographical Memoirs* 89 (2007): 85.

[37] Jermy, "Insect-Host-Plant Relationship--Co-Evolution or Sequential Evolution?."

[38] *Insect-Plant Interactions*. (Washington, DC: National Academy of Sciences, 1969).

[39] See Chapter Two on Williams' isolation of juvenile hormone. The isolation of juvenile hormone also inspired some trepidation, at least in the case of Rachel Carson, who learned of Williams' work while she was still working on *Silent Spring*. She wrote to him, worried that this newly discovered insecticide would obviate the work that she had already put into her manuscript. Citing the *Life* magazine article that brought Williams'

"natural insecticide" could be both potently effective and highly specific suggested that pests might be controlled without the larger-scale environmental destruction wrought by synthetic pesticides. In fact, John Siddall of the Syntex Corporation presented a paper at the insect/plant conference, reporting on the company's efforts to produce a synthetic hormonal insecticide.[40] The work of Syntex would have been particularly interesting to Williams, since the company had been founded, in part, upon the promise of insect juvenile hormone.[41] Overall, little mention of the evolution of these compounds can be found in either *Insect-Plant Interactions* or *Biochemical Interactions Among Plants*.

Like Whittaker's keynote address, however, Williams' was an attempted to address some of the larger themes in insect-plant interaction research, offering a characteristic synthesis of basic and applied perspectives on the evolution of plant secondary compounds. To this end, Williams cited not only his experience in the lab at Harvard, but also his recent foray into the Amazon, where he was captivated by the Rio Negro, a river that earned its name thanks to the tannins that fill its water, turning it black. Williams was "amazed to note the absence of aquatic insects in the Rio Negro…in marked contrast to the abundance of aquatic insects" in the other tributaries of the Amazon. The Rio Negro, he found, was a veritable "river of plant-derived pesticides," which induced many of the same reactions in insects as the juvenile hormone that he and

---

discovery into the public sphere [Albert Rosenfeld, "The Ultimate Weapon in an Ancient War," *Life* 45, no. 14 (1958).], Carson wrote, "If the LIFE article may be accepted at face value, much of what I am about to say may be academic." Letter from Rachel L. Carson to Carroll M. Williams, 5 October 1958, Carroll M. Williams Papers, Accession 12265, Harvard University Archives.

[40] J.B. Siddall, "Synthetic Studies on Insect Hormones," in *Insect-Plant Interactions* (Washington, DC: National Academy of Sciences, 1969).

[41] Carroll M. Williams Papers, Accession 12265, Harvard University Archives.

Sláma had studied together at Harvard.[42] The economic promise of such compounds arose from Williams' observation that "insect hormones constitute 'weak spots' in their physiological armor and open them to attack by specific materials from which they have little defense or prospect of evolving defense."[43] For this evolutionary reason, then, plant chemistry "is the place to look for a whole battery of selective hormonally active pesticides."[44]

Thus, one of the most interesting aspects of this pair of IBP conferences was how intently it was focused on applied questions, and yet how clearly it attracted the interest of biologists who could relate its content to broad questions about the origin and ecological function of evolutionary adaptations. Community interactions provided a nexus at which contentious notions about nature, technological manipulation, and control all collided. And while most of the papers presented at the conference talked little about evolutionary adaptation, they represent the context within which the theory of coevolutionary adaptation came into being. Thus, the notion of "natural insecticide" enters coevolutionary theory by way of biological control. And while plants "controlling" pest insects constitutes an oversimplified and proximate description of a phenomenon in which an evolutionary ecologist reads rich biological and historical layers, the unadulterated *instrumentality* of this construction had its effect. It was through the power of language like this, of control, and of chemical weapons and evolved tools, that a newly technological notion of adaptation, rooted especially in the human

---

[42] Carroll M. Williams, "Perspectives in Insect-Plant Interactions," in *Insect-Plant Interactions* (Washington, DC: National Academy of Sciences, 1969), 86.
[43] Ibid., 87.
[44] Ibid., 86.

endeavor of agriculture, took shape. Molecules had already been transformed into tools with which biological phenomena could be altered. This process of "molecularization" reflected, as I noted in Chapter One, historian Phil Pauly's notion of the "engineering ideal," which had infiltrated biological thinking in the early 20th century. Molecules were tools that both humans and plants could use, and while coevolutionists studied them in a historical context, as an adaptive response to insect predators, the sense of action and agency that toxic molecules carried was shared by the organisms that produced them.

The 29th Annual Biology Colloquium and *Biochemical Coevolution*

In contrast to the papers of the IBP conferences described above, the six papers of the 29th Annual Biology Colloquium at Oregon State were focused explicitly on evolutionary dynamics and the history of interactions between organisms. Like most work in coevolutionary studies at the time, the papers analyzed, in Ehrlich's words, "patterns of interaction," reciprocal ecological and evolutionary interactions "between two groups of organisms [that] do not exchange genetic information but which do have a close and evident ecological relationship."[45] Ehrlich led the conference with a discussion of a number of such systems. Like Janzen's analogies between acacia-ants and secondary plant compound, evolutionary adaptation gave Ehrlich a tool with which he could draw out the similarities between a disparate variety of interactions, from the relationships between predator and prey and between ticks and rabbits."[46] Most strikingly, he asserted that relationships between herbivorous insects and plants also

---

[45] Ehrlich, "Coevolution and the Biology of Communities," 1.
[46] Ibid., 3.

represented, in parallel, such selectional races.[47] Ehrlich knew that the image of a caterpillar munching on a leaf evoked an entirely different notion of interaction from the image of a lion hunting a gazelle. As I suggested above, the discordance between these two ideas of predatory behavior was a perceptual challenge that coevolutionists would take up time and again: "All biologists," Ehrlich wrote, "are familiar with the sharp senses and speed of the antelope [and] the stealth and fangs of the tiger."[48] To describe lions and caterpillars in similar terms was, simply put, a cognitive leap that even some biologists were not immediately prepared to make.

To support this cognitive leap, Ehrlich focused especially upon Feeny's graduate work on winter moth larvae, characterizing the relationship between oak trees and larvae as a "tight selectional race." "If the oaks can evolve ways of depositing tannins even earlier, or produce other defenses, the moths will lose the race, unless the moths can evolve a way of dealing with the oak's defenses."[49] Next, Ehrlich cited Janzen's graduate work on the acacia-ant system, where "ants serve as substitutes for the usual defensive mechanisms of acacias…the bitter-tasting chemicals which are characteristic of other

---

[47] Oddly, Ehrlich writes here that the "plant-herbivore system" is a "homologue" of the "predator-prey system" (Ibid.). In evolutionary terms, to identify the two systems as homologous to each other would be to attribute their similarities to shared ancestry, rather than to adaptive change in response to similar selective pressure (which would make them analogous).

[48] Ibid. In support of the idea of plant-insect relationships as "selectional races," he cited the work of both Janzen and Feeny, both already making their names in the study of coevolutionary phenomena.

[49] Ibid. While the race metaphor became increasingly common as the development of coevolutionary theory expanded beyond the study of insects and herbivores, it was more common for Ehrlich to invoke the language of economic entomology, identifying secondary compounds as "plant pesticides" (Ibid.).

acacias."[50] In both cases, coevolution makes sense of the system of ecological interaction by positing powerful reciprocal selective pressure operating between the organisms. Moreover, the systems were dynamic—the process of adaptation continued, and even today, winter moths might just "lose the race."

According to Ehrlich, seeing these relationships as dynamically evolving avoided the pitfalls of "physiological ecology," and of "being seduced into 'explanations,' such as 'competition from X limits the distribution of Y.'"[51] Such "explanations" explained nothing at all, in Ehrlich's view, constituting simple statements of fact. Instead, coevolutionary theory challenged biologists to ask how such limits came to be and how they might be shifting in response to selection; to ask, in other words, about the *ultimate* causes of biological phenomena, rather than the *proximate* causes.[52] Searching for ultimate causation motivated Ehrlich, like other coevolutionists, to focus on the space of interaction between organisms, enabling him to draw evocative parallels between winter moth larvae and tigers, or antelopes and oak trees.

Of the five remaining papers, all but one spanned equally broad taxonomic gulfs, addressing the evolution of symbioses between invertebrates and algae, plants and fungi, and orchids and bees.[53] Brower presented his research on monarch butterflies' ability to

---

[50] Ibid.

[51] Ibid., 10.

[52] See introduction to Chapter Three for an explanation of this distinction.

[53] The one exception was Muller's paper [Cornelius H. Muller, "The Role of Allelopathy in the Evolution of Vegetation," in *Biochemical Coevolution: Proceedings of the Twenty-Ninth Annual Biology Colloquium, April 26-27, 1968*, ed. Kenton L. Chambers (Corvallis: Oregon State University Press, 1970).], which focused on plant evolution. I will not address Muller's disagreement with coevolutionary biologist here, as this constitutes the main focus of the final section of this chapter.

safely sequester the toxic cardiac glycosides produced by their main food source, the American milkweed.[54] He hypothesized that in the coevolutionary race between monarchs and milkweeds, monarchs were ahead: Not only could they tolerate milkweed toxins, but they chose milkweed preferentially as a food plant and stored the plant's toxins within their own bodies, making monarchs unpalatable to their own predators.[55] Brower had demonstrated this experimentally from a variety of angles, including artificially selecting for a population of monarchs that would feed (though they could not thrive) upon cabbage. Blue jays captured from the wild had apparently long ago learned to avoid monarchs and avoided eating even these cabbage-fed butterflies. But jays placed on an "extreme food deprivation schedule" overcame their revulsion and learned to eat the monarchs, which, indeed, carried no cardiac glycosides. Later, the same jays were presented with monarchs fed on milkweed, which they unhesitatingly accepted, only to be rewarded with "a period of severe vomiting."[56] Brower's study used many of the standard biochemical techniques to analyze the chemical contents of milkweed and of monarchs fed on milkweed. But the degree to which he employed animal experimentation was unusual in coevolutionary studies. Moreover, he also exploited pharmacological techniques far more than most coevolutionists, using assays developed for the detection of digitalis, "including guinea-pig ileum and suspended frog heart

---

[54] Brower was first mentioned in Chapter 3. He was one of the American scientists who visited Oxford when Feeny was a student and influenced his ideas about coevolution.
[55] Lincoln P. Brower, "Plant Poisons in a Terrestrial Food Chain and Implications for Mimicry Theory," in *Biochemical Coevolution: Proceedings of the Twenty-Ninth Annual Biology Colloquium, April 26-27, 1968*, ed. Kenton L. Chambers (Corvallis: Oregon State University Press, 1970), 70.
[56] Ibid., 73.

infusions, lethal dose determinations for cats via the intravenous route, and emetic dosages for starlings and pigeons via the oral route," in order to confirm the presence of toxic and emetic levels of cardiac glycosides in extracts taken from monarchs raised on milkweed.[57] And this "remarkable example of coevolution" was made even more interesting by the presence of mimicry amongst species of butterflies that had adapted to feeding on other, non-toxic food sources.[58] An additional level of adaptation, which Brower tested with additional feeding experiments,[59] only strengthened further the notion of adaptive chemical defense. Even if the monarch had overcome the defenses of the milkweed, the potency of the defense was verified by its selective value for butterflies. Brower also foreshadowed an important future focus for coevolutionary research, examining the geographical variation in food sources for monarchs along their long migration route, and correlating this variation with variation in the palatability of monarchs themselves. In some areas of North America, monarchs would eat nonpoisonous milkweed, leading Brower to acknowledge, "it is most likely that the palatability heterogeneity of Monarch populations is constantly changing in both space and time."[60] The inherent flexibility of coevolved relationships over both geographical space and ecological and evolutionary time scales would become a critical element of

---

[57] Ibid., 71.
[58] Ibid., 75.
[59] Ibid., 76.
[60] Ibid., 78.

coevolutionary theory in the following decades,[61] a topic that I address in the final chapter of my dissertation.

Brower also invoked the commonly cited theme of ecological damage from agricultural chemicals in his introduction. “The cycling of chemical substances through terrestrial and freshwater ecosystems has attracted much attention in recent years as a result of the ever-increasing use of pesticides,” he wrote. Nonetheless, “[n]otwithstanding this recent dramatic example, the idea that naturally occurring poisons are transferred from plant to herbivores and thence to predators is nearly a decade old.”[62] Like many other coevolutionists, Brower drew a parallel between anthropogenic pesticides and the natural ones produced by plants, a parallel that, like so many other coevolutionary analogies, emphasized the shared function of repelling predators. The biological analogy easily extends into the human realm: antelopes are to poisonous plants as poisonous plants are to human-synthesized pesticides. Thus, in coevolutionary theory, it remained difficult to tell where the boundary between natural chemicals and artificial chemical lay.

By and large, the papers of *Biochemical Coevolution* demonstrate that by the late 1960s, coevolution had become a topic of general interest to evolutionary biologists. The notion that the diversity of life could be explained by the proliferation of such intimately evolved relationships and, moreover, that theoretical bridges could be built so clearly from one kingdom to another, made coevolutionary theory appear a promising

---

[61] John N. Thompson, *The Coevolutionary Process* (Chicago: The University of Chicago Press, 1994).

[62] Brower, "Plant Poisons in a Terrestrial Food Chain and Implications for Mimicry Theory," 69.

explanation for a wide variety of phenomena. It satisfied the evolutionary ecologists' desire to look beyond the physiological details of ecosystems and ask *how* and *why* they had come to be. And it insisted, in part through the use of the evocative language that I analyze in the next section, that both insects and plants were active ecological participants, and both possessed the evolutionary agency to shift the dynamics of their mutual interactions.

The Language of Coevolutionary Studies

In 1971, Whittaker and Feeny published a collaborative paper in *Science* that brought together their respective botanical and entomological knowledge, as well as Feeny's molecular expertise.[63] In this paper, "Allelochemics: Chemical Interactions between Species," they gave a detailed account of many of the most common classes of secondary plant compounds, including their botanical distribution, chemical properties, and molecular structure, describing adaptive scenarios and positing evolutionary hypotheses for the emergence of these plant compounds.[64] Ecologically, Whittaker and Feeny described the "natural environment" as a "maze of chemical stimuli, unappreciated by man but of vital importance for the survival of many plant and animal species."[65] But how did this maze arise? Reflecting the same moderate tone exhibited in Whittaker's presentation for the IBP conference, they described the process of random genetic

---

[63] This paper was jointly written—Whittaker and Feeny each took responsibility for the sections that were most relevant to their respective areas of expertise (Feeny. Interview by author. Digital Audio Recording. Ithaca, NY, 12 November 2007.).
[64] Whittaker and Feeny, "Allelochemics: Chemical Interactions between Species."
[65] Ibid.: 760.

change, followed by natural selection that led to the evolution of plants' "chemical defenses":

> The metabolism of a plant species produces wastes and some chemical accidents, substances that may result from mutation and are not part of normal metabolism, but are not so deleterious that the genes determining them are promptly selected out of the gene pool. Some of these wastes and accidents are unpalatable to the animals consuming the plants. Selection by reduced consumption of more effectively protected individuals of the plant species increases the concentration of these substances in the tissues of descendent individuals.[66]

Alongside this measured, standard account of evolutionary change by natural selection, however, Whittaker and Feeny also invoked common martial metaphors, describing the process of reciprocal adaptation between organisms as a series of "biochemical combats" happening over evolutionary time.[67] Moreover, they were among the first to use the term "arms race" to describe this process. While some insects use enzymes called mixed-function oxidases to break down plant-produced toxins, once species of chrysanthemum has evolved an inhibitor of these oxidases, a compound that represented, to their minds, "a further turn to the evolutionary arms race between plants and insect."[68]

Metaphors and analogies are particularly productive as conduits for communication between different disciplinary traditions.[69] This was certainly the case in

---

[66] Ibid.: 767.
[67] Ibid.: 763.
[68] Ibid.: 759. Berenbaum claimed, in interview, that they were the first to use the "coevolutionary arms race" (Berenbaum. Interview by author. Digital audio recording. Champaign-Urbana, IL, 19 April 2007.).
[69] James J. Bono, "Science, Discourse, and Literature: The Role/Rule of Metaphor in Science," in *Literature and Science: Theory & Practice*, ed. Stuart Peterfreund (Boston: Northeastern University Press, 1990); Mary B. Hesse, *Revolutions and Reconstructions in the Philosophy of Science* (Bloomington: Indiana University Press, 1980); ———,

coevolutionary studies, where classic examples communication between entomology and botany include Ehrlich's collaboration with Raven,[70] and Whittaker and Feeny's co-authored paper. In these cases, and in the conferences that brought together many different scientists to discuss coevolution, metaphors and analogies served as a medium by which botanical and zoological approaches could be bridged, creating linkages that—reciprocally—bolstered the strength of the metaphors themselves and of adaptive evolutionary theory.[71]

But even as a metaphor helps build connections, it also "selects, emphasizes, suppresses, and organizes" elements on both sides of the metaphorical relationship,

---

"Models, Metaphors and Truth," in *Knowledge and Language: Metaphor and Knowledge*, ed. F.R. and J.J.A. Mooij Ankersmit (Dordrecht: Kluwer Academic Publishers, 1993); Karin D. Knorr, "The Scientist as Analogical Reasoner: A Critique of the Metaphor Theory of Innovation," in *The Social Process of Scientific Investigation*, ed. Roger and Richard Whitley Krohn (Dordrecht: Kluwer Academic Publishers, 1980); Sabine Maasen, Everett Mendelsohn, and Peter Weingart, "Metaphors: Is There a Bridge over Troubled Waters?," in *Biology as Society, Society as Biology: Metaphors*, ed. Sabine Maasen, Everett Mendelsohn, and Peter Weingart, *Sociology of the Sciences* (Dordrecht: Kluwer Academic Publishers, 1995); Sabine Maasen, "Who Is Afraid of Metaphors?," in *Biology as Society, Society as Biology: Metaphors*, ed. Sabine Maasen, Everett Mendelsohn, and Peter Weingart, *Sociology of the Sciences* (Dordrecht: Kluwer Academic Publishers, 1995); Sabine and Peter Weingart Maasen, *Metaphors and the Dynamics of Knowledge* (London: Routledge, 2000).

[70] Ehrlich and Raven, "Butterflies and Plants: A Study in Coevolution." Ehrlich also collaborated with and another California botanist, Dennis Breedlove, on a paper researching the effects of butterfly predation on populations of lupine discussed in the next section (Breedlove and Ehrlich, "Coevolution: Patterns of Legume Predation by a Lycaenid Butterfly."). Potent martial language featured particularly strongly in the collaboration between Ehlrich and Raven. In the Scientific American piece citied in Chapter Two, in particular, they made heavy use of "battle-hardened plants" and "chemical warfare" [Paul R. Ehrlich and Peter H. Raven, "Butterflies and Plants," *Scientific American* 216, no. 6 (1967).].

[71] As Lily Kay argues, when metaphors create new connections, their "potency" may be "enhanced through their disciplinary linkages and social valences" [Lily E. Kay, *Who Wrote the Book of Life? A History of the Genetic Code*, ed. Timothy Lenoir and Hans Ulrich Gumbrecht, Writing Science (Stanford: Stanford University Press, 2000).].

influencing the future direction of research.[72] Evelyn Fox Keller's analysis of "gene action" illuminates how notions about how biological entities work can influence the direction and emphasis of scientific research.[73] In Keller's account of T.H. Morgan's genetics lab, she recounts how the Morgan lab "did more than develop the techniques and practices of genetics" with their work on *Drosophila*, "they also forged a way of talking" that gave genes "both ontological and temporal priority." The gene was granted biological *agency* that relegated the cytoplasm to the role of "by-product." Thus, the "conceptual framework" advanced by Morgan served to limit the types of questions, explanations, and organisms thought valid within the discipline of genetics. According to Keller, this framework also elided the developmental processes that link genotype to phenotype, effectively diminishing the disciplinary influence of embryology.[74] This "discourse of gene action," then, was both practical and political, making Morgan's work quite successful even as it altered the terms of scientific communication across disciplinary lines.

In the remainder of this chapter, I will take a look at a conflict that arose between coevolutionists like Ehrlich and Janzen, both trained as entomologists, and UC-Santa Barbara botanist and allelopathy proponent Cornelius Muller. While this was a conflict over evolutionary processes, the language of the conflict was equally important. The

---

[72] Max Black, *Models and Metaphors: Studies in Language and Philosophy* (Ithaca: Cornell University Press, 1962).
[73] Evelyn Fox Keller, *Refiguring Life: Metaphors of Twentieth-Century Biology* (New York: Columbia University Press, 1995); ———, *Making Sense of Life: Explaining Biological Development with Models, Metaphors, and Machines* (Cambridge: Harvard University Press, 2002).
[74] Keller, *Refiguring Life: Metaphors of Twentieth-Century Biology*.

tropes of “waste” and “warfare” came to represent, respectively, Muller’s conception of allelopathy and the coevolutionists’ conception of insect-plant interactions. More than mere signposts for theoretical positions, or explanations intended for a general audience, I argue here that such supposed "figures of speech" played an important role in the genesis of coevolutionary studies, giving the “conceptual framework” of coevolutionary theory, in Keller’s words, “both ontological and temporal priority.”

Much scholarship in the field of science studies supports the contention that analogical and metaphorical reasoning can serve as generators of scientific change. Rhetorician Mary Hesse has suggested that all scientific theories function as “metaphorical redescriptions” of natural phenomena.[75] Likewise, sociologist of science Karin Knorr Cetina argues that metaphor is only the most extreme example of the analogical reasoning that scientists use all of the time, and that research is often oriented by the “opportunities” that such analogical reasoning provides.[76] After all, evolutionary biology has long been rife with such “opportunities,” as Darwin’s use of analogical reasoning[77] and Wright’s “adaptive landscapes”[78] demonstrate. In a historiographical example directly relevant to this project, historian of biology Nicholas Rasmussen argues that plant physiologists’ conception of plant hormones before World War II constrained

---

[75] Hesse, *Revolutions and Reconstructions in the Philosophy of Science*.

[76] Knorr, "The Scientist as Analogical Reasoner: A Critique of the Metaphor Theory of Innovation."

[77] Gillian Beer, *Darwin's Plots: Evolutionary Narrative in Darwin, George Eliot and Nineteenth-Century Fiction, 2nd Ed.* (Cambridge: Cambridge University Press, 2000).

[78] Michael Ruse, "Adaptive Landscapes and Dynamic Equilibrium: The Spencerian Contribution to Twentieth-Century American Evolutionary Biology," in *Darwinian Heresies*, ed. Abigail Lustig, Robert J. Richards, and Michael Ruse (Cambridge: Cambridge University Press, 2004).

their research because plant hormones were solely seen as *stimulants*. This "conceptual obstacle" obscured their potential as herbicides. Not until the wartime effort to boost agricultural production did hormones make the transition from *stimulant* to *toxin*.[79] In this case then, the context of war stimulated a new language and a new way of thinking about plant hormones, which in turn allowed scientists to conceptualize and experiment with those hormones in new ways. Gregg Mitman addresses a similar shift in his paper on ragweed pollen, describing how ragweed came to be seen as a polluting "pollen-factory," with its emissions considered "poison."[80] In both cases, human relationships with nature played a pivotal role in how these natural substances were conceptualized.

In the case of coevolution, analogical reasoning had already been fruitful for coevolutionary biologists. Janzen, in particular, had built analogical bridges between plant secondary compounds and populations of ants in the construction of his first adaptive argument. And the literal truth of these analogies (for, again, he insisted upon the word *analogy*, rather than metaphor) was not in doubt for him. Even the literal truth of the arms race analogy, with all its Cold War connotations, was not in doubt. To Janzen's mind, "coevolution is like a military escalation between Russia and the United States…I don't care who's interacting with who. I'm focused on the interaction...And the military system has a lot of active things that you can analogize with. Because, what is it? It's competition for resources. That's what military is, it's I get it or you get it…the

---

[79] Nicolas Rasmussen, "Plant Hormones in War and Peace: Science, Industry, and Government in the Development of Herbicides in 1940s America," *Isis* 92, no. 2 (2001).
[80] Gregg Mitman, "When Pollen Became Poison: A Cultural Geography of Ragweed," in *The Moral Authority of Nature*, ed. Lorraine and Fernando Vidal Daston (Chicago: The University of Chicago Press, 2004).

world is full of that kind of competition."[81] Similarly, Feeny asserted that the prevalence of martial metaphors in coevolutionary studies was "not surprising—because it's war out there," and "nature is vicious." "What about all of the natural pesticides? We eat them all of the time. You get this worldview of a peaceful and harmonious planet until we come along and mess it all up. We have—but other species would make a mess if they could."[82] In other words, these analogies were not merely vivid figures of speech. To coevolutionists, they represented a critical aspect of interactions in nature, the natural world as it truly *is*. Environmental historian Edmund Russell has thoroughly demonstrated that the development and application of synthetic organic insecticides is indelibly linked, in ideology and practice, to the development of modern chemical warfare between human societies.[83] Here I exploit this linkage to show how the ideology and practices of such molecular technology proceeded to permeate the development of late-20th century evolutionary theory.

---

[81] Feeny. Interview by author. Digital Audio Recording. Ithaca, NY, 12 November 2007.

[82] Ibid. Feeny's student May Berenbaum, an important coevolutionary biologist who I will introduce in Chapter 5, likewise states that the language of the arms race was "completely appropriate." It was, after all, "the middle of the Cold War" (Berenbaum. Interview by author. Digital audio recording. Champaign-Urbana, IL, 19 April 2007.). Berenbaum coauthored a paper in 1981 with her graduate advisor Feeny, using this very metaphor in the title, "Toxicity of Angular Furanocoumarins to Swallowtail Butterflies: Escalation in a Coevolutionary Arms Race?" [May Berenbaum and Paul Feeny, "Toxicity of Angular Furanocoumarins to Swallowtail Butterflies: Escalation in a Ceovolutionary Arms Race?," *Science* 212 (1981).].

[83] Edmund Russell, *War and Nature: Fighting Humans and Insects with Chemicals from World War I to Silent Spring* (Cambridge: Cambridge University Press, 2001).

It's important to note that while metaphors of warfare have been an important part of evolutionary biology since Darwin's time,[84] the language of insecticide use and pest control was by far the most important trope in the development of coevolutionary studies. Human society had sloppily polluted the environment with such chemicals. Nevertheless, the language of insecticides and the molecular model of *highly specialized* "chemical defense" that characterized the "warfare" of coevolutionary theory implied a level technological control and reciprocal calibration that set it apart from the classic Victorian model of "[n]ature, red in tooth and claw."[85] The coevolutionary arms race could amount to a stalemate or a continuing series of reciprocally responsive adjustments. In fact, in the words of Whittaker and Feeny, "It is not simply true that nature is red in tooth and claw." Not only are the "means of antagonism between animals…more varied than carnage," but the evolution can just as easily result in "differentiation toward the reduction of competition important."[86] The classical ecological notion of "balance" reemerges here,[87] defined (in the case of plants, for example) as a highly "sensitive"

---

[84] Beer, *Darwin's Plots: Evolutionary Narrative in Darwin, George Eliot and Nineteenth-Century Fiction, 2nd Ed*; Ruse, "Adaptive Landscapes and Dynamic Equilibrium: The Spencerian Contribution to Twentieth-Century American Evolutionary Biology."

[85] Alfred Lord Tennyson, *In Memoriam A. H. H.*, 1850. Michael Ruse, *The Darwinian Revolution: Science Red in Tooth and Claw, 2nd Ed.* (Chicago: University of Chicago Press, 1999).

[86] Whittaker and Feeny, "Allelochemics: Chemical Interactions between Species," 757.

[87] For a general overview of this concept throughout history, see the following paper (by an ecologist): Frank N. Egerton, "Changing Concepts of the Balance of Nature," *Quarterly Review of Biology* 48 (1973).

balance between the metabolic costs of producing toxic defenses and the selective effects of insect predation.[88]

In paying close attention to language of coevolutionary research, then, I am not just examining how scientists communicated with each other or promoted their ideas (though they certainly did both of these things). I am examining how, through the use of language, and particularly analogies, coevolutionists shaped how biologists see the world of interspecific interactions, transforming picky insects and passive plants into partners and adversaries engaged in a coevolutionary, biochemical "arms race." Equally important was the transformation of plant secondary compounds from passive "wastes" or functionless "by-products" to active adaptations for chemical warfare with insects. This was not an easy transformation, as I discuss below, because it created tensions with scientists like Muller who saw the interactions of plants with animals to be less important than the excretion of toxic "wastes." But for entomologists in particular, the notion of relegating potent biologically active molecules to the category of passive wastes or by-products ran counter to the mounting power and prevalence of molecular analysis and the "molecularization" that had been a part of insect physiology and economic entomology since the time of Fraenkel.

Language as a point of contention

In November of 1968, Ehrlich and botanist Dennis Breedlove coauthored a new paper on butterfly food plants. They specifically singled Muller out as an ecologist who

---

[88] Whittaker and Feeny, "Allelochemics: Chemical Interactions between Species," 763 & 768.

denied the adaptive value of plant toxins.[89] Muller was already well aware that his view of secondary compounds diverged from that of Ehrlich and other coevolutionary biologists. In 1967, when Chambers recruited him to present at the upcoming 29th Annual Biology Colloquium in Corvallis, Muller accepted, acknowledging that his perspective was likely to be quite different from that of the other conference participants."[90] Muller's paper, which directly follows Ehrlich's in *Biochemical Coevolution*, tested the hypothesis of allelopathy in the soft chaparral communities of the Santa Ynez Valley, near Santa Barbara. He attempted to explain an arresting pattern of growth in theses communities, where the chaparral shrubs grow in concentrated stands, each bordered by a distinctive "bare zone," devoid of vegetation. Adjacent to the bare zone is a "zone of inhibition," where vegetation grows sparsely, which gradually gives way to flourishing, uninhibited grasses.[91]

In this paper, Muller studied a toxin released by the chaparral, focusing exclusively on structure of the plant community. In closing, he remarked, "The omission here of discourse on animal participation does not reflect lack of consideration…Rather it is likely that each of these processes will be found to function in both groups [i.e., animals and plants] and that most of them operate also between groups.[92]

---

[89] D.E. Breedlove and P.R. Ehrlich, "Plant-Herbivore Coevolution: Lupines and Lycaenids," *Science* 162 (1968).

[90] Letter from C.H. Muller to Kenton Chambers, Cornelius H. Muller Collection, CCBER, UCSB.

[91] Muller, "The Role of Allelopathy in the Evolution of Vegetation."

[92] Ibid., 29.

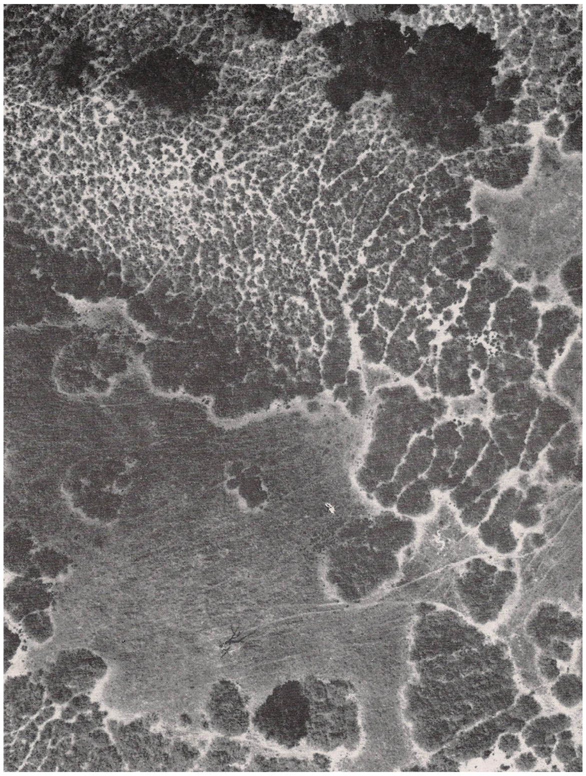

Figure 4: This aerial photo of chaparral was featured on the cover of *Science* when Muller published his research in 1968.[93] [From Cornelius H. Muller, "Volatile Growth Inhibitors Produced by Aromatic Shrubs." Science 143 (1964): 471-473. Reprinted with permission from AAAS.]

To coevolutionists, who insisted that any study of an ecological community was not complete unless it considered both animals and plants, Muller's concluding generalization would have seemed quite weak. And his further assertions that plant secondary compounds were "primarily" wastes, that their most biologically important feature was their excretion as useless by-products of metabolism, drew the ire of biologists like Ehrlich and Breedlove, who saw plant secondary compounds as *primarily* defenses, that is, adaptively evolved characters of plants that exist today solely because of the benefit they convey to plants during natural selection.

---

[93] Cornelius H. Muller, "Volatile Growth Inhibitors Produced by Aromatic Shrubs," *Science* 143 (1964).

Toxic compounds produced by plants have been understood in various ways throughout the past century. Because phytotoxins are considered *secondary* compounds, meaning that they are not directly involved in primary metabolic processes, it was easy to accept, throughout the early 20th century, that these compounds were metabolic wastes, by-products serving no biological function. While some naturalists periodically suggested their defensive function,[94] most chemists and botanists regarded their presences in plants a mystery, "never satisfactorily explained."[95] Agricultural practices, on the other hand, forced farmers and agronomists to take toxic secondary compounds far more seriously—they were poisons: sometimes useful, as when they were isolated and used as insecticides like pyrethrin; and other times destructive, as when they accumulated in the soil, gradually decreasing crop yield or choking growth entirely. In the 1930s, the term *allelopathy* was coined to describe this latter type of biochemical interaction between plants.[96] But documenting the phenomenon in crops proved far easier than in diverse, uncontrolled natural populations. Consequently, allelopathy was long seen as an artifact of agricultural practice and treated with skepticism by many ecologists, including

---

[94] Ernst Stahl, *Pflanzen Und Schnecken : Eine Biologische Studie Über Die Schutzmittel Der Pflanzen Gegen Schneckenfrass* (Jena: G. Fischer, 1888); E. Verschaffelt, "The Cause Determining the Selection of Food in Some Herbivorous Insects," *Proceedings of the Royal Academy, Amsterdam* 13 (1910).

[95] Gottfried S. Fraenkel, "The Raison D'être of Secondary Plant Substances," *Science* 129 (1959): 1466.

[96] Richard W. Halsey, "In Search of Allelopathy: An Eco-Historical View of the Investigation of Chemical Inhibition in California Coastal Sage Scrub and Chamise Chaparral," *Journal of the Torrey Botanical Society* 131 (2004): 343; Hans Molisch, *Der Einfluss Einer Pflanze Auf Die Andere, Allelopathie (the Influence of One Plant on Another, Allelopathy* (Jena: Verlag von Gustav Fischer, 1937).

Muller himself.[97] But sometime in the late 1950s, as Muller recalled, he received a "well-deserved jolt" from an undergraduate in a field course, who drew his attention to the bare zone around stands of chaparral, and asked if it might be allelopathic.[98] This conspicuous pattern galvanized Muller, who began his study of chaparral in 1961.[99]

For coevolutionists, who insisted on the adaptive value of plants compounds, the notion that plants leached a toxic waste, a by-product of other metabolic processes, into the soil, which then *just happened* to inhibit the growth of other plants, seemed the epitome of non-evolutionary thinking. In fact, to them, the idea represented the classic misperception of plants, cited at the beginning of this chapter, that they are "passive and benign"[100] and, in Ehrlich's words, "just sit[ting] around defenseless, waiting to be eaten!"[101] As in Rasmussen's historical account of plant hormones wartime, certain "conceptual obstacles" seem to have prevented some biologists from regarding plants as active and agentive in their environments. These obstacles were theoretical and practical, and also—inextricably—disciplinary. Janzen had cause to remark upon this, reflecting upon his time as a graduate student, when he moved between the botanists and entomologists of Berkeley. When I asked him how these disciplinary groups reacted to his application of the same evolutionary principles to both plants and animals, he said,

> That's what I was dinged for at Berkeley. I was told explicitly in the Botany Department at Berkeley, "Dan, you're"—almost word-for-word what you just

---

[97] Muller, "The Role of Chemical Inhibition (Allelopathy) in Vegetational Composition."
[98] Cornelius H. Muller, "This Week's Citation Classic: The Role of Chemical Inhibition (Allelopathy) in Vegetational Composition," *Current Contents* 45 (1982).
[99] Muller, "Volatile Growth Inhibitors Produced by Aromatic Shrubs."
[100] Whittaker, "The Biochemical Ecology of Higher Plants."
[101] Ehrlich, "Coevolution and the Biology of Communities," 3.

> said—"you're inferring about plants from what you know about animals." And I said, "Sure, they're organisms!"…but a lot of it is, again, maintaining guild structure [guild structure among humans, i.e., *disciplines*]. You don't want to recognize that there are analogies with the other guilds.[102]

Thanks to their own long disciplinary history in the "economic" research sector, entomologists faced no "conceptual obstacle" to seeing the adaptive value of secondary compounds. To the contrary, their knowledge of insecticides invited them to consider "the primary role of plant biochemicals as herbivore poisons."[103] Using the powerful analogies of insecticide and chemical warfare, they bridged Kingdom Animalia and Kingdom Plantae, making adaptive arguments relevant to both. And, critically, this transformation of plant chemicals was transferred to the plants themselves—no longer passive, plants could be seen as *defending* themselves from herbivorous attack. This practice of pointing out the evolutionary costs and benefits of plant characters, where they had long been ignored would come to characterize Janzen's career.[104]

---

[102] Daniel H. Janzen. Interview by author. Digital Audio Recording. Philadelphia, PA, 4 December 2007.

[103] Breedlove and Ehrlich, "Plant-Herbivore Coevolution: Lupines and Lycaenids." Here note their use of the word "primary," just as Muller uses the word "primary" to distinguish the biological importance of a phenomenon.

[104] For example, Janzen wrote a lot about seeds. The reproductive costs of producing seeds had long been neglected, according to Janzen, and seeds were considered merely plant "products." Janzen's papers on seeds referred to them as "babies," again using an analogy with animals in order to reinforce the sense that plants are subject to the same selective forces as animals [Daniel H. Janzen, "How Many Babies Do Figs Pay for Babies?," *Biotropica* 11 (1979).]. Another interesting scenario in which Janzen used evolutionary biology to draw connections between plants and animals was in his writing about the nature of the biological "individual," in which he compares dandelions and aphids, writing, "an aphid is the annual dandelion of the insect world" [———, "What Are Dandelions and Aphids?," *The American Naturalist* 111, no. 979 (1977): 588.]. As Janzen wrote in 1977, "All of the contemporarily fashionable ideas about parental investment, optimal parentage, sibling rivalry, etc. all apply to plants as well as to

Nonetheless, as suggested by Janzen's quotation above, botanists did not all react warmly to the assertions of entomologists about plant evolution. Muller, for his part, saw Ehrlich and Breedlove's criticism of his own allelopathic work as a product of "unswerving zoocentrism."[105] Janzen joined forces with Breedlove and Ehrlich in 1969, emphasizing the selective advantage that a "metabolic waste" might confer if it were only "slightly toxic, deterrent, hallucinogenic, [or] distasteful" to an insect predator.[106] Breedlove, Ehrlich, and Janzen were applying neo-Darwinian logic to their subject, arguing, like other coevolutionists, that the metabolically costly compounds conferred a benefit to plants that more than compensated for the energetic expense.

In contrast, Muller asserted, "the toxic compounds of plants involved in allelopathy, as well as in the repulsion of pathogens, insects, and browsing animals, are primarily metabolic wastes." This designation might appear at first to deprive plants of causal agency in their environment. However, in identifying excretion as a primary function, Muller demanded that biologists consider toxins in terms of the plant's own immediate—or, to his mind, *primary*—needs, which reflected physiological function rather than evolutionary history. His comparison of plants and animals further reveals the primacy of physiological mechanisms, as well as the basis for his accusation of "zoocentrism" in the coevolutionists' claims: "Animal bodies have prominent muscular devices by means of which they eject metabolic by-products and avoid autointoxication. Because plants lack any such structures, it had been widely held that they do not

---

animals" [Janzen, "Promising Directions of Study in Tropical Animal-Plant Interactions," 733.].

[105] Daniel H. Janzen and Cornelius H. Muller, "Coevolution," *Science* 165 (1969).

[106] Ibid.

excrete."[107] In other words, in asserting that plants excrete waste, just like animals, Muller felt that he was correcting a misconception based on a zoological bias—a bias that had led biologists to disregard the imperatives of plant life. Like Janzen, Muller used an analogy between animals and plants to support his claim, but his focus on physiology led him to an entirely different conclusion.

Though debates about the "primary" functions of secondary compounds might give the impression that this conflict consisted largely of rhetorical flourishes, Muller's ideas about allelopathy were certainly based upon extensive field experimentation. When he began his alleopathic research in 1961, his first bioassays tested whether the aromatic shrubs of chaparral could actually inhibit the growth of other plants. Particularly toxic, he found, was *Salvia leucophylla*, or purple sage. After tracing the production of a toxin to the leaves of *Salvia*, he suggested that it might be volatile, able to vaporize and easily diffuse outward through the air, since the effects of inhibition were evident as far as ten meters away from the shrub. And, indeed, the germination of grass seeds and the growth of seedlings were both inhibited when they were merely sealed in an enclosed space with crushed sage leaves. Using the first gas chromatograph on the Santa Barbara campus, Muller soon identified a number of volatile, toxic terpenes, which could be collected from the air around *Salvia* both in the lab and in the field.[108] The distinctive geography of chaparral communities, the localization of toxic terpenes in the leaves of *Salvia leucophylla*, and the terpenes' ability to volatilize and travel across space, all supported

---

[107] Muller, "The Role of Allelopathy in the Evolution of Vegetation," 23.

[108] ———, "The Role of Chemical Inhibition (Allelopathy) in Vegetational Composition."

Muller's hypothesis that a toxic chemical gradient generated a corresponding gradient of growth inhibition.

Yet the geography of the community also suggested the possibility of animal influence, a factor that Muller did not immediately discount. Since grazing herbivores take cover from predators under the shrubs, it was logical to assume that they would not travel very far from this cover to feed. The intensity of their feeding in this protected area might account for the formation of the bare zone. In 1965, Muller's group began an investigation of animal activity. First, they placed the seeds of various native grasses in specific points along the gradient extending out from the shrubs. They accounted for the eaten seeds and restocked them at dawn and dusk, in order to distinguish between diurnal herbivores like birds, and nocturnal ones like rodents. They also took advantage of the distinctive geographical zones by building exclosures—cages to exclude herbivores—across the different types of vegetation. They established, as Muller's student Roger del Moral wrote in an unpublished report, that "even in the area fully protected from any grazing, the species are inhibited to about half of normal size. However, they are much larger than herbs immediately adjacent, exposed to full grazing pressure. The implication from this is that grazing accentuates the differences caused by the toxic effects."[109] In other words, grazing was certainly a factor in community structure, but not nearly as strong as factor as allelopathy was thought to be.

---

[109] Roger del Moral, "The Activities of Birds and Rodents in Relation to Vegetation Patterning About *Salvia leucophylla*," 20 May 1966, unpublished paper prepared for the course Zoology 113B, CCBER, UCSB.

But Del Moral's summary of grazing pressure in the bare zone was unpublished and Muller's public statements about the role of animals, such as the conclusion of his paper for *Biochemical Coevolution*, were unsatisfactory to coevolutionary biologists. In October 1970, Muller received a direct challenge Stanford University, where Ehrlich and Raven both still taught: a letter from graduate student Bruce Bartholomew.[110] The attached manuscript, already accepted for publication in *Science*, attempted to refute Muller's conclusions by asking a single narrow question: "whether animal activity alone could account for the bare zone." Bartholomew's methods for detecting animal activity, though simplified, were quite similar to Muller's. Rather than using a mix of native seeds in his feeding experiments, Bartholomew used only non-native millet seeds, detecting diurnal and nocturnal feeding intensity, but not food preferences. He installed exclusion cages similar to the Muller group's. But instead of measuring the height of the various grass species throughout the year, he collected all of the grass within the cage at once and measured its total biomass. Thus, he was unable to distinguish between inhibitory effects on seed germination and growth at different points during the year.[111]

Bartholomew's general results agreed with Muller's: Feeding intensity was significantly higher near the stands of shrubs and in the bare zone. His conclusions, however, were drastically different. Bartholomew, who had not examined the effects of chaparral biochemistry in his study, claimed that animal grazing was strong enough to account—alone—for the bare zone. In his reply to the paper, coauthored with del Moral,

---

[110] Bruce Bartholomew to Cornelius H. Muller, 16 October 1970, C.H. Muller Papers, CCBER, UCSB.

[111] Bruce Bartholomew, "Bare Zone between California Shrub and Grassland Communities: The Role of Animals," *Science* 170 (1970).

Muller characterized Bartholomew's paper as a "'single-factor' explanation of the phenomenon," concluding, "There is no universal solution to a problem with so many variables, and certainly there is no acceptable simplistic one."[112] Hence, one reasonable explanation for the conflict is the complexity of California chaparral. Muller's group considered a variety of interacting factors, finding chemical inhibition to be the strongest and most consistent, while Bartholomew had restricted himself to the study of only one factor.

Privately, Muller blamed Bartholomew's contradictory conclusion on the perspective promoted by the biology program at Stanford. In a letter that I believe he never typed or sent, Muller accused Stanford scientists Raven and Harold Mooney of mistreating Bartholomew, inducing him to "produce a paper that neither of you quite had the nerve to undertake."[113] From this allegation, we understand that Muller viewed the Bartholomew paper as an extension of his continuing conflict with the Stanford group over the origin and function of plant toxins. And, indeed, though Bartholomew began his paper with a single objective, to study the role of animals in the bare zone, he did not hesitate to speculate on the adaptive value of the toxic terpenes of *Salvia leucophylla*, suggesting that these compounds might be repellants, preventing animals from grazing on the chaparral shrubs. In other words, Muller's passive allelopathic excretions had

---

[112] Cornelius H. Muller and Roger Del Moral, "Role of Animals in Suppression of Herbs by Shrubs," *Science* 173 (1971).

[113] Cornelius H. Muller to Peter Raven and Harold Mooney, handwritten and undated, CCBER, UCSB. I am led to believe that this was never sent for two reasons: First, typed copies of Muller's outgoing letters were carefully preserved, yet there is no typed copy of this letter; and, second, a typed letter, addressed only to Raven and dated 8 December 1970, is contained in the same file. This second letter appears to be a second draft, as it includes much of the same phrasing, with a *slightly* less accusatory tone.

become, in Bartholomew's paper, adaptations against herbivory. In attributing both the formation of the bare zone *and* the evolution of plant toxins to the activity of animals, Bartholomew asserted their ecological and evolutionary dominance in the development of California chaparral.

A great deal of space for collaboration existed within coevolutionary studies. After all, coevolutionists, in general, attempted to consider both plants and animals, and Muller himself had attempted to assess the effects of both in the structure of chaparral communities. Whittaker, time and again, gave credit to both coevolutionary and allelopathic theory, believing them to be complementary ways of approaching communities. But in the debate between Muller and coevolutionary biologists, a resolution was difficult to find. In part, this was due to the centrality of figurative language and the importance of analogies to both allelopathy and coevolution. While coevolutionists of all disciplinary backgrounds could rally around "chemical defense" and "natural insecticides," these terms provided an impenetrable barrier to an ecologist who considered plant toxins to be "wastes." Thus the language that had proven so fruitful for coevolutionists excluded Muller's contribution to the understanding of community evolution.

Even these divergent perceptions of secondary compounds might have bee. reconcilable—after all, the evolutionary scenario in which secondary compounds were purported to have arisen originally much resembled Muller's conception of waste excretion. But the critical difference between them lay in the evolutionary history that followed that origin. To coevolutionists, the idea that natural selection for the wastes' defensive value had sustained and further developed these compounds over millennia meant that their adaptive value was of *primary* importance. To Muller, the original physiological value of waste excretion remained of *primary* importance. Allelopathy and coevolutionary theory also diverged in considering the costs of toxin production. To Muller, since these were merely "by-products," they incurred no metabolic costs to the plants. To coevolutionists, however, these were costly "weapons," on par with the energy expenditure required, for instance, to produce food supporting a colony of defensive ants. Therefore, real theoretical differences remained, tied in large part to the difference between a plant physiological perspective and an evolutionary ecological perspective.

But it's also clear that the personal and scientific mingled inextricably in this conflict. In his correspondence with Whittaker, Muller seethed about "Ehrlich and his cronies,"[114] fuming that "no enemy of a plant, be it a member of any kingdom…has the power to wave a magic wand over a plant and impel it to initiate the production of a new chemical compound."[115] The implication that coevolutionists wanted to grant animals a magical evolutionary wand exposes Muller's own sense of vulnerability, an awareness of his own loss of agency in ecology: Coevolutionary theory was on the ascendant, while allelopathy floundered. Whittaker continued to take the moderate approach exhibited by his presentation for the IBP conference, believing that the two perspectives were compatible, but his reply to Muller makes it clear that this debate was more than an

---

[114] Cornelius H. Muller to Robert H. Whittaker, 4 February 1969, C.H. Muller Papers, Cheadle Center for Biodiversity and Ecological Restoration (CCBER), University of California, Santa Barbara (UCSB).

[115] Ibid., 23 January 1969.

isolated squabble between Stanford and Santa Barbara. Though the lines of dispute were not neatly drawn between botanists and zoologists, Whittaker agreed that some ecologists were overeager to promote an animal-centered theory of toxic plant compounds, writing, "I am in contact here with people who might, like Ehrlich, [want] to construct an issue to the effect that secondary substances are not wastes at all; I do not agree."[116] The emerging coevolutionary account of plant toxins gave animals a much greater role in plant evolution, and in granting greater agency to animals, C.H. Muller saw a loss of agency for both plants and plant ecologists. As in Keller's account of "gene action," carefully crafted discourse may grant priority to particular scientific practices, theoretical stances, and disciplines or styles of investigation. Necessarily, the process also disempowers alternative perspectives.[117] Thus, privileging one metaphorical conception over another can create or reinforce boundaries both internal and external to scientific discourse, and generate conflict amongst scientists. The persuasive discourse of coevolution, already generating a large amount of enthusiasm in the late 1960s, promoted the ideas of coevolutionists in a way that left little space for allelopathy.

Conclusion

The year 1968 was clearly a banner year for coevolutionary research and enthusiasm. At the same time, societal concerns about the pollution and anthropogenic

---

[116] Robert H. Whittaker to Cornelius H. Muller, 28 January 1969, C.H. Muller Papers, CCBER, UCSB.

[117] Keller, *Refiguring Life: Metaphors of Twentieth-Century Biology*; ———, *Making Sense of Life: Explaining Biological Development with Models, Metaphors, and Machines*.

environmental damage were coming to a head. In fact, it was also in 1968 that the challenges of global overpopulation became a mainstream concern, with the publication of Ehrlich's *The Population Bomb*.[118] Widespread cultural concern over the spread of synthetic chemicals, particularly insecticides,[119] generated a wave of support for ecological research, including the International Biological Program. While the simultaneous swell of interest in coevolutionary research certainly reflected the growing influence of modern evolutionary theory in ecological research, it also represented a growing interest in understanding how chemicals mediate relationships between organisms. Connections between research on the evolution of natural chemicals and the effects of synthetic chemicals were a product of the history of entomological and insect physiological research, but they also signified a new awareness of humanity's place in the natural environment. From both a cultural vantage point and a scientific vantage point, it became increasingly clear that not only are human not separate from the nature, but we are deeply entrenched in it, equal participants in ecological interactions and evolutionary dynamics.

Thus, in formulating analogies between animals and plants, and between human interactions and nonhuman interactions, coevolutionary biologists were taking part in a larger cultural exercise, working out ideas about ourselves and how we relate to nature. In describing insects and plants locked in warfare, anthropomorphic notions were

---

[118] Paul R. Ehrlich, *The Population Bomb* (New York: Ballantine Books, 1968).
[119] Paolo Palladino, *Entomology, Ecology and Agriculture: The Making of Scientific Careers in North America, 1885-1985* (Amsterdam: Harwood Academic Publishers, 1996); John H. Perkins, *Insects, Experts, and the Insecticide Crisis: The Quest for New Pest Management Strategies* (New York: Plenum Press, 1982).

projected onto these organisms, giving them a new level of agency in their environments. Simultaneously, as I argue in the case of Muller and his conflict with the coevolutionists, the language used by coevolutionists had a way of feeding back upon human social interactions. As in any metaphorical or analogical relationship, the traffic of ideas went both ways. Just as Janzen transgressed supposed boundaries between what animals could do and what plants supposedly could not do, he also transgressed disciplinary boundaries, formulating new ways of thinking and talking about insect-plant interactions that affected the way humans interacted and thought about interactions themselves.

Recent scholarly literature on anthropomorphism interrogates this interchange. In introducing their volume *Thinking With Animals: New Perspectives on Anthropomorphism*, Lorraine Daston and Gregg Mitman write, “When humans imagine animals, we necessarily reimagine ourselves, so these episodes [of anthropomorphic thinking] reveal a great deal about notions of the human.”[120] Plants, by contrast, without the “roaming autonomy movement implies,” do not allow us to so easily analogize across species boundaries.[121] But in the case of coevolutionary theory, the practice of reasoning *adaptively* stretched the boundaries of what Daston and Mitman call “shape-changing across species.”[122] If plants could share selective pressures with animals, they could also share adaptive solutions to those pressures.

---

[120] Lorraine Daston and Gregg Mitman, "Introduction: The How and Why of Thinking with Animals," in *Thinking with Animals: New Perspectives on Anthropomorphism*, ed. Lorraine and Gregg Mitman Daston (New York: Columbia University Press, 2005), 6.
[121] Ibid., 13.
[122] Ibid., 6.

In “thinking with animals” by using analogies of pest control and warfare, coevolutionists helped reconfigure the biological understanding of the evolution of community structure by insisting that both plants and insects must be considered as equally active participants. Their adaptive arguments and metaphors alike asserted, against a series of “conceptual obstacles,” that insects are a strong selective force on plants and, conversely, plants are a strong selective force on insects. Moreover, the practice, theory, and the ideology carried over with the language of pest control, a technological notion of pest control was built into coevolutionary theory. Insects became themselves expert "phytochemists” in order to negotiate the chemical geography of their environment,[123] and plants produced highly specialized, carefully calibrated “natural insecticides.” In this construction of coevolved relationships, ideas about human technology and natural interactions were both reciprocally transformed.

In the final chapter, I expand upon this reciprocal transformation, showing how coevolutionary scientists enthusiastically supported increasingly broad applications of coevolutionary theory both within biology and beyond its bounds, in the broader human culture. At the same time, the same scientists engaged in efforts to reform coevolutionary studies, providing clearer definitions and more critical analyses. Both expansion and reform drove the coevolutionary studies from the 1970s onward, offering new ideas about dynamic change in both ecosystems and human culture.

---

[123] H.F. Van Emden, "Aphids as Phytochemists," in *Phytochemical Ecology*, ed. J.B. Harborne (London: Academic Press, 1972).

Chapter 5

"When is it coevolution?": Expansion and reform in coevolutionary theory from the 1970s onward

In the decade after the many coevolution conferences of 1968, studies of coevolution only proliferated. Attempts to better characterize coevolutionary processes theoretically and to document them experimentally also increased. Many evolutionary ecologists turned a more critical eye on coevolution, which had, to some people's minds, come to represent another instance of the indiscriminate application of adaptationist Neodarwinian theory, a set of "just-so" stories told about the ostensibly infinite capacity of natural selection to generate adaptations perfectly suited to their biological function.[1]

Perhaps even more worrying to coevolutionists like Janzen were attempts to apply coevolutionary theory to an ever-widening array of interactions between organisms. Interest in insect-plant relationships arose originally in response to the observation that particular insects ate particular plants preferentially—even plants that appeared to repel herbivory by most other insects. These closely paired plants and insects suggested a highly specialized relationship. By contrast, other insects seemed to be able to eat a multitude of different plants. Infamous crop pests like the southern armyworm drew attention to this generalized mode of herbivory. These forms of specialism and

---

[1] For an example of this type of critique of evolutionary theory at the time, see: Stephen Jay Gould and Richard C. Lewontin, "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme " *Proceedings of the Royal Society of London, Series B* 205, no. 1161 (1979): 706. For attempts to defend the "adaptionist" logic of coevolutionary accounts, see: J.R.G. Turner, "Adaptation and Evolution in Heliconius: A Defense of Neodarwinism," *Annual Review of Ecology and Systematics* 12 (1981).

generalism, central to the study of plant-insect relationships became, likewise, central to the study of coevolution. Yet, empirically demonstrating specialized or generalized insect-plant interactions, much less understanding their evolutionary history, was far more challenging than observing and recording the plethora of different insect-plant relationships that exist in the natural world. After Ehrlich and Raven's 19764 paper, the tendency to claim coevolution in any given insect-plant pairing quickly overwhelmed the ability of biologists to verify such claims. In 1980, Janzen published a one-page paper in Evolution, entitled "When is it Coevolution?"[2] The paper was a "call for more careful attention to the use of 'coevolution' as word and concept."[3] The "conspicuous misuses" to which Janzen drew attention hinged particularly upon the consequences of historical contingency, rather than evolution. Many species of organisms likely began interacting thanks to patterns of migration or geological changes resulting in the reorganization of ecological communities. "It is commonly assumed that a pair of species whose traits are mutualistically congruent have coevolved," Janzen wrote. Consider the possibility, however, that an animal that migrating into a new habitat "with its dietary preferences already established" may merely be fortunate enough, by chance rather than coevolution, to find a fruit that perfectly suits its tastes, thus becoming a most effective seed-disperser for the plant. No reciprocal evolutionary change has occurred between the species of plant and animal. This type of scenario—of historical contingency, rather than coevolution—could result in any number of intimate interspecies interaction, including parasitism or herbivory. "When this occurs, it is those species that are most exactly

---

[2] Daniel H. Janzen, "When Is It Coevolution?," *Evolution* 34, no. 3 (1980).
[3] Ibid.: 611.

congruent which will appear most coevolved yet are likely to be the least coevolved." Thus, though the enthusiasm that drove biologists to look anywhere everywhere for coevolved relationships between insects and plants had been fruitful for coevolutionary studies, the tendency to *see* coevolved relationships anywhere and everywhere could be, in contrast, damaging to coevolutionary theory. "In summary," Janzen wrote, "I plead for the retention of the usefulness of 'coevolution' by removing it from synonymy of usage with 'interaction,' 'symbiosis,' 'mutualism,' and 'animal-plant interaction.'"[4] Janzen, himself a builder of coevolutionary enthusiasm, demanded a more rigorous, approach to the still-growing field. In other words, he asked biologists to ask more critically, "When is it Coevolution?"

In this chapter, I examine many different ways of answering this question. Two trends persisted within the broad body of "coevolutionary theory" through the 1970s and into the 1980s. One was the expansive, all-encompassing sense that at its most basic level, *most* evolution was coevolution. This notion was so generally compelling that coevolution quickly escaped the confines of scientific discourse and entered the cultural sphere, where it became a tool for explaining and guiding human culture using biological precepts. The second trend is represented by Janzen's critical question above. Even as coevolutionary theory seemed to be expanding, many coevolutionists attempted to rein it in, refining definitions and encouraging a more rigorous approach to hypothesis-testing and data-gathering.

---

[4] Ibid.

In the first half of this chapter I examine how scientific and popular notions about nature and human evolution hybridized, creating new opportunities for coevolutionary biologists to provide lessons for human society based upon coevolutionary theory. Most common was the notion that humans were subject to coevolution just like other organisms. Humans could coevolve with other species, an idea made all the more convincing by the fact that humans had obviously sparked evolution in other species, as in the evolution of insecticide resistance in pest insect populations. But while reciprocal human evolution, in response to evolutionary change in other species, might be genetic, it might also be cultural. Insecticide resistance had arisen in response to the technology of insecticide application, which was a product of human culture. Reciprocal human evolution in response to insecticide resistance would likely be, for better or worse, also a form of cultural evolution. These coevolutionary dynamics meant that humans were, in part, transgressors who polluted the environment with the help of increasingly powerful technologies. At the same time, technology could also be understood as a human adaptation for interaction, and human interaction and influence could be seen as an increasingly pivotal component of multiple coevolutionary systems.

In the second half of this chapter, I examine how coevolutionary theory quickly grew in popularity within the sphere of evolutionary ecology. This growth motivated scientists to build more interdisciplinary connections, showing the broad relevance of coevolutionary theory throughout biology. But it also motivated scientists like Janzen to work at reforming coevolutionary theory, emphasizing the importance of clear definitions, testable hypotheses, and experimental data. Here I will draw attention to the types of analysis and evidence that were brought to bear upon interactions between different species. At stake in these attempts at reform was the scientific vitality of the very concept of coevolution itself. Echoing Janzen's plea of 1980, evolutionary biologists Douglas Futuyma and Montgomery Slatkin wrote in 1983, "Coevolution, too broadly defined becomes equivalent to evolution."[5] If this were the case, what repercussions could it have for the coherence of "coevolutionary theory" and for the field of research that came to be known as "coevolutionary studies"?

Human technology, gene-culture coevolution, and the "gardenification" of nature

Even as coevolutionary theory provided an explanation for chemically mediated relationships between insects and plants in nature, coevolutionists found that humans could not be excluded from these interactions. Human society had already changed the geographical and chemical landscape of nature and, in so doing, provoked evolutionary change, undeniably writing itself into the ecological interactions of communities. Seeing humans as an integral part of coevolved nature had multiple cultural ramifications. The place of humans in nature has long been in flux, subject to multiple scientific and humanistic interpretations. Are humans the children of a benevolent or perhaps vengeful nature? Or are humans the wise stewards of nature, a gift bequeathed to us for both care

---

[5] Douglas J. Futuyma and Montgomery Slatkin, "Introduction," in *Coevolution*, ed. Douglas J. Futuyma and Montgomery Slatkin (Sunderland, MA: Sinauer Associated Inc., 1983), 2.

and subjugation?[6] Finally, in the 1960s, growing awareness of the repercussions of industrial and agricultural pollution suggested, instead, that humans are the destructive enemies of nature. Coevolutionary theory presented one way to formalize and interrogate the quality of the interactions between humans and other organisms, both within the bounds of scientific inquiry and outside those bounds, in the cultural realm.

Coevolutionary scientists found opportunities in both realms to make suggestions about human behavior. These suggestions could be either proscriptive or prescriptive. Below, I first examine the pessimistic, proscriptive mode of understanding human society's coevolved relationship with the rest of nature. Then I investigate the optimistic, prescriptive mode, which appears to have been even more common than the proscriptive mode, despite the immediacy of society's struggles with issues of pollution and habitat destruction. Humanity's technological tools could generate toxins far more potent than plants' secondary compounds, capable of contaminating entire ecosystems and traveling up food chains, with their toxic effects magnified at each level. But these same tools could also be used to generate positive interactions with other species, alleviating destruction and reaffirming humanity's ability to act as participants in, interactors with, or—perhaps, with care—stewards of nature.

In previous chapters I have mentioned the sense, shared by many coevolutionary scientists that the recreational use of plant secondary compounds was tantamount to, in

---

[6] Lorraine Daston and Fernando Vidal, eds., *The Moral Authority of Nature* (Chicago: University of Chicago Press 2004); Carolyn Merchant, *The Death of Nature: Women, Ecology, and the Scientific Revolution* (San Francisco: Harper & Row, 1990).

Feeny's words, "falling into a trap of being poisoned by a plant defense."[7] Closely allied with this conviction was a deep concern with industrial and agricultural chemical pollution: humans were actively using highly active molecular agents, both synthetic and natural, to poison the environment and themselves. No coevolutionary scientist was more vehemently convinced of this danger than R.H. Whittaker. Whittaker identified industrial and agricultural pollution as a form of human "autotoxicity," the term used by ecologists and agronomists to describe plants that harm themselves by leaching high levels of secondary compounds into their own immediate environment. Moreover, the concept of autotoxicity linked pollution to what Whittaker perceived as a scourge of drug use in American youth, a form of autotoxicity that made use of other species' evolved poisons. In both cases, pollution and drug use, humans were losing the "selectional race," falling victim to coevolved enemies, the most powerful of which was our own culture and technology.

In teaching and writing alike, Whittaker explored the effects of human-synthesized chemicals on the environment and society, using the lenses of allelopathy and coevolution to interpret what he believed to be an example of "community retrogression."[8] In a paper prepared for the 1971 meeting of the International Association

---

[7] Paul P. Feeny. Interview by author. Digital audio recording. Ithaca, NY, 12 November 2007. An interesting contrast with this perspective is provided by Ehrlich, who writes that it is amusing to speculate that plants bearing hallucinogens may practice 'chemopsychological warfare' against their enemies!" (Cited in Chapter Two also, Paul R. Ehrlich and Peter H. Raven, "Butterflies and Plants," *Scientific American* 216, no. 6 (1967): 105.).

[8] Whittaker, Robert H. "Community Retrogression and its Measurements," Robert Harding Whittaker Papers (RHW Papers), Cornell University Library, Division of Rare and Manuscript Collections, Ithaca, NY (Cornell DRMC).

for Phytosociology, Whittaker examined just this theme, presenting "Community Retrogression and its Measurement" for a symposium entitled "*Vegetation als anthropoökologisher Gegenstand*" (roughly translated as "Vegetation as anthropogenic-ecological subject").[9] Thus, not only did Whittaker believe that communities were being altered anthropogenically, he also asserted that the change was directional and markedly negative. It may seem self-evident that the destruction wrought by human enterprise deserves this interpretation. But the perturbing effects of environmental damage might just as easily be seen as a disordered chaos. Whittaker intended something far more specific than chaotic destruction when he used the word "retrogression." In implying this negative directionality, he clearly invoked the antithesis of the classical ecological model of succession, which embodied *progress*—from a relatively simple community of mosses and other colonizing plants to a complex community of plants, dominated by mature, long-lived trees.[10] However, Whittaker's conception of natural progress (and regress) was even more complex than this. Much of his career was devoted to studying the process by which ecological communities were assembled in this study he challenged the classical successional notion that community development occurred in a predetermined, progressive manner.[11] Instead, Whittaker's engagement in the debate over allelopathy

---

[9] Translation by Stephanie Diezmann, personal communication, 9 September 2009.

[10] This progressive, organismic view of community composition is classically represented by the ideas of Frederic Clements. On Clements' view and challenges to it, see: Gina Rumore, *A Natural Laboratory, a Nation Monument: Carving out a Place for Science in Glacier Bay, Alaska, 1879-1959, Ph.D. Dissertation* (University of Minnesota, 2009), 206-241.

[11] Whittaker countered the Clementsian paradigm that asserted that succession was analogous to the development of an individual organism or, alternatively, to the

and coevolution had familiarized him with coevolution. Coevolutionary theory suggested that, given the right circumstances, organismal and community evolution could be directional. After all, the "coevolutionary arms race," with its heightening of plants' toxicity and the concomitant heightening of insects' resistance, was a profoundly directional model of evolution.[12] Thus, disruption of a natural community by human toxins could cause something more noteworthy than mere ecological disintegration—it could cause retrogression.

Whittaker's manuscript for "Community Retrogression and its Measurement" focused narrowly on the ways that "industrial civilization" alters natural communities of nonhuman organisms, through the "accumulation of toxic materials…extinction of less tolerant species, [(and compensatory spread, and in some cases evolutionary change, of more tolerant species)].[13] But in other similar manuscripts he directly expressed his despair of and disdain for the "retrogressive" effects that "industrial civilization" had upon the human community itself. In 1970, Whittaker presented a lecture, "The Biosphere: living system and man's arena" for a Cornell course, "Biology and Society." After extensive discussion of the poisons produced by human technology, both agricultural and industrial, Whittaker placed them in the context of the general concept of "The Waste Problem," which he couched in just the terms C.H. Muller would have used

---

phylogenetic history of organisms. See, for example: Whittaker, R.H. "Evolution of Natural Communities," RHW Papers, Cornell DRMC.

[12] Futuyma and Slatkin, "Introduction."This is also a prominent feature of R. Dawkins and J.R. Krebs, "Arms Races between and within Species," *Proceedings of the Royal Society of London, Series B* 205, no. 1161 (1979).

[13] The parenthetical statement quoted here in brackets was originally typed in the manuscript but later crossed out. Whittaker, "Community Retrogression and its Measurement," manuscript, RHW Papers, Cornell DRMC, Ithaca, NY.

to define allelopathy: "All living systems produce wastes and toxins of which they must dispose." And Whittaker's conception of a "living system," was sufficiently broad to include not only human society, but the technological systems of human society. "Man and his industry are a living system," he wrote, "a great if not monstrous system."[14] And like all living systems, Whittaker argued, toxins build up when populations become too high. Here, then, Whittaker demonstrated that he had begun to apply ecological and evolutionary ideas to human society.

Thus far, Whittaker's claims may seem similar to those of many environmentalists and socially engaged ecologists in the 1960s and 1970s, who argued that the global "population explosion" was having detrimental effects upon ecological and human social stability.[15] But in 1971, he saw an opportunity to expand his analysis further and to reach a far larger community than a colloquium audience or a classroom of Cornell students. In Chapter Four, I introduced "Allelochemics: Chemical Interactions between Species," Whittaker and Feeny's collaborative effort in *Science* to unite coevolutionary theory and biochemical data. This paper has since been heavily cited in the coevolutionary literature and is thought to be the first published instance of the "coevolutionary arms race."[16] It also served as a platform for Whittaker to link plant secondary compounds, industrial and agricultural pollution, and recreational drug use, in

---

[14] Whittaker, R.H. "The Biosphere: living system and man's arena," Lecture for course "Biology and Society," Cornell University, 14 September 1970, p.10. RHW Papers, Cornell DRMC.

[15] Ehrlich is one of the most well-known examples of such socially engaged ecologists. See, for example: Paul R. Ehrlich, *The Population Bomb* (New York: Ballantine Books, 1968).

[16] Cited as such in: May Berenbaum. Interview by author. Digital audio recording. Champaign-Urbana, IL, 19 April 2007.

a section of the paper first entitled "Allelochemistry of the Human Community," and later renamed, for publication, "Autotoxicity and Civilization."[17] For Feeny, over the course of an unusually lengthy period of revisions, the addition of this section, particularly with its heavy-handed conservative social critique, came as a surprise. A period of negotiation between the co-authors ensued, and the final, published draft became a considerably tempered version of Whittaker's first draft,[18] the manuscript of which is found in Cornell's archives. The published version still contains references to "the increasing abuse" of intoxicating plant secondary substances and its consequential "contributions to psychological erosion among members of a wealthy and complex civilization," which seems an unusual claim to be found in an oft-cited scientific paper. The assertion of "psychological erosion" seems mild, however, in comparison with the original version, which cited the "alkaloids and other compounds [that] have long been used for their halucinogenic [*sic*] properties, [and] certain mushrooms and hashish [used] for the arousal of the berserker's readiness for murder."[19] Most of these drugs, he pointed out, were plant secondary compounds and "may be thought the plant world's revenge on an animal (or its society) grown arrogant in use of the world and incompetent in self-regulation."[20] Similarly, Whittaker wrote of humanity's "great enterprise in antibiosis,"[21] the application of toxic chemicals to control pest insects and the release of toxic by-

---

[17] Whittaker, R.H. "Autoxicity and Civilization" manuscript, RHW Papers, Cornell DRMC.

[18] Feeny. Interview by author. Digital audio recording. Ithaca, NY, 12 November 2007.

[19] Whittaker, R.H. "Autoxicity and Civilization" manuscript, RHW Papers, Cornell DRMC.

[20] Ibid.: 2.

[21] Ibid.: 2; Whittaker and Feeny, "Allelochemics: Chemical Interactions between Species," 766.

products of industrial processes into the environment. In the published paper, Whittaker concluded, “Civilized man is consequently faced with a phenomenon new in history—progressive toxication of the biosphere. We are cast, like some pathogens and successional species, in the role of an unstable dominant population that can effect its own demise by autotoxicity and degradation of the environment.”[22] Again, then, Whittaker invoked coevolution (in the case of pathogens) and ecological community assembly (in the case of successional species) in an attempt to understand the biochemical predicament that human society and its technological tools had created. In contrast to coevolved biochemical relationships in nature, which were frequently defined in terms of their great adaptive value, humans were in the process of evolving highly maladaptive biochemical relationships. As he wrote elsewhere, “Western man has found a new way to relate to his environment; it is not a strategy but a game that might be likened to chemical Russian roulette.”[23]

In the final version of the 1971 paper, Whittaker excised all remaining references to what he called “cultural self-poisoning,”[24] presumably in response to Feeny’s admonishment. But in other venues he continued to extrapolate ecological and evolutionary theory to human culture. In presenting the “Evolution of Natural Communities” at the 31st Biology Colloquium at Oregon State University in 1971, he relegated his remarks on human communities to a “Coda” at the end of the paper. Again Whittaker wrote of human society as a natural community, which, in its recent extreme

---

[22] Ibid.
[23] Whittaker, R.H. Undated, untitled manuscript, p. 477, RHW Papers, Cornell DRMC.
[24] Whittaker, R.H. “Autoxicity and Civilization” manuscript, p. 3, RHW Papers, Cornell DRMC.

expansion, had grown increasingly unhealthy. But here he focused on the psychological effects of this expansion. Not only did he assert the negative impact of aural and visual pollution, but also he lamented the advent of highly organized social systems, used to manage large populations of humans. Applying his own concepts of ecological niche differentiation to human society, he observed the necessity of "increasing complexity of organization—increasing diversification—and subdivision of corporations and public agencies…[and the] increasingly narrow and diverse specialization of individuals."[25] In the growing complexity of human societal niches, Whittaker did not see prosperity or stability, but a diminishment of human life, a concomitant heightening of the self-indulgent qualities cited above, and an impossibly heavy burden on the organizing principles that held the community together. In other words, to Whittaker's mind, the products of technological sophistication—amongst which were increasingly unmanageable population sizes, and increasingly potent toxins of all kinds—led to societal disintegration. Moreover, this human social and environmental predicament fit neatly within the theoretical framework of ecology and evolutionary biology. "Tragedy too," he wrote, "can be an evolutionary product."[26]

But where Whittaker saw the seeds of social destruction, other coevolutionary scientists were more sanguine. One general perspective on human coevolutionary interactions can be termed "gene-culture coevolution," a term that fits the conceptions of

---

[25] Whittaker, R.H. "Evolution of Natural Communities," p. 11, RHW Papers, Cornell DRMC. On Whittaker's development of the "niche," see: Robert H. and Simon A. Levin Whittaker, ed., *Niche: Theory and Application* (Stroudsberg, Pennsylvania: Dowden, Hutchinson & Ross, Inc., 1975).
[26] Ibid.: 13.

both Ehrlich and Janzen. In this evolutionary model, human culture, including technological application, is subject to coevolution with the genes of humans and of other organisms. Whittaker would have endorsed a form of gene-culture coevolution, but that is where his similarities to Ehrlich and Janzen ended. Both of the latter emphasized the human ability to consciously use technology in *positive* interactions with other organisms. Below, I use Ehrlich's early influence upon counterculture icon Stewart Brand to demonstrate how rapidly the compelling notion of coevolution entered the American cultural vocabulary, as force for positive social and cultural change. Next, I argue that Janzen used coevolutionary theory to formulate a highly interactive model for conservation. In contrast to the proscriptive lessons that Whittaker drew from evolutionary ecological theory, Ehrlich and Janzen both generated culturally persuasive and positively prescriptive lessons.

Throughout the 1970s, Ehrlich became increasingly socially engaged, arguing for the application of ecology and evolutionary biology to aid in heightening agricultural output, conquering insecticide resistance, preserving natural resources, and controlling the ballooning global population.[27] It should already be clear that Ehrlich believed science held the solutions to many societal conundrums. In Chapter Two, I cited his cautionary "Lessons from Coevolution" for the control of agricultural pests with pesticides, which had for so long "proceeded largely as if Charles Darwin had never

---

[27] Anne E. Ehrlich and Paul R. Ehrlich, "Ehrlichs' Guide to the Apocalypse: Food," *The CoEvolution Quarterly* 2 (1974); Ehrlich, *The Population Bomb*; Paul R. Ehrlich, "We're Standing at the Edge of the World," *National Wildlife* October-November (1970); ———, "An Ecologist Standing up among Seated Social Scientists," *The CoEvolution Quarterly* 31 (1981); ———, "Human Natures, Nature Conservation, and Environmental Ethics," *BioScience* 52, no. 1 (2002).

lived."[28] Thus, Ehrlich described the evolution of pesticide resistance as a human failure to evolve culturally, in response to our own "coevolutionary race with our competitors."[29] To Ehrlich, cultural evolution in human society may provoke biological evolution, just as the technological application of agricultural toxins provoked the evolution of insecticide resistance in pest populations. But the human capacity to evolve culturally also offered the possibility of true coevolution: human culture, including human technology, could respond reciprocally to biological evolution. By this model of gene-culture coevolution, human cultural attributes, including wisely applied technologies, were transformed into evolutionary adaptations. And it is from this model that Ehrlich drew his conviction that humans may—with effort and intentionality—evolutionary alter the trajectory of our relationship with the rest of nature.[30]

The work cited immediately above reflects Ehrlich's more recent efforts to share the "lessons" of ecology and evolution. But his earlier writings and his influence upon Stewart Brand, early environmentalist and architect of *The Whole Earth Catalog* in the 1960s,[31] demonstrate that Ehrlich's broader notions about human coevolution had entered the cultural sphere long before he began to write explicitly about cultural evolution. Brand was an undergraduate at Stanford when Ehrlich had only just begun his career

---

[28] Paul R. Ehrlich, *Human Natures: Genes, Culture, and the Human Prospects* (Washington, DC: Island Press, 2000), 281.

[29] Ibid.

[30] Ibid; Ehrlich, "Human Natures, Nature Conservation, and Environmental Ethics."

[31] The Whole Earth Catalog was a compilation of ideas and "tools" to help readers negotiate the natural and technological environments. See: Andrew Kirk, *Counterculture Green: The Whole Earth Catalog and American Environmentalism* (Lawrence: University Press of Kansas, 2007); Fred Turner, *From Counterculture to Cyberculture: Stewart Brand, the Whole Earth Network, and the Rise of Digital Utopianism* (Chicago: University of Chicago Press, 2008).

there. “Assistant Professor Ehrlich supervised my tarantula ‘research’ at Stanford in 1959,” Brand writes, “when the Stanford Biology Department was still mostly molecular biology and an ecologist was hard to find.”[32] But it was not until 1964, with Ehrlich and Raven’s publication of “Butterflies and Plants: A Study in Coevolution,”[33] that Brand gleaned from Ehrlich what he would later call the “founding metaphor” of his magazine *The CoEvolution Quarterly*. In contrast to much of the environmental movement, which fostered a fear of technology as the source of environmental problems, *The CoEvolution Quarterly* portrayed technology as a tool with which humans might live harmoniously with the natural environment, a perspective that Brand seems to have maintained through the present day.[34] Within Brand’s conception, human technology became an adaptation for interaction between humans and other organisms in nature. Just as Janzen argued that the relationship between the acacia and acacia-ants was an evolutionary adaptation for defense, human behaviors and modes of technological interaction with other species could also be adaptations.[35] When *The CoEvolution Quarterly* was first published in 1974, Brand presented a synopsis of Ehrlich and Raven’s 1964 paper within the cover of the magazine, describing the “predator-prey relationship of caterpillars and plants.” In

---

[32] Stewart Brand, "Introduction To: Coevolution and the Biology of Communities," in *News That Stayed News, 1974-1984: Ten Years of the Coevolution Quarterly*, ed. Art Kleiner and Stewart Brand (San Francisco: North Point Press, 1986).

[33] Paul R. Ehrlich and Peter H. Raven, "Butterflies and Plants: A Study in Coevolution," *Evolution* 18, no. 4 (1964).

[34] John Tierney, "An Early Environmentist, Embracing New 'Heresies'," *New York Times*, 27 February 2007.

[35] A concept that some evolutionary biologists came to call the “extended phenotype,” [see, for example: Richard Dawkins, *The Selfish Gene* (Oxford: Oxford University Press, 1976); Richard Dawkins and Daniel Dennett, *The Extended Phenotype: The Long Reach of the Gene* (Oxford: Oxford University Press, 1999).], in that some adaptive elements of the phenotype are not directly “coded” for in the genotype.

coevolving, “the eaters and the eaten progressively evolved in close response to each other.” But, as Brand emphasized, coevolutionary theory focuses on the interaction, the space between the organisms, rather than the organisms themselves: “What evolved really was the relationship, stably dynamic, unpredictable and sure.” Below, in a segment he titled “A Coevolutionary Game,” Brand outlined Janzen’s research on acacia-ants and Browers work on monarch butterflies and milkweed. “So long as everyone gets some victory and some defeat,” he concluded with an egalitarian moral from nature, “the game never stops.”[36]

In christening his new magazine about human technology and nature with the word “coevolution,” Brand implied that humans too could achieve a “stably dynamic” relationship with the rest of nature. Brand eschewed the distinction between natural and artificial, or natural and human, which other environmentalists embraced when they emphasized, in his words, “preserving the ecology.” For this phrase, of *preservation*, “suggests something quite perfect—static, knowable, oriented backward, unwelcoming to human foolishness…unreal.” In contrast, by Brand’s estimation, ecology must consider the “whole system.” Coevolutionary theory, even better than mere ecology, represented to Brand the “whole system in TIME.” In other words, Brand had integrated the deeply dynamic change implicit in the process of coevolution, and its emphasis on interaction, into his own philosophy of human betterment and environmental protection. To Brand, coevolutionary theory applied as much to humans as to any other species. Moreover, because of the evolutionary capacity of human culture—and especially technology—

---

[36] Stewart Brand, ""Coevolution"," *The CoEvolution Quarterly* 2 (1974).

coevolutionary theory also suggested the importance of "systematic self-education which feeds on constant imperfection. We coevolved watchers and meddlers are not left out of it."[37] Contrary to Whittaker's conception, then, human technology did not have to function toxically. Instead, as a coevolved part of nature, it could represent a force for wise, targeted manipulation of nature.

Ehrlich's own contributions to *The CoEvolution Quarterly* demonstrate just this principle. While Ehrlich wrote several articles for the magazine,[38] a letter published in 1978 eloquently illustrates his positive attitude toward the manipulation of nature with technology. In the midst of concern over the possible health and environmental dangers of recombinant DNA, Ehrlich wrote as "a professional biologist"—stepping in, in other words, as the voice of scientific reason—supporting the "scientists involved," who had "behaved admirably," and arguing for the continuation of recombinant DNA research, despite the resistance of notable environmentalist and public interests groups.[39] Not only was Ehrlich convinced that the risks were low, but he was particularly irritated and "depressed" by the rhetoric that implied that recombinant DNA was a bad idea because it constituted "meddling with evolution." "*Homo sapiens* has been meddling with evolution in many ways and for a long time," Ehrlich responded. "We started in a big way when we domesticated animals and plants. We continue every time we alter the

---

[37] Ibid.

[38] For example: Ehrlich and Ehrlich, "Ehrlichs' Guide to the Apocalypse: Food."; Ehrlich, "An Ecologist Standing up among Seated Social Scientists."

[39] Paul R. Ehrlich, "Recombinant DNA, Paul Ehrlich, and Friends of the Earth," *The CoEvolution Quarterly* 17 (1978): 24.

environment."[40] And based upon "evidence that bacterial species have been swapping DNA among themselves for a very long time," he contended that recombinant DNA techniques could hardly constitute the "evolutionarily novel experiments" that the naysayers claimed. In other words: manipulation of nature is itself natural—even technological manipulation. To emphasize the positive value of this particular technology, Brand introduced Ehrlich's letter, describing the possible environmental *benefits* of this new technology. One application of recombinant DNA could allow the Environmental Protection Agency to test the carcinogenicity of new chemicals for a fraction of the current cost and in a fraction of the current testing time.[41] Not only was technological manipulation of nature itself quite natural, but it also allowed humans to care for themselves and other organisms more effectively.

Like Ehrlich, Janzen also began applying evolutionary and ecological theory to human social and cultural challenges early in his career. As I have recounted in past chapters, he saw coevolutionary theory as an explanatory framework for understanding human warfare and cultural conflict. However, like Ehrlich, Janzen also came to see coevolutionary theory as a solution to human problems, and, by the 1980s, he began to incorporate it into his own distinctive ethos of ecological preservation and restoration. This philosophy of conservation focused on interactions as *the* most important aspect of ecological communities—including the interactions of humans with other organisms. In a 1977 paper for the *Annals of the Missouri Botanical Garden*, Janzen emphasized the importance of creating "cultural rules for the preservation of interactions," instead of

---

[40] Ibid.: 25.
[41] Ibid.: 24.

rules for “the preservation of participants.”[42] Here the importance of interactions to both the basic science and the application of coevolutionary studies becomes abundantly clear: Interactions between all kinds of organisms are central to the understanding and conservation of functioning ecosystems.

In 1984, Janzen won the Royal Swedish Academy of Sciences’ Crafoord Prize for his work in coevolution, an honor that he commemorated by presenting a lecture entitled “The most coevolutionary animal of the them all.”[43] And the “most coevolutionary animal,” Janzen claimed, is the human. Like Ehrlich, Janzen saw the cultural practices and technological tools of domestication as evolved adaptations for interaction. Just as and ant was an extension of the acacia’s evolutionary repertoire, humans “have quite literally captured the genomes of hundreds of species of plants and animals, cleared the world of many of their competitors and consumers, and put them to work making products.”[44]

But, as Janzen was quick to point out, despite this suite of useful interactions and the evolutionary history that we share with our coevolutionary partners, our behavior toward the environment has proceeded to destroy increasing numbers of interspecific interactions. The extension of coevolutionary theory to include human “coevolution with our agricultural animals and plants” is hardly surprising, considering Janzen’s use of

---

[42] Daniel H. Janzen, "Promising Directions of Study in Tropical Animal-Plant Interactions," *Annals of the Missouri Botanical Garden* 64, no. 4 (1977): 706.

[43] See http://www.crafoordprize.se for more information; Janzen, Daniel H. “The most coevolutionary animal of them all,” Lecture given upon receipt of the 1984 Crafoord Prize. Text available at: http://fusion.sas.upenn.edu/caterpillar/index.php?action=retrieve&article=Janzen,1984Crafoord.pdf. Accessed on 9 September 2009.

[44] Ibid.:16.

evolutionary analogies to understand adaptation across different species and even different kingdoms of organisms. But it might seem an unlikely foundation for a conservation philosophy. Nonetheless, Janzen, like Ehrlich, saw intentional intervention on the part of humans as a form of cultural evolution that could respond reciprocally to biological change; i.e., gene-culture coevolution. "The simple question is, do we come up with a new [cultural] program [for interacting with other species], or do we follow tradition and let a consequence select for a new program?" Janzen's clear implication was that humans must steer our own cultural evolutionary trajectory.[45]

Over time, Janzen more fully developed his notion of the coevolved human by asserting that the human genome could "contain" thousands of wild species. "Why can't the wild tropical species be left 'out in the wild' to fend for themselves?" Janzen would ask in 1998. "Because the wild is at humanity's mercy. Humanity now owns life on earth," he answered.[46] In my interview with Ehrlich, he told me that anthropogenic effects are an unavoidable part of all ecological research because there is no place on earth untouched by humans besides, perhaps, the very depths of the Marianas Trench.[47] Likewise, Janzen asserted that "there is no footprint-free world."[48] Brand suggested, similarly, that the idea of a nature untouched and unresponsive to human action was "unreal."[49] In other words, incorporating the dynamically interactive theory of

---

[45] Ibid.:18.

[46] Daniel H. Janzen, "Gardenification of Wildland Nature and the Human Footprint," *Science* 279, no. 5355 (1998): 1312.

[47] Daniel H. Janzen. Interview by author. Digital Audio Recording. Philadelphia, PA, 4 December 2007.

[48] Ibid.

[49] Brand, ""Coevolution"."

coevolution into a philosophy of human cultural interaction and environmentalism required full acceptance of the idea that we humans have written ourselves completely into nature that the human role as integral *interactors* must be acknowledged not only in ecological and evolutionary study of nature, but also in efforts to protect nature. From this basis, Janzen developed the notion of the "gardenification" of nature, in which the preservation of nature necessarily implies active human intervention.[50] According to Janzen, only "[b]y recognizing and relabeling wildland nature as a garden," and by laboring to provide "all of the traits that we have long bestowed on a garden—care, planning, investment, zoning, insurance, fine-tuning, research, and premeditated harvest," can nature be preserved.[51]

Not only is the "gardenification" of nature predicated on a model of coevolutionary change between interacting species, but it is also clearly a method of intervening—technologically—in the operations of nature. In essence, nature is redefined as the process and product of organismal interactions, whether those interactions are achieved by behavioral, biochemical, technological, or any other means. As with much of coevolutionary theory, then, the boundaries are subverted between what we might otherwise perceive as distinctly *natural* or *artificial*.

For many coevolutionists, the broad application of coevolutionary theory to the global environmental cause seems a step in the right direction. May Berenbaum, a student of Feeny's and a prominent coevolutionary researcher whose work will be

---

[50] Janzen, "Gardenification of Wildland Nature and the Human Footprint."; Daniel H. Janzen, "Gardenification of Tropical Conserved Wildlands: Multitasking, Multicropping, and Multiusers," *Proceedings of the National Academy of Science* 96, no. 11 (1999).

[51] Janzen, "Gardenification of Wildland Nature and the Human Footprint," 1312.

discussed below, told me that she was “happy to the see the word [coevolution]” in such wide circulation. Most critically, “it’s a recognition of reciprocity. To use the word coevolution is an explicit recognition that interactions are somehow different from living things in isolation.”[52] For Ehrlich, this outcome must certainly be gratifying, as he and Raven heavily emphasized the reciprocity of interactions in their original 1964 paper.[53]

Nonetheless, coevolutionary research, as a domain of lab and the field study, does have boundaries that are safeguarded by expert scientists, like any other disciplinary social grouping. After all, Janzen, of “The most coevolutionary animal of them all” fame is far better known amongst his professional peers for asking, “When is it Coevolution?”[54] And Ehrlich, acting in his dual capacity as environmentalist and public scientist, has taken the time to carefully delineate between true coevolution in its “strict biological context” and efforts to apply the general idea of coevolution globally to living and nonliving systems. The Gaia Hypothesis, developed by independent scientists James Lovelock in the 1970s, posited that the biosphere and the atmosphere of Earth function together like one large organism.[55] When proponents of the Gaia Hypothesis implied that

---

[52] Berenbaum. Interview by author. Digital audio recording. Champaign-Urbana, IL, 19 April 2007.
[53] Ehrlich and Raven, "Butterflies and Plants: A Study in Coevolution."
[54] Janzen, "When Is It Coevolution?."
[55] James E. Lovelock, "Letter to the Editors: Gaia as Seen through the Atmosphere," *Atmospheric Environment* 6 (1972); Lynn Margulis and Gregory Hinkle, "The Biota and Gaia: 150 Years of Support for Environmental Sciences," in *Scientists on Gaia*, ed. Stephen H. Schneider (Cambridge: The MIT Press, 1991). In fact, three years later, Lynn Margulis introduced the idea to a larger audience in an article for *The CoEvolution Quarterly*. Brand proudly announced that the magazine was “the first non-specialist American publication to carry the Gaia Hypothesis,” Lynn Margulis and James E. Lovelock, "The Atmosphere as Circulatory System of the Biosphere - the Gaia Hypothesis," *The CoEvolution Quarterly* 5 (1975).

climate and life have “coevolved” in response to each other, Ehrlich felt compelled to speak out, contributing “Coevolution and Its Applicability to the Gaia Hypothesis” to a 1991 volume of collected papers.[56] In this paper, Ehrlich clearly expressed his appreciation for the Gaia Hypothesis and even likened it to his own work, writing, “I think the Gaia Hypothesis, in similar way [to his and Raven’s paper], has brought home to scientists and laypeople alike the great importance of interactions between living and nonliving parts of the biosphere.”[57] However, while the prime importance of interactions certainly united multiple cultural and scientific notions about coevolution, this central element was not a basis on which to extrapolate coevolutionary theory to the climate. Ehrlich drew a clear line between non-living variable and living organisms, which “evolve” in very different ways. “The essence of biological evolution is self-replication with variation and then differential reproduction of the variants…There are no similar mechanisms in the physical world.”[58] In other words, even for scientists like Ehrlich, who seemed to so broadly apply coevolutionary theory to the human world, the scientifically pressing question, “When is it coevolution?,” was fundamental. In the next section of this chapter, I examine some of the ways that coevolutionary scientists both asked and answered this very question in the 1970s and 1980s.

---

[56] Paul R. Ehrlich, "Coevolution and Its Applicability to the Gaia Hypothesis," in *Scientists on Gaia*, ed. Stephen H. Schneider (Cambridge: The MIT Press, 1991).
[57] Ibid., 20.
[58] Ibid., 21.

"When is it Coevolution?"

Public interest in coevolution was a mere shadow of the growing enthusiasm for coevolutionary theory within science in the 1970s and 1980s. This enthusiasm motivated scientists to continue in their attempt to demonstrate the broad relevance of coevolutionary theory throughout biology. But it also motivated them to refine the goals and methods of coevolutionary studies. These goals were not mutually exclusive. After all, in the currency of modern science, little is worth more than a body of theory and models that are generalizable across multiple natural systems. Thus, many coevolutionists focused on attempts to synthesize the many varied and particular instances of coevolutionary adaptation that made up the burgeoning field. As in previous chapters, professional meetings and volumes of collected papers provide an excellent sampling of the diversity of coevolutionary research and attempts at synthesis, which engendered a sense of scientific reform in coevolutionary studies, that thrived concurrently with continued efforts to build increasingly strong interdisciplinary bridges betweens specialized groups of scientists like botanists and zoologists, and biologists and chemists.

In addition, coevolutionists also faced the general critique that evolutionary biology relied too heavily upon hypothetical adaptive scenarios.[59] Efforts to increase empirical data, demonstrating reciprocal natural selection in action, arose in response. Berenbaum's work provides an example of a long-term, concerted effort to abide by these rigorous scientific standards by focusing her research program, from graduate school

---

[59] Gould and Lewontin, "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme ".

onward, on the coevolved relationship between wild parsnips and the parsnip webworm. Through her own application of her advisor Feeny's methodology, combining biochemistry, ecology, evolutionary biology, and—more recently—protein- and gene-level analyses, Berenbaum has turned the interaction between the wild parsnip and parsnip webworm into a model system for coevolution.

In August of 1973, the first International Congress of Systematic and Evolutionary Biology was convened in Boulder with the explicit hope of building bridges between different groups of biologists. "As specialists," secretary of the steering committee (and botanist) James Reveal wrote, "each of us can contribute directly or indirectly to all areas of biology, and the time is now when the communication gap between botany and zoology must be closed."[60] It was wholly appropriate, then, that one very popular symposium session at the conference should bring together botanists and zoologists around the topic of "Coevolution of Animals and Plants."[61] When the papers from the symposium were published two years later, editors Lawrence E. Gilbert and Raven wrote in the introduction, "there is no other volume focusing on the dynamic aspects of animal-plant coevolution."[62] The timeliness of such a volume became

---

[60] James L. Reveal, "The First Internation Congress of Systematic and Evolutionary Biology," *Taxon* 21, no. 4 (1972): 491.

[61] Lawrence E. Gilbert and Peter H. Raven, eds., *Coevolution of Animals and Plants: Symposium V; First International Congress of Systematic and Evolutionary Biology; Boulder, Colorado; August 1973* (Austin: University of Texas Press, 1975). One reviewer of the published volume from this conference wrote that the "expanding interest" in coevolution "was reflected by the large audience at the symposium where these papers were first presented," Barbara L. Bentley, "Review: Coevolution of Animals and Plants," *The Quarterly Review of Biology* 51, no. 3 (1976): 432.

[62] Lawrence E. Gilbert and Peter H. Raven, "General Introduction," in *Coevolution of Animals and Plants: Symposium V; First International Congress of Systematic and*

abundantly clear when, only four years later, the second edition of the book was issued, with no substantial revisions, showing that demand remained high, and *Coevolution of Animals and Plants* remained the only volume of its kind on the market.[63] And certainly, more than any other volume of collected papers discussed thus far in this dissertation, *Coevolution of Animals and Plants* blended a botanical and zoological perspective and stayed focused on the *evolution* of inter-kingdom interactions. The biologists involved were nearly evenly split along botanical and zoological lines and the papers made a distinct effort to speak to workers trained on either side of this disciplinary divide—a quality that was specifically emphasized by the editors in selecting papers for the symposium and volume.[64] And according to one reviewer, the authors were largely successful in this respect, forcing the "distinctions between 'botanist' and 'zoologist,' or 'biochemist' and 'ecologist' [to] break down."[65] This effort was especially important because, as the reviewer for *Systematic Botany* wrote, "Botanists have paid little attention to the role of animals as selective agents in plant evolution." While Ehrlich and Raven's 1964 paper meant that "in that last ten years much attention has been paid to this subject," it has been, "alas mostly by zoologists and biochemists."[66] Another reviewer commented on the persistent botanical notion that plants operated mostly independently

---

Evolutionary Biology; Boulder, Colorado; August 1973, ed. Lawrence E. Gilbert and Peter H. Raven (Austin: University of Texas Press, 1975), ix.

[63] Lawrence E. Gilbert, "Editor's Note on the Second Edition," in *Coevolution of Animals and Plants, Second Edition*, ed. Lawrence E. Gilbert and Peter H. Raven (Austin: University of Texas Press, 1980).

[64] Gilbert and Raven, "General Introduction," x.

[65] Bentley, "Review: Coevolution of Animals and Plants," 432.

[66] Otto T. Solbrig, "Review, Costs and Benefits: Coevolution of Animals and Plants," *Systematic Botany* 1, no. 4 (1976): 393.

of animals, which nevertheless “were the welfare recipients of the [plants’] largesse.” For those botanists “who still cling to the ‘green plant’s burden,’” *Coevolution of Animals and Plants* “may come as a surprise.”[67] For, as the book demonstrates, “no species evolves in a vacuum,” and interaction between animals and plants impacts both sides of the equation.[68]

The contributors’ efforts to advance and reform coevolutionary studies were perhaps less successful, leading one reviewer to write, “plant-animal coevolution is a rich, promising field of investigation still in its infancy.”[69] Gilbert and Raven had hoped to publish “studies that stressed the process rather than the products of coevolution.”[70] This goal was critical; the *products* of coevolution, those remarkable “gee-whiz”-inducing coadaptations between different species, had consumed so much of biologists’ attention for so long that little was understood of how they came to be. Despite this ideal, however, it’s clear that few biologists knew yet how to approach such a task. Lincoln Brower, himself a coevolutionary biologists, reviewed the volume, commenting that though the authors “were charged to weave together a diversity of fascinating botanical and zoological information, much of it new, in support of coevolution as process,”[71] the

---

[67] Peter Bernhardt, "Review: Coevolution of Animals and Plants," *Bulletin of the Torrey Botanical Club* 104, no. 3 (1977): 286.
[68] Ibid.: 287.
[69] Solbrig, "Review, Costs and Benefits: Coevolution of Animals and Plants," 394.
[70] Gilbert and Raven, "General Introduction," x.
[71] Lincoln P. Brower, "Review: Coevolution of Animals and Plants," *Science* 190, no. 4213 (1975): 455.

book's main "weakness lies in a loss of focus on the central theme set out by the editors, namely, coevolution as an important process in community evolution."[72]

Nevertheless, Brower also asserted that *Coevolution of Plants and Animals* "must be regarded as an important contribution to modern evolutionary ecology."[73] A few papers in particular stood out in their attempts to present specific hypotheses about coevolution that could be effectively tested in a variety of different ecological communities. According to Gilbert and Raven, these papers "may be regarded as the beginning of a process of generalization across ecosystems that will eventually make possible effective and useful model-building in the area of coevolutionary studies."

Like much of coevolutionary studies until this point, these papers emphasized costs and benefits, the currency of *fitness*, which was central to Neodarwinian evolutionary theory. Janzen's first coevolutionary argument had been based on the premise that producing secondary compounds and supporting ant populations were both energetically taxing endeavors, made adaptively possible only because they *cost less* than the damage that undefended trees would suffer from herbivores. Increasingly, coevolutionists (and evolutionary biologists in general) attempted to formalize the costs and benefits of various adaptive characteristics, as one way of illuminating and—crucially—measuring the process of coevolution.[74] For instance, if the cost of seed predation were higher for a plant than the cost of producing a toxin in its seed coat, then

---

[72] Ibid.: 456.

[73] Ibid.

[74] Bernd Heinrich, "The Role of Energetics in Bumblebee-Flower Interrelationships," in *Coevolution of Animals and Plants: Symposium V; First International Congress of Systematic and Evolutionary Biology; Boulder, Colorado; August 1973*, ed. Lawrence E. Gilbert and Peter H. Raven (Austin: University of Texas Press, 1975).

this net benefit would, over many generations of evolution, engender a selective pressure for toxin production.

Doyle McKey, a graduate student of Janzen's, contributed a paper to the session, making generalizations about the seed dispersal *strategies* of plants. His approach reflected a trend in evolutionary biology, where particular ecological characteristics often found in conjunction were characterized as recognizable strategies that made evolutionary "sense" under particular ecological circumstances. Surveying a number of plant genera, McKey hypothesized that two "alternative compromises were open to a plant in its dispersal strategy."[75] "It is theoretically obvious," he wrote, "that plants should evolve to minimize the cost of their dispersal, and indeed much has been written about the poor nutritional value of most fleshy fruits[76]…However, it is just beginning to be appreciated that fruits vary widely in their nutrient content and that, while many fruits are mostly sugar and water, some fruits contain relatively high concentrations of expensively produced nutrient."[77] In formalizing the two alternative dispersal strategies, McKey also drew upon a recent ecological hypothesis that organisms tend to reproduce according to two general strategies. By the first strategy, r-selection, offspring tend to be numerous and relatively inexpensive to produce. In contrast, by the second strategy, K-

---

[75] Doyle McKey, "The Ecology of Coevolved Seed Dispersal Systems," in *Coevolution of Animals and Plants: Symposium V; First International Congress of Systematic and Evolutionary Biology; Boulder, Colorado; August 1973*, ed. Lawrence E. Gilbert and Peter H. Raven (Austin: University of Texas Press, 1975), 186.

[76] Because nutrients are thought, like toxic secondary compounds, to be energetically expensive compounds for a plant to synthesize, a fruit with low nutritional value would have a relatively low cost of fruit production and, therefore, low cost of attracting a dispersing animal.

[77] McKey, "The Ecology of Coevolved Seed Dispersal Systems," 171.

selection, offspring require large investments of energy and, thus, fewer are produced.[78] Applying this general theory to the domain of coevolution between plants and seed dispersers, McKey proposed a low-quality dispersal strategy, in which a large number of inexpensive seeds are produced, typically employing wind pollination or dispersal by unspecialized opportunistic herbivores. By this strategy, many seeds may be dispersed into inappropriate environments, but the cost of such a loss is relatively low. The high-quality strategy, by contrast, would be more likely to result from tight coevolution: small numbers of high-investment seeds are produced and typically dispersed by specialized fruit-eating animals, a method that better guaranteed that seeds would find a viable new home.[79] McKey's formulation presented new options for experimentally studying coevolved systems by manipulating elements of different plants' dispersal strategies. It also fit coevolutionary specialization (between high-quality fruit-producers and specialized seed-dispersers) and generalization (between low-quality fruit-producers and generalized seed-dispersers) into a larger theoretical framework, applying mainstream ecological and evolutionary theory to coevolutionary systems.

Feeny, on the other hand, generated a new theoretical framework for specialism and generalism. It was in his paper for *Coevolution of Plants and Animals* that he first compared general plant defense strategies, using what he would later dub "plant

---

[78] Robert MacArthur and Edward O. Wilson, *The Theory of Island Biogeography* (Princeton: Princeton University Press, 1967), 203.
[79] McKey, "The Ecology of Coevolved Seed Dispersal Systems," 186.

apparency" theory.[80] He posited that the defensive strategy of some plant species could be classified as "hard to find," while the defensive strategy of others could be classified as "bound to be found." He described these strategies in the terms of evolutionary ecology, carefully assessing their adaptive value over the course of both ecological time and evolutionary time. Communities composed of "hard to find" plants, usually successional herb species like the wild parsnip that he and Berenbaum would study in great detail, tend to have "rather specific chemical defenses." In fact, "the more chemically diverse" the plants making up a "hard-to-find" the community, "the harder it is for non-adapted insects to colonize new plant species and for adapted plant specialist insects to find their hosts." In ecological time, then, these plants may "escape" from insect herbivores by growing to maturity before their predators can do the most damage, or being masked among a diverse community of other plants. And in evolutionary time, the evolution of increasingly potent chemical defense may allow them to stay just ahead in the coevolutionary race that they run with their specialized insect predators.[81] Because many "agricultural crop varieties have originated from" such plants, "[i]t is interesting to speculate as to whether the vulnerability of crops to insect herbivores (in the absence of synthetic chemical defenses supplied by man) may result from planting in monoculture species which have evolved chemical defenses appropriate to communities in which the

---

[80] Paul Feeny, "Plant Apparency and Chemical Defense," in *Recent Advances in Phytochemistry, Volume 10: Biochemical Interaction between Plants and Insects*, ed. James W. Wallace and Richard L. Mansell (New York: Plenum Press, 1976).

[81] ———, "Biochemical Coevolution between Plants and Their Insect Herbivores," in *Coevolution of Animals and Plants: Symposium V; First International Congress of Systematic and Evolutionary Biology; Boulder, Colorado; August 1973*, ed. Lawrence E. Gilbert and Peter H. Raven (Austin: University of Texas Press, 1975), 13.

optimum strategy is being hard to find…Moreover, such natural chemical defenses may have been further reduced over the centuries by man's selection for increased yield or improved flavor."[82] In the case of many agricultural crops, Feeny suggested, human cultural practices—agricultural practices, to be specific—undermine the evolved defenses of the very plants we cultivate and hope to protect from predation.

Instead of being lost in the biochemically diverse crowd, plant species that have adopted the "bound to be found" strategy are large and long-lived, like the oak trees that Feeny studied as a graduate student. Because of their size they are "bound to be found" by insect herbivores in ecological time. And because of their lifespan, they are "bound to be found" in evolutionary time. As in Feeny's oaks, most of these species have generalized defenses against herbivory: toxic compounds and leaf toughness that make them difficult to eat for most insects. When such generalized "quantitative" defenses play a more important role in plant defense than "qualitative," highly specific chemical defenses, plants are expected to be less subject to tight coevolutionary races with insects.[83]

In articulating these two strategies for plant defense, Feeny provided a generalizable hypothesis that could be tested in a variety of ecological communities. This was an indispensable service for a field of study striving to find ways to test for true coevolution and to understand the process of coevolution itself. And like McKey's, Feeny's theoretical framework attempted to make further sense of generalism and specialism in plant-insect interactions.

---

[82] Ibid., 14.
[83] Ibid.

As mentioned above, Feeny would later dub this hypothesis “plant apparency,” which he explained in much greater detail only two years later, for a volume of *Recent Advances in Phytochemistry* entitled “Biochemical Interaction Between Plants and Insects.”[84] This 1976 volume held yet another attempt at synthesis, with a collaboration between zoologist David Rhoades and botanist Rex Cates, “Toward a General Theory of Plant Herbivore Chemistry.”[85] This theory, like Feeny’s “apparency,” correlated specialized plant chemical defenses with the ability of insects to find the plant, gauged by the plant’s “predictability and availability.”[86] All of these coevolutionary biologists, then, were attempting to solve the problem of specialism and generalism in relationships between insects and plants: When, in other words, do interactions between insects and plants constitute tight coevolution? And when do they represent general defensive phenomena, the product of “diffuse” coevolution between large groups of predator and prey species?

Such efforts to provide testable hypotheses and generalizable theory for coevolution were indeed critical for the further development of the field. But perhaps even more pressing was the need for more empirical evidence. In 1979, Janzen collaborated again with plant physiologist and phytochemist Gerald Rosenthal,[87] to edit

---

[84] Feeny, "Plant Apparency and Chemical Defense."
[85] David F. Rhoades and Rex G. Cates, "Toward a General Theory of Plant Antiherbivore Chemistry," in *Recent Advances in Phytochemistry, Volume 10: Biochemical Interaction between Plants and Insects*, ed. James W. Wallace and Richard L. Mansell (New York: Plenum Press, 1976).
[86] Ibid., 205.
[87] Janzen’s earlier collaboration with Rosenthal was addressed in Chapter Three. They worked on a study of L-canavanine, a potent plant toxin that interferes with insect protein synthesis by mimicking the amino acid L-arginine. Gerald A. Rosenthal,Daniel H.

the first edition of what would be become an indispensable guide to plant-insect interactions, *Herbivores: Their Interaction with Secondary Plant Metabolites*.[88] Janzen's chapter, "New Horizons in the Biology of Plant Defenses,"[89] contained a characteristic mix of naturalistic insights and practical advice. His emphasis on collaboration between ecologists and chemists only grew stronger,[90] and he wrote that the study of coevolution needs a "team" of scientists from multiple disciplines, "or a person who thinks like a team."[91]

Janzen also presented a number of suggestions for the collection of more and better empirical data, to help his colleagues escape the "morass of untestable hypotheses."[92] One of the techniques Janzen suggested, reminiscent of the work of insect physiologists Fraenkel and Dethier, who shaped the foundation for coevolutionary studies in the 1950s, was the creation of "realistic" artificial diets, to which different combinations of secondary compounds could then be added, in order to gauge their effects.[93] Janzen suggested a more original methodology when he proposed studying "extinct interactions," between extant plant species and their extinct specialized

---

Janzen, and D.L. Dahlman, "Degradation and Detoxification of Canavanine by a Specialized Seed Predator," *Science* 196 (1977).

[88] Gerald A. Rosenthal and Daniel H. Janzen, eds., *Herbivores: Their Interaction with Secondary Plant Metabolites* (New York: Academic Press, Inc., 1979).

[89] Daniel H. Janzen, "New Horizons in the Biology of Plant Defenses," in *Herbivores: Their Interaction with Secondary Plant Metabolites*, ed. Gerald A. Rosenthal and Daniel H. Janzen (New York: Academic Press, Inc., 1979).

[90] Ibid., 333.

[91] Ibid., 338.

[92] Ibid., 333.

[93] Ibid., 338.

herbivores, by experimenting with the effects of introduced herbivores.[94] Finally, Janzen suggested controlled experiments using artificial herbivory at levels that mimicked the degree of herbivory seen in natural populations of plants, in order to more directly measure the effects of herbivory—an important issue, since some biologists continued to hold firm in their conviction that herbivory in nature (in contrast to herbivory in agricultural settings) had little effect on the fitness of plants.[95] In other words, Janzen had many suggestions for experimentation and data collection, many of which were nearly as interventionist as the model of conservation that he was developing.

One more practical suggestion that Janzen offered was the design of long-term research projects focusing on particular groups of tightly interacting animal and plant species. As an example, Janzen cited Feeny's work on crucifers and umbellifers.[96] It was in this domain that Feeny's student Berenbaum was already beginning to excel, learning from Feeny how to "think like a team," and beginning her own detailed investigation into the interaction between wild parsnip and parsnip webworms. Berenbaum's work would, over the course of the next few decades, turn her subject of research into a model system for coevolution: a testing ground for coevolutionary hypotheses and a generator of empirical data. Moreover, Berenbaum's work has formed a bridge between the first generation of coevolutionary research and the next generation, in which the meticulous analysis of gene expression is combined fruitfully with a global perspective on the role of historical contingency in coevolution.

---

[94] Ibid., 333.
[95] Ibid., 342.
[96] Ibid., 338.

As a Yale undergraduate with a variety of biological interests, Berenbaum suffered from "an inability to decide among equally pleasant alternatives."[97] Plants and insects alike riveted her, and it wasn't until Feeny visited, giving a seminar on his own research, that she realized, "I don't have to choose. If I worked with Feeny, I would never have to make up my mind. And that's basically what I did."[98] Upon entering graduate school at Cornell in 1975, Feeny handed her a volume on the biochemistry of the Umbelliferae, the family of plants that includes parsnips,[99] and instructed her to find a thesis project therein. Mining this phytochemists' tome, two particularly interesting classes of plant secondary compounds stood out to Berenbaum: the coumarins and the furanocoumarins. While it was clear that while much was known already about the biochemical properties and the synthesis of these compounds, "it appeared as if no one had actually examined their effects on insects." And this particular confluence of known and unknown "provided opportunities for hypothesis testing in the context of coevolution."[100] Within the Umbelliferae, Berenbaum soon began to focus on wild parsnips and their specialized predators, parsnip webworms. Like most model organism systems used in biology,[101] the natural qualities of this coevolved interaction made it well

---

[97] Berenbaum. Interview by author. Digital audio recording. Champaign-Urbana, IL, 19 April 2007.

[98] Ibid.

[99] Also known as the Apiaceae. This family also includes other aromatic herbs, such as parsley, cilantro, dill, and fennel.

[100] Berenbaum. Interview by author. Digital audio recording. Champaign-Urbana, IL, 19 April 2007.

[101] On the construction of model organisms in biology, see: Angela N. H. Creager, *The Life of a Virus: Tobacco Mosaic Virus as an Experimental Model, 1930-1965* (Chicago: University of Chicago Press, 2002); Robert E. Kohler, *Lords of the Fly: Drosophila Genetics and the Experimental Life* (Chicago: University of Chicago Press, 1994); Karen

suited to become, in Berenbaum's own words, a "model system for coevolution." Wild parsnip is "a plant with relatively few other enemies," while parsnip webworm is "an insect with virtually no other hosts." In addition, "it's an interaction where the life histories are more or less synchronous—you have a biennial plant and a univoltine insect, an insect that attacks the reproductive structures, so it has a clear effect on fitness. I mean—it's ideal."[102] In retrospect, the system seems, indeed, "ideal" for testing of coevolutionary hypotheses and the generation of empirical data. Berenbaum would be the first to admit, however, that a first-year graduate student is unlikely to immediately recognize the qualities of an ideal model system. She picked the parsnip/webworm less for its superlative value to science and more for her own convenience: "I picked it because, um, I didn't drive in graduate school and I needed to walk to a field site and right behind the dairy barn—the dairy store, at Cornell, right across from my office in the insectary, was this big field of wild parsnip, infested with webworms. And that is why I started working on webworms. Not very dramatic."[103]

Since 1975, though, Berenbaum has clearly established that drama is not a necessary element of an effective model system. Beginning with familiar methods of biochemical analysis and insect rearing on artificial diets, Berenbaum soon demonstrated the toxicity of the furanocoumarin xanthotoxin to that notorious generalist predator of plants, the southern armyworm, and hypothesized about the adaptations allowing the

---

Rader, *Making Mice: Standardizing Animals for American Biomedical Research, 1900-1955* (Princeton: Princeton University Press, 2004).

[102] Berenbaum. Interview by author. Digital audio recording. Champaign-Urbana, IL, 19 April 2007. "Univoltine" means that the parsnip webworm reproduces one generation per year.

[103] Ibid.

parsnip webworm to tolerate the toxin. Adhering to Janzen's requirement that an artificial diet be "realistic,"[104] Berenbaum's bioassay organisms fed on xanthotoxin levels "within the range found in plants producing their own furanocoumarins."[105] The xanthotoxin diet halted the development of the armyworms and eventually killed them. Critically, light bulbs were used that mimicked natural daylight—xanthotoxin acts toxically only in the presence of ultraviolet light, crosslinking the DNA of the insect,[106] which is a very effective defense, since DNA molecules that have been crosslinked together cannot be replicated. Thus, the toxicity of the wild parsnip's xanthotoxin provided "experimental support to the coevolutionary hypothesis that plants 'escape' from adapted enemies by altering their chemical phenotype—that is, by evolving biogenetic pathways which produce ecologically novel secondary compounds."[107] As for the adapted predators of the parsnip webworms, the winning step in their "coevolutionary arms race" with wild parsnips was not biochemical, but behavioral. From the infested field of wild parsnips that Berenbaum mentions above, she collected insects, like the parsnip webworm, which live successfully on wild parsnips, nestled inside rolled leaves or under a shelter of webbing, which they string across parsnip flower heads. "Because a rolled leaf fails to transmit detectable amounts of ultraviolet light (as tested in an ultraviolet spectrophotometer), it appears that the leaf-rolling habit, common to many Microlepidoptera, may have been a preadaptation for feeding on plants containing

---

[104] Janzen, "New Horizons in the Biology of Plant Defenses," 338.

[105] May Berenbaum, "Toxicity of a Furanocoumarin to Armyworms: A Case of Biosynthetic Escape from Insect Herbivores," *Science* 201, no. 4355 (1978): 532.

[106] Ibid.: 533.

[107] Ibid.: 532.

furanocoumarins."[108] Starting with biochemical data, Berenbaum gradually expanded the experimental data pertaining to parsnip and its predator, until both sides of the relationship could be seen clearly.

But the "arms race" between insects and parsnips didn't end there. In a paper coauthored with Feeny in 1981, "Toxicity of Angular Furanocoumarins to Swallowtail Butterflies: Escalation in a Coevolutionary Arms Race?,"[109] Berenbaum documented a biochemical adaptation in the parsnips—one aimed very specifically at insect species that had already adapted to xanthotoxin. While xanthotoxin had a broad toxicity for many different species of insects (as is demonstrated by its effect on the generalist armyworm), this second furanocoumarin, angelicin, has little toxicity for most insects. Swallowtail butterflies, on the other hand, already adapted to umbellifers containing xanthotoxin, assiduously avoid those with angelicin. Feeding experiments confirmed that for the swallowtail, while angelicin has toxic effects, xanthotoxin does not.[110] However, the possibility remained that a further turn to the arms race could free insects from this constraint also: a species of swallowtail butterfly in Newfoundland had been found to feed on toxins like angelicin, suggesting that it had "evolved to specialize on umbelliferous hosts that are largely unexploited by its congeners."[111] Berenbaum's

---

[108] Ibid.: 533.

[109] May Berenbaum and Paul Feeny, "Toxicity of Angular Furanocoumarins to Swallowtail Butterflies: Escalation in a Ceovolutionary Arms Race?," *Science* 212 (1981). Note that at this point, Berenbaum had just begun her appointment at the University of Illinois Urbana-Champaign.

[110] Ibid.: 929.

[111] Ibid.

research thus traced coevolution as it happened in real time, as well as expanding her study in order to consider the coevolved system on a global scale.

The same year, Berenbaum published a paper in *Ecology*, synthesizing her own already impressive body of data in order to better understand the role of plant secondary chemistry in shaping the structure of ecological communities. In other words, how important are different types of plant toxins in determining the range of insects that live and feed on specific plants? In order to answer this question, Berenbaum correlated factors with potential for structuring the community of insects—namely, habitat preferences, taxonomic relationships, and secondary chemicals—with the populations of insects found on different plants. Clustering the plant species with respect to each of these factors and then comparing each factor with insect faunae revealed that "neither taxonomy nor habitat preference could account for similarities in insect faunae."[112] Instead, these correlations showed "strong evidence for the role of secondary chemistry in organizing the structure of insect communities."[113]

---

[112] May Berenbaum, "Patterns of Furanocoumarin Distribution and Insect Herbivory in the Umbelliferae: Plant Chemisry and Community Structure," *Ecology* 62, no. 5 (1981): 1261.

[113] Ibid.: 1264.

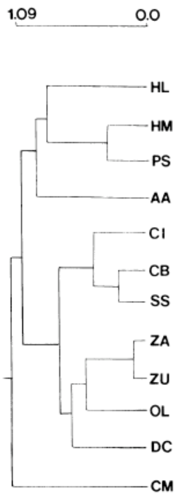

FIG. 5. Cluster analysis depicting similarity of plant species with respect to their insect fauna using weighted data (see text).

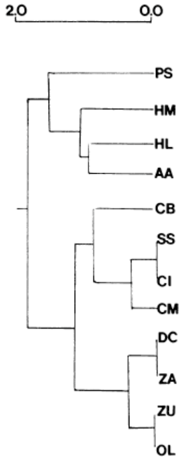

FIG. 6. Cluster analysis depicting similarity of plant species with respect to their furanocoumarin chemistry (dihydrofuranocoumarins ranked at 1, linear furanocoumarins at 2, angular furanocoumarins at 3, in accordance with number of enzymatic steps involved in biosynthesis; see text for explanation).

Figure 5: In both images, letter-pairs represent species of plants (HL= *Heracleum lanatum*, for example). In Figure 5,[114] species are clustered according to the similarity of the insect faunae that feeds on them. In Figure 6,[115] species are clustered according to the similarity of their secondary compound constituents. The close match between these two cluster analyses (compared to the cluster analyses done for the other factors, habitat preference and taxonomical similarity) shows that the distribution of chemical characteristics in the plant community is most closely correlated with the distribution of insect species. (Images used by permission of the Ecological Society of America.)

Here, then, Berenbaum applied a mass of empirical data in order to test a hypothesis about specialized relationships between insects and plants—a hypothesis that could be similarly tested in many other plant communities.

Her growing body of data gave Berenbaum a firm foundation from which to make progressively more synthetic claims about insect-plant coevolution. In a 1983 paper for *Evolution*, “Coumarins and Caterpillars: A Case for Coevolution,” she remarked upon a persistent “lack of empirical data” for the various steps in the coevolutionary process, which has been a “subject of considerable criticism.” “It is difficult, if not impossible,”

---

[114] Ibid.: 1261.
[115] Ibid.: 1262.

she wrote, “to prove coevolution—indeed, it has even proved difficult simply to define it (Janzen 1980).” Her own work, however, beginning with the 1978 paper cited above, “provides a case study,” in other words, a model system, “with either direct or circumstantial evidence for each part of the coevolutionary process.”[116] The steps, as posited originally by Ehrlich and Raven in 1964, should seem familiar by now. First, through mutation, plants produce a novel biochemical agent, which then deters some insects from feeding.[117] Next, plants, having “escaped” from the pressure of herbivory, undergo rapid adaptive radiation, evolutionarily diversifying.[118] The insects, like the plants, are subject to genetic change, and mutants arise that can, by one means or another, tolerate or avoid some novel plant compounds, thereby evolving the ability to feed on previously protected plants.[119] Finally, just as plants did before them, insects undergo adaptive radiation, taking advantage of the feeding opportunities that their evolved tolerance to phytochemicals provides.[120] One by one, Berenbaum addressed each of these steps, relying almost exclusively upon her own data to demonstrate the occurrence of each. “Despite its limitations in scope,” she concludes, “this system—coumarin-containing plants and associated herbivores—can serve as a paradigm for similar systems, i.e., plants containing ‘qualitative’ toxins (sensu Feeny, 1976) and their associated herbivores.”[121] Hence, less than a decade after starting graduate school,

---

[116] ———, "Coumarins and Caterpillars: A Case for Coevolution," *Evolution* 37, no. 1 (1983): 163.

[117] Ibid.: 163-166.

[118] Ibid.: 163, 166-167.

[119] Ibid.

[120] Ibid.: 163, 169.

[121] Ibid.: 175.

Berenbaum was already well on her way to marshaling the empirical data necessary to support of "models" and "paradigms" that could help orient future coevolutionary research.

To a large extent, coevolutionary scientists responded proactively to calls to sharpen and refine their research with generalizable theory, testable hypotheses, and a stronger empirical foundation. But, as I quoted at the beginning of this chapter, even in 1983, Futuyma and Slatkin had cause to worry that coevolution may yet be defined too loosely, writing, in their own edited volume, "Coevolution, too broadly defined, becomes equivalent to evolution."[122] This book constituted landmark collection of coevolutionary analysis and synthesis, outlining new methods and theory, in particular the use of phylogenetic data to better compare the evolutionary history of host plants with their associated insects.[123] But even here, a decade after the symposium that spawned Gilbert and Raven's *Coevolution of Animals and Plants*, Futuyma and Slatkin remarked that much of coevolutionary research still focused mostly on adaptations, the *products* of coevolution, rather than on the *process*.[124] Furthermore, while interest in coevolution remained high,[125] a coherent discipline of "coevolutionary studies" did not appear to be

---

[122] Futuyma and Slatkin, "Introduction," 2.

[123] Charles Mitter and Daniel R. Brooks, "Phylogenetic Aspects of Coevolution," in *Coevolution*, ed. Douglas J. Futuyma and Montgomery Slatkin (Sunderland, MA: Sinauer Associated Inc., 1983).

[124] Futuyma and Slatkin, "Introduction," 5.

[125] For exampled the Futuyma and Slatkin volume was only one of two books entitled *Coevolution* published in 1983, Matthew H. Nitecki, ed., *Ceovolution* (Chicago: The University of Chicago Press, 1983).

taking distinct shape.[126] Was it a continued lack of scientific rigor, or was it the apparent omnipresence of coevolutionary phenomena, the sense that most evolution might be considered coevolution? After all, as Feeny told me recently, “Coevolution is a matter of degree rather than kind—every community—everything is exerting some sort of selective pressure on its neighbors. Coevolution is incredibly—it’s almost so broad as to be useless.”[127] In fact, it’s so widely applicable that scientists like Ehrlich and Janzen could unabashedly apply it directly to the operation of human society. How could a concept so expansive provide the basis for a cohesive disciplinary community?

As for the hybrid methodology crafted by Feeny and continued by Berenbaum: In Berenbaum’s own words, the response was “a little disappointing.” In the mid-1970s to early 1980s, “chemistry was becoming much more accessible to everyone. And [yet] relatively few people picked up the gauntlet. And that’s still true today…there is so much to be learned but very few people have, kind of, taken on the challenge, taken up the challenge of learning the methodology. More have actually moved into molecular work.”[128] Under the rubric of “chemical ecology,” some training programs have been established, but few in the United States. Feeny, for one, has found himself flying frequently to Germany in recent years, where he was involved in the establishment of the

---

[126] For example, Dawkins and Krebs’ 1979 paper (Dawkins and Krebs, "Arms Races between and within Species.") shows the broad relevance of coevolutionary theory—yet, this paper, despite the fact that it refers to the “coevolutionary arms race,” makes no reference to the literature of herbivorous insect-plant interactions discussed in this dissertation. Thus, it simultaneously shows the spread of the concept of “coevolution” and the lack of a cohesive (i.e., in this case, with an academic citation record that is shared by most practitioners) disciplinary structure forming around the concept.

[127] Feeny. Interview by author. Digital audio recording. Ithaca, NY, 12 November 2007.

[128] Berenbaum. Interview by author. Digital audio recording. Champaign-Urbana, IL, 19 April 2007.

Max Planck Institute for Chemical Ecology—the kind of institute that, for decades, he has strived to establish at Cornell, to no avail.[129]

Geographic mosaics, molecular genetics, and coevolutionary studies beyond 1983

Despite these challenges, however, the expansive body of coevolutionary theory has continued to grow—becoming an increasingly broad and global concept and, at the same time, an increasingly rigorous scientific concept. More recently, coevolutionists have begun to seriously address another core element of Janzen's question, "When is it coevolution?" One of the challenges in studying coevolution is the fact, as Janzen writes, that "plants are anachronisms."[130] Having evolved in the past, there is no guarantee that the interactions we see today between plants and insects reflect the interactions under which particular plant traits originated. Extinction and migration of both plants and animals over the millennia have switched and shifted relationships that evolved under very different circumstances in a different place and time. Fully accepting that ecological communities are composed and evolve under these conditions of extreme historical contingency makes the study of coevolution that much more difficult. In the 1990s, evolutionary biologist John Thompson coined the phrase "geographic mosaic" to describe the highly varied global patterns of specialized relationships that result from such a large amount of historical contingency. "Studies of neither local populations alone nor species as a whole can capture the dynamics of evolving interactions," Thompson writes. "Associations between species are molded by local conditions, and these associations are

---

[129] Feeny. Interview by author. Digital audio recording. Ithaca, NY, 12 November 2007.
[130] Janzen, "New Horizons in the Biology of Plant Defenses," 333.

then often reshaped over evolutionary time as some populations become extinct and other exchange genes. Hence, the outcomes within local populations—whether escalating arms races or intricate mutualisms—are often only the raw material for the patterns that develop and the processes that take place over larger geographic scales."[131] In other words, even when a close association between two species is seen in one geographic area, that relationship may not be generalizable: everything is context-dependent.

Berenbaum and her colleague Arthur Zangerl are also applying the wild parsnip model system to take local studies of parsnip predators to a global scale. Not only have they examined multiple populations of wild parsnips in North America,[132] but they have also attempted to examine the historical interaction between parsnips and parsnip webworms by analyzing the furanocoumarin content of herbarium specimens. They compared wild parsnip collections made in North America before the introduction of parsnip webworm (in the last half of the 19th century) with collections made after the introduction of the webworm and collections made during the same period in Europe, where parsnips and webworms originally coevolved. Zangerl and Berenbaum discovered that the introduction of the webworm in North America had stimulated a concomitant rise in furanocoumarins in North American populations of wild parsnips. Not only does this reveal a geographic mosaic of relationships between parsnips and webworms on a global scale, but it has important implications for the introduction of natural predators in biocontrol programs: Sometimes predators will serve to only strengthen invasive weeds,

---

[131] John N. Thompson, *The Coevolutionary Process* (Chicago: The University of Chicago Press, 1994), 289.
[132] Arthur Zangerl and May Berenbaum, "Phenotype Matching in Wild Parsnip and Parsnip Webworms: Causes and Consequences," *Evolution* 57, no. 4 (2003).

by triggering an increase in their previously coevolved defenses.[133] As Berenbaum told me in an interview, “you don’t have to be on your home turf to evolve.” And evolution takes different routes in different contexts.

This case demonstrates not only the contextuality of coevolution itself, but the contextuality of scientific research: “I’ve been studying [this system] for thirty years,” Berenbaum said, “and we now discover [that] what, in the early ‘80s, was a bad system because it was introduced, is now a great system because it’s invasive. So—same system, different context.”[134]

Demonstrating of the value of the parsnip/webworm system as a model for coevolution and the value of taking a global view on locally contingent evolutionary interactions, Zangerl and Berenbaum have recently expanded their research to New Zealand, where the webworm invaded in 2004. In studying parsnip seed production and secondary compounds constituents, they confirmed that the introduction of the webworm had a severe effect on the fitness of parsnip populations, and that the expression of toxin secondary compounds by the parsnips was changing rapidly in response to selection.[135] All of Berenbaum and Zangerl’s research shows that the evolutionary arms race never ends—making ecological interactions an endless source of evolutionary innovation.

---

[133] ———, "Increase in Toxicity of an Invasive Weed after Reassociation with Its Coevolved Herbivore," *Proceedings of the National Academy of Science* 102, no. 43 (2005).

[134] Berenbaum. Interview by author. Digital audio recording. Champaign-Urbana, IL, 19 April 2007.

[135] Arthur Zangerl,M.C. Stanley, and May Berenbaum, "Selection for Chemical Trait Remixing in an Invasive Weed Aftee Reassociation with a Coevolved Specialist," *Proceedings of the National Academy of Science* 105, no. 12 (2008).

Finally, to Berenbaum's great satisfaction, the very molecular methods she mentioned above have provided new analytical access to those evolutionary innovations.[136] Here "molecular" refers not to the historical process of molecularization in the first half of the 20th century,[137] but to the molecular *genetic* methods of the last half of the 20th century and beyond.[138] Here Berenbaum truly bridges the traditional, first-generation methods of coevolutionary studies and the new generation. She has focused particularly on "environmental response genes," like those that code for the enzymes that allow insects to detoxify plant compounds, cytochrome P-450 monooxygenases. In fact, cytochrome P-450 monooxygenases are involved not only in the detoxification of furanocoumarins, but also in their synthesis by wild parsnips. As she wrote in a 2002 paper entitled "Postgenomic Chemical Ecology: From Genetic Code to Ecological Interactions," "Molecular approaches now allow chemical ecologists to characterize specifically those biochemical innovations postulated to lead to adaptation and diversification in plant/insect interactions." In other words, molecular genetic methods allow for a critical innovation in coevolutionary studies: the investigation of the elusive *process* of coevolution itself. Moreover, as for Berenbaum's molecularizing predecessor Gottfried Fraenkel, interactions between organisms have not become subservient to

---

[136] In my interview with Berenbaum, she cites the immense importance of looking directly at the process that generates the "biochemical innovations" that make coevolution possible (Berenbaum. Interview by author. Digital audio recording. Champaign-Urbana, IL, 19 April 2007.)

[137] See Chapter One.

[138] See, for example: Jean-Paul Gaudillière and Hans-Jörg Rheinberger, eds., *From Molecular Genetics to Genomics: The Mapping Cultures of Twentieth-Century Genetics*, Routledge Studies in the History of Science, Technology, and Medicine (London: Routledge, 2004).

molecules. While molecular genetic tools have much value for coevolutionary studies, ecologists and evolutionary biologists also still have much to show molecular biologists. Only chemical ecologists, Berenbaum claims, at home in an "inherently multidisciplinary field" and accustomed to seeing molecules as elements within a larger context of organismal and community interaction, "can begin to hazard a guess as to the function of the macromolecules that provide the blueprints for behavior and ecology."[139] In other words, molecules have meaning only within their larger ecological context.

Conclusion

Throughout the 1970s and 1980s, coevolutionary scientists found a multitude of ways to both ask and answer Janzen's pressing question, "When is it coevolution?" Among these were increasingly rigorous experimental methods, more thorough knowledge of specific coevolved model systems, and more informative and generalizable theoretical frameworks. The impetus toward scientific reform that motivated these this sharpening of definitions and research goals was met by an equally strong drive to broaden coevolutionary theory, applying it to the human cultural context. While these extensions of "coevolution" to human culture fell clearly outside the bounds of scientific discourse, many coevolutionary scientists were complicit, or even active, in their popularization. The growing acknowledgement of the importance of reciprocal interactions both inside and outside science was gratifying to many of these biologists.

---

[139] May Berenbaum, "Postgenomic Chemical Ecology: From Genetic Code to Ecological Interactions," *Journal of Chemical Ecology* 28, no. 5 (2002): 891.

Moreover, coevolutionary theory did appear to offer useful lessons—again, hinging upon this central element of reciprocal interaction—for the betterment of human culture, particularly in how it related to the rest of nature. Some, like Whittaker, saw a cautionary moral in coevolutionary theory, suggesting that humans were "autotoxically" poisoning ourselves and other species with both natural and synthetic toxins. In other words, in the process of gene-culture coevolution, humans were losing the coevolutionary "arms race" with our own toxic technology. Others, however, saw gene-culture coevolution in a far more optimistic light, as an opportunity for proactive positive cultural change, which would have manifold positive consequences for humans and the organisms with which we coevolve. Ehrlich and Janzen both built a philosophy of conservation upon this premise, which reached the broader cultural sphere, particularly through the iconoclastic venue of *The CoEvolution Quarterly*.

The ethos behind *The CoEvolution Quarterly* represents the notion of nature that coevolutionary scientists like Ehrlich and Janzen developed in the course of their work. Not only is a pure, unsullied form of nature an impossible construction, but the technology of humans, far from being an intruder in nature, could only be part of nature. Just as plants had genetically evolved toxic means of defending themselves against insects, so had humans culturally evolved toxic means of defending themselves—and their crops—against insects. In both cases, insects had evolved in response. And the coevolutionary arms race was on going.

But human cultural adaptation, unlike biological evolution, could respond to human intention and effort, and this was the key to a coevolutionist's view of conservation. In a sense, the technology of *control* had become part of the warp and weave of coevolutionary theory. Reciprocally, coevolutionary theory had also become part of the warp and weave of cultural notions of technology and environmental change. Acknowledging humans as part of nature, interacting with other organisms and provoking change, implies both only the destructive potential of industrial and agricultural pollution *and* the judicious and evolutionarily progressive use of technology. And saving nature means controlling it—managing it like a garden.

An increasingly global perspective on the evolution of organismal interactions required that coevolutionary scientists also begin to fully acknowledge the importance of historical contingency. This meant that ecological interactions observed at the local level, within narrow, specific geographical ranges, had to be understood as products of unique evolutionary and ecological processes. Thus, knowledge about particular coevolved relationships could not easily be generalized over multiple populations of interacting organisms. Thompson's geographic mosaic model accommodated these insights in a fresh way, while building on what I see as the core principle and strength of coevolution, both in its scientific pursuit and its cultural extensions: dynamic reciprocal change. As Berenbaum told me, "It seems to be inherent in ecology, to polarize. And I think it might be because everything is so debatable. When phenomena are not repeatable, easily repeatable, opinions tend to get polarized. Because there's ambiguity. You don't have people questioning fundamental chemical principles, because they are endlessly repeatable. Very few ecological phenomena are endlessly repeatable. I mean, you can do the same study one state over, one county over, and get a different result. So, it's hard to be—it's hard to definitively rule out anything because of this problem with repeatability."[140] Within this context, where local differences can change everything, yet global theory is still idealized, a model of dynamic, responsive change may be the only viable one.

Nonetheless, for all its lack of disciplinary coherence, the general success of coevolutionary theory seems impressive to today's coevolutionists. A measure of that success, according to Berenbaum, is that—finally—"people are beginning to realize now that the terrestrial plant diversity we see around us would not exist without insect diversity."[141] And that, as I have documented in past chapters, is no small feat.

---

[140] Berenbaum. Interview by author. Digital audio recording. Champaign-Urbana, IL, 19 April 2007. Berenbaum continued here, saying that ecologists "know their particular corner of the world very well and that corner of the world is more predictable because of their greater familiarity with that corner of the world. But how generalizable it is…?" When I suggested that she was striving to be familiar with many different "corners of the world," she replied that, "as a consequence, I'm kind of on thin ice a lot. I don't know as much about butterflies as a butterfly systematist, I don't know as much about phytochemistry as a phytochemist. You know, so, being on the interface is kind of a—you have to keep moving, or the ice breaks."

[141] Ibid.

Conclusion

In this dissertation, I have argued that the rapidly growing domain of coevolutionary studies, from the 1960s onward, was rooted in the same fields where crop plants grew, and where agronomists, farmers, and economic entomologists first discovered the ability of chemical agents to cause evolution in insect populations. The ability of humans to cause such widespread evolutionary change—through unintentional, *natural* selection—had profound effects for both basic biological knowledge and for how we, as humans, see our place in nature. Most significantly, humans became participants in nature, both as subjects and as causal agents of evolutionary change. Molecules, whether produced by plants or by humans, were a form of natural technology: evolutionary adaptations for community-level interactions.

Foundational to this shift, and to coevolutionary studies as a whole, was the early-20th-century process of molecularization, by which physiologists gained an increasingly sophisticated knowledge of molecules and a belief in the important role that molecules played in society. In the words of Lily Kay, molecularization allowed the "conceptualization of life as a technology,"[1] and, consequently, the conceptualization of molecules as natural tools. Moreover, this shift did not reduce all biological phenomena to mere epiphenomena of microscopic master molecules. To the contrary, the molecular work of insect physiologists like Gottfried Fraenkel promoted a highly interactive interpretation of the ecological relationships between insects and plants. An awareness of

---

[1] Lily E. Kay, *Who Wrote the Book of Life? A History of the Genetic Code*, ed. Timothy Lenoir and Hans Ulrich Gumbrecht, Writing Science (Stanford: Stanford University Press, 2000).

molecules moving through both time and space, as integrated parts of organisms that shared intimate interactions with other organisms, lent a historical dimension to this research that belies the claims many scholars make about reductionism in 20th-century molecularization.

It is in this recasting of molecules as natural tools that Pauly's engineering ideal is most relevant. As in his study, coevolutionary researchers found motivation in both social goals and in the pursuit of so-called "pure" science. While evolutionary research on relationships between insects and plants was a form of basic biology, there is no doubt that it also drew from a wellspring of agricultural data and had direct relevance to agricultural practices. Moreover, in the hands of insect physiologists and entomologists, plant compounds became active, isolable agents—“natural insecticides” that could be extracted and manipulated. Synthetic insecticides were a technology engineered by humans and natural insecticides were a technology engineered by natural selection. And the potential of this natural technology for future evolutionary engineering, by humans, was as much a part of coevolutionary studies as insect physiology and biochemistry.

Through the dialectic between molecular and evolutionary practices described above, coevolutionary studies blossomed in the late 1960s and throughout the 1970s. Critical to this growth was the meeting of multiple disciplines, most notably ecology with evolutionary biology, and biology with chemistry. Both of these pairings had their challenges. In particular, changes on ecological and evolutionary time scales were difficult to synthesize. But rapid evolution in insect populations began to bridge the gap between ecological time and evolutionary time. Furthermore, the methods of molecularization allowed coevolutionists like Daniel Janzen and Paul Feeny to trace chemical compounds through ecological and evolutionary space and time. Janzen and Feeny saw molecules not as the ultimate causes for complex biological interactions, but as handles with which they could grasp the dynamics of those interactions and understand the ultimate causation of their evolutionary histories. Through this work, biochemical interactions themselves were transformed into a form of evolutionary adaptation.

Thus, the existence of a natural technology, evolved by plants in order to repel or poison insects, began to make natural sense of the synthetic poisons engineered by humans. In this fashion, the repercussions of insecticide research became a part of coevolutionary theory, building a sense of “chemical control” into nature and—conversely—of adaptive “natural insecticides” into human efforts to control pest insects.

My analysis concurs with more recent scholarship by both Pauly and Russell. Pauly's history of horticulture in the United States reclaims the word "culture" as "an umbrella term for efforts at biotic improvement."[2] As with the engineering ideal, then, culture is about the control of nature. However, just as in my account, the responsive abilities of organisms become just as critical to biological change as human intention is. Pauly emphasizes "the extent to which organisms have been evolutionary actors adapting themselves to the conditions created by people…Plants, insects, and fungi pursued their own reproductive and evolutionary strategies, and some moved successfully in and out of cultured settings." Here he even cites coevolution as an explanation for the success of

---

[2] Philip J. Pauly, *Fruits and Plains: The Horticultural Transformation of America* (Cambridge: Harvard University Press, 2007), 6.

such opportunistic weeds.[3] In other words, in human efforts to manage other organisms, nature and culture blur, and the agency of all participating organisms is felt.

Similarly, Russell promotes a new form of historical investigation that he has dubbed "evolutionary history," in which the interplay between biotic evolutionary change and human cultural history plays a central role. "Many of us think of evolutionary ideas as tools for biologists, not humanists," Russell writes. "But humans have shaped the evolution of countless species for millennia, reshaping human experience as well as the genes of other species."[4] As in my account, Russell features the evolution of insecticide resistance as a primary example of this evolutionary interaction between culture and nature, writing, "Artificial evolution—and thus anthropogenic evolution—has been [both] unintentional and intentional."[5] From this sentence it becomes clear, however, how dramatically my perspective diverges from Russell's. Dobzhansky was not being careless when he wrote that the evolution of insecticide resistance was a form of natural selection. Humans had *unintentionally* exerted a selective pressure upon pest insect populations, a distinctly different form of selection from the *intentional*, artificial selection of domestication. In claiming that the evolution of insecticide resistance was the result of some form of unintentional artificial selection, Russell reinforces the boundary between nature and humanity, rather than undermining it. "Artificial" remains the byword for "what humans do." In an edited volume on "evolutionary history," Russell reinforces this division between the natural and the human, writing, "humans and

---

[3] Ibid., 7.
[4] Edmund Russell, "Evolutionary History: Prospectus for a New Field," *Environmental History* 8, no. 2 (2003): 205.
[5] Ibid.: 207.

nature have been molding each other for millennia."[6] A review of the book indicates that this is a trend continued throughout the collection of essays, where the definition of nature "simply appears to be everything that is not human."[7]

By contrast, I suggest that the reciprocal interchange between insecticide research and coevolutionary theory had the power to undermine simplistic distinctions between natural and unnatural, and between humans and nature. When plants' adaptations came to be seen as weapons in a global, historical war against pests, it changed the very character of the war itself. And when biologists drew evocative analogies between human-insect interactions and plant-insect interactions, they formulated a new body of theory that could unify both types of evolutionary interactions. In describing insects and plants locked in warfare, anthropomorphic notions were projected onto these organisms, giving them a new level of agency in their environments. Simultaneously, the language used by coevolutionists had a way of feeding back upon human social interactions. Thus, in using the powerfully suggestive language of warfare to describe interactions between plants and insects, coevolutionary biologists were taking part in a larger cultural exercise, working out ideas about ourselves and how we relate to nature. In other words, humans use technology to interact with nature, both responding to and provoking evolutionary change because we are a part of nature.

---

[6] ———, "Introduction: The Garden in the Machine: Toward an Evolutionary History of Technology," in *Industrializing Organisms: Introducing Evolutionary History*, ed. Susan Schrepfer and Philip Scranton (London: Routledge, 2003), 6.
[7] Dorothee Brantz, "Review: Industrializing Organisms: Introducing Evolutionary History," *Journal of the History of Biology* 38 (2005): 644.

As coevolutionary theory gained prominence within evolutionary biology, it also gained cachet outside of science. Coevolutionary biologists played a large role in the dissemination of coevolutionary ideas, offering lessons for society based upon their understanding of coevolution. Some, like Robert Whittaker, warned that humans were “autotoxically” poisoning ourselves and other species with both natural and synthetic toxins, thereby losing the coevolutionary “arms race” with our own toxic technology. Others, like Janzen and Ehrlich, saw the implications of coevolution for society far more optimistically. The human capacity to evolve culturally—in technological application or any other cultural respect—represented an opportunity to establish a more mutualistic relationship with the rest of life on earth. "Pure" nature, separate from humans, is an impossibility. Acknowledging our embeddedness in nature required us to also see our responsibility toward the rest of nature, a responsibility that could be fulfilled with the help of technology. Both of these coevolutionists established a philosophy of conservation on this basis. Saving nature means controlling it, managing it like a garden.

At the same time, coevolutionary biologists also worked to reform coevolutionary studies from the inside, calling for a more critical approach to Janzen's question, "When is it coevolution?" Approaching this question more rigorously meant assimilating the importance of historical contingency into coevolutionary studies: The most convincing apparent cases of tight, pairwise coevolution could easily be the result of species coming together entirely by chance. Because the globe is composed of an almost infinite variety of different evolutionary contexts, a "geographic mosaic," it became apparent that ecological interactions observed at a local level, within narrow, specific geographical ranges, had to be understood as products of unique evolutionary and ecological processes. Nonetheless, the core value of *interaction* remains, and is strengthened by the acknowledgment that the unique set of interactions that defines each geographical area on earth has its only special ecological and evolutionary repercussions.

At the beginning of this dissertation I claimed that in the development of coevolutionary studies, *knowing* was inextricable from *doing*. In other words, knowledge about the natural world was deeply marked by the human process of interacting with and altering the world. What emerged from this union of knowing and doing was not an attenuated form of knowing, weakened by a confusion of priorities introduced by doing. Instead, what emerged was a fuller form of knowledge, one that could not avoid seeing the involvement of humans in the natural world that they strove to understand, making the natural world a profoundly interactive place. More than anything else, this is what gives coevolutionary theory its compelling quality and its broad relevance. While the aftermath of destructive human action is unavoidable in such an interactive world, it also offers the promise of continual change. The coevolutionary race never ends. And rather than an ominous warning that we will always be running from the repercussions of our actions, the endless race suggests that opportunities for changing the outcome of coevolution with our fellow organisms—for the better—always remain.

Bibliography

Ackert, Lloyd T. "The Role of Microbes in Agriculture: Sergei Vinogradskii's Discovery and Investigation of Chemosynthesis, 1880–1910." *Journal of the History of Biology* 39 (2006): 373-406.

Allen, Garland E. "A Century of Evo-Devo: The Dialectics of Analysis and Synthesis in Twentieth-Century Life Science." In *From Embryology to Evo-Devo: A History of Developmental Evolution*, edited by Manfred D. Laublicher and Jane Maienschein, 123-167. Cambridge: The MIT Press, 2007.

Andrewartha, H.G., and L.C. Birch. *The Distribution and Abundance of Animals*. Chicago: University of Chicago Press, 1954.

Apple, Rima D. *Vitamania: Vitamins in American Culture*. New Brunswick, NJ: Rutgers University Press, 1996.

Bartholomew, Bruce. "Bare Zone between California Shrub and Grassland Communities: The Role of Animals." *Science* 170 (1970): 1210-1212.

Beer, Gillian. *Darwin's Plots: Evolutionary Narrative in Darwin, George Eliot and Nineteenth-Century Fiction, 2nd Ed.* Cambridge: Cambridge University Press, 2000.

Bell, E.A., and Daniel H. Janzen. "Medical and Ecological Considerations of L-Dopa and 5-Htp in Seeds." *Nature* 229 (1971): 136-137.

Bell, E.A., and J.R. Nulu. "L-Dopa and L-3-Carboxy-6,7-Dihydroxy-1,2,3,4-Tetrahydroisoquinoline, a New Imino Acid, from Seeds of *Mucuna Mutisiana*." *Phytochemistry* 10 (1971): 2191-2194.

Belt, Thomas. *The Naturalist in Nicaragua*. London: E. Bumpus, 1888.

Bentley, Barbara L. "Review: Coevolution of Animals and Plants." *The Quarterly Review of Biology* 51, no. 3 (1976): 431-432.

Berenbaum, May. "Coumarins and Caterpillars: A Case for Coevolution." *Evolution* 37, no. 1 (1983): 163-179.

———. "Genetic Variation in Cytochrome P450-Based Resistance to Plant Allelochemicals and Insecticides." In *Herbivores: Between Plants and Predators*, edited by H. Olff, V.K. Brown and R.H. Drent, 55-84. Oxford: Blackwell, 1999.

———. "Patterns of Furanocoumarin Distribution and Insect Herbivory in the Umbelliferae: Plant Chemisry and Community Structure." *Ecology* 62, no. 5 (1981): 1254-1266.

———. "Postgenomic Chemical Ecology: From Genetic Code to Ecological Interactions." *Journal of Chemical Ecology* 28, no. 5 (2002): 873-896.

———. "Toxicity of a Furanocoumarin to Armyworms: A Case of Biosynthetic Escape from Insect Herbivores." *Science* 201, no. 4355 (1978): 532-534.

Berenbaum, May, and Paul Feeny. "Toxicity of Angular Furanocoumarins to Swallowtail Butterflies: Escalation in a Ceovolutionary Arms Race?" *Science* 212 (1981): 927-929.

Berenbaum, May R., and Arthur Z. Zangerl. "Facing the Future of Plant-Insect Interaction Research: Le Retour À La ‘‘Raison D’être’’." *Plant Physiology* 146 (2008): 804-811.

Bernhardt, Peter. "Review: Coevolution of Animals and Plants." *Bulletin of the Torrey Botanical Club* 104, no. 3 (1977): 286-287. *Biochemical Interactions among Plants*. Washington, DC: National Academy of Sciences, 1971.

Black, Max. *Models and Metaphors: Studies in Language and Philosophy*. Ithaca: Cornell University Press, 1962.

Bonner, James. "The Role of Toxic Substances in the Interactions of Higher Plants." *The Botanical Review* 16 (1950): 51-65.

Bonner, John Tyler. "The Chemical Ecologyof Cells in the Soil." In *Chemical Ecology*, edited by Ernest Sondheimer and John B. Simeone, 1-19. New York: Academic Press, 1970.

Bono, James J. "Science, Discourse, and Literature: The Role/Rule of Metaphor in Science." In *Literature and Science: Theory & Practice*, edited by Stuart Peterfreund, 59-90. Boston: Northeastern University Press, 1990.

Borell, Merriley. "Organotherapy, British Physiology, and Discovery of the Internal Secretions." *Journal of the History of Biology* 9, no. 2 (1976): 235-268.

Borrello, Mark E. "Synthesis and Selection: Wynne-Edwards’ Challenge to David Lack." *Journal of the History of Biology* 36 (2003): 531-566.

Brady, John. "J.S. Kennedy (192-1993): A Clear Thinker in Behavior's Confused World." *Annual Review of Entomology* 42 (1997): 1-22.

Brand, Stewart. ""Coevolution"." *The CoEvolution Quarterly* 2 (1974): cover.

———. "Introduction To: Coevolution and the Biology of Communities." In *News That Stayed News, 1974-1984: Ten Years of the Coevolution Quarterly*, edited by Art Kleiner and Stewart Brand, 3. San Francisco: North Point Press, 1986.

Brantz, Dorothee. "Review: Industrializing Organisms: Introducing Evolutionary History." *Journal of the History of Biology* 38 (2005): 641-645.

Breedlove, D.E., and P.R. Ehrlich. "Coevolution: Patterns of Legume Predation by a Lycaenid Butterfly." *Oecologia* 10 (1971): 99-104.

———. "Plant-Herbivore Coevolution: Lupines and Lycaenids." *Science* 162 (1968): 671-672.

Brower, Lincoln P. "Plant Poisons in a Terrestrial Food Chain and Implications for Mimicry Theory." In *Biochemical Coevolution: Proceedings of the Twenty-Ninth Annual Biology Colloquium, April 26-27, 1968*, edited by Kenton L. Chambers. Corvallis: Oregon State University Press, 1970.

———. "Review: Coevolution of Animals and Plants." *Science* 190, no. 4213 (1975): 455-456.

Brower, Lincoln P., Jane Van Zandt Brower, and Joseph M. Corvino. "Plant Poisons in a Terrestrial Food Chain." *Proceedings of the National Academy of Science* 57, no. 4 (1967): 893-898.

Brown, Gordon. "Foreword." In *Radicals and Reformers: A Century of Fabian Thought*, edited by Mark Thomas and Guy Lodge, 4-5. London: Fabian Society, 2000.

Buhs, Joshua Blu. "The Fire Ant Wars: Nature and Science in the Pesticide Controversies of the Late Twentieth Century." *Isis* 93 (2002): 377-400.

———. *The Fire Ant Wars: Nature, Science, and Public Policy in Twentieth-Century America*. Chicago: University of Chicago Press, 2004.

Carter, Herbert E., P.K. Bhattacharyya, Katharine R. Weidman, and Gottfried S. Fraenkel. "Chemical Studies on Vitamin B(T). Isolation and Characterization as Carnitine." *Archives of Biochemistry and Biophysics* 38 (1952): 405-416.

Ceccatti, John S. "Biology in the Chemical Industry: Scientific Approaches to the Problem of Insecticide Resistance, 1920s-1960s." *AMBIX* 51, no. 2 (2004): 135-147.

———. "Resisting Insects: Shifting Strategies in Chemical Control." *Endeavour* 28, no. 1 (2004): 14-19.

Chadarevian, Soraya de. "Following Molecules: Hemoglobin between the Clinic and the Laboratory." In *Molecularizing Biology and Medicine: New Practices and Alliances, 1910s-1970s*, edited by Soraya de Chadarevian and Harmke Kamminga, 171-202. Amsterdam: Harwood Academic Publishers, 1998.

Chadarevian, Soraya de, and Jean-Paul Gaudillière. "The Tools of the Discipline: Biochemists and Molecular Biologists." *Journal of the History of Biology* 29 (1996): 327-330.

Chadarevian, Soraya de, and Harmke Kamminga. "Introduction." In *Molecularizing Biology and Medicine: New Practices and Alliances, 1910s-1970s*, edited by Soraya de Chadarevian and Harmke Kamminga, 1-16. Amsterdam: Harwood Academic Publishers, 1998.

Chapman, R.F. "Entomology in the Twentieth Century." *Annual Review of Entomology* 45 (2000): 261-285.

Cittadino, Eugene. "Ecology and the Professionalization of Botany in America, 1890-1905." *Studies in the History of BIology* 4 (1980): 171-198.

Collins, James P. "'Evolutionary Ecology' and the Use of Natural Selection in Ecological Theory." *Journal of the History of Biology* 19 (1986): 257-288.

Collins, James P., John Beatty, and Jane Maienschein. "Introduction: Between Ecology and Evolutionary Biology." *Journal of the History of Biology* 19, no. 2 (1986): 169-180.

Cornel, Anthony, Matthew Stanich, Rory McAbee, and F. Mulligan. "High Level Methoprene Resistance in Hte Mosquito Ochlerotatus Nigromaculis (Ludlow) in Central California." *Pest Management Science* 58, no. 8 (2002): 791-798.

Creager, Angela N. H. *The Life of a Virus: Tobacco Mosaic Virus as an Experimental Model, 1930-1965*. Chicago: University of Chicago Press, 2002.

Daston, Lorraine, and Gregg Mitman. "Introduction: The How and Why of Thinking with Animals." In *Thinking with Animals: New Perspectives on Anthropomorphism*, edited by Lorraine and Gregg Mitman Daston, 1-14. New York: Columbia University Press, 2005.

Daston, Lorraine, and Fernando Vidal, eds. *The Moral Authority of Nature*. Chicago: University of Chicago Press 2004.

Dawkins, R., and J.R. Krebs. "Arms Races between and within Species." *Proceedings of the Royal Society of London, Series B* 205, no. 1161 (1979): 489-511.

Dawkins, Richard. *The Selfish Gene*. Oxford: Oxford University Press, 1976.

Dawkins, Richard, and Daniel Dennett. *The Extended Phenotype: The Long Reach of the Gene*. Oxford: Oxford University Press, 1999.

Demerec, Milislav. "Development of Bacterial Resistance to Chemicals." In *Conference on Insecticide Resistance and Insect Physiology*. Washington, DC: National Academy of Sciences, National Research Council, 1952.

Dethier, Vincent. "Chemical Interactions between Plants and Insects." In *Chemical Ecology*, edited by Ernest Sondheimer and John B. Simeone, 83-102. New York: Academic Press, 1970.

Dethier, Vincent G. *Man's Plague? Insects and Agriculture*. Princeton, NJ: The Darwin Press, Inc., 1976.

Dethier, Vincent G, Gottfried S. Fraenkel, and Reginald S. Painter. "The Physiological Relations between Insects and Their Foodplants." In *Symposia of the Ixth International Congress of Entomology (Amsterdam)*, 81-105. Amsterdam: DR W. Junk, Publishers, 1953.

Dethier, Vincent G. "Chemical Factors Determining the Choice of Food Plants by Papilio Larvae." *The American Naturalist* 75, no. 756 (1941): 61-73.

———. *Chemical Insect Attractants and Repellents*. Philadelphia: The Blakiston Company, 1947.

———. "Gustation and Olfaction in Lepidopterous Larvae." *Biological Bulletin* 72 (1937): 7-23.

———. "Host Plant Perception in Phytophagous Insects." In *Symposia of the Ixth International Congress of Entomology (Amsterdam)*, 81-89. Amsterdam: DR W. Junk, Publishers, 1953.

Dobzhansky, Theodosius. *Genetics and the Origin of Species*. New York: Columbia University Press, 1937.

———. "Summary of Remarks of Th. Dobzhansky." In *Conference on Insecticide Resistance and Insect Physiology*, 86-88. Washington, DC: National Academy of Sciences, National Research Council, 1952.

Doel, Ronald E. "Oral History of American Science: A Forty-Year Review." *History of Science* 41 (2003): 349-378.

Dunn, Rob. *Every Living Thing: Man's Obsessive Quest to Catalog Life, from Nanobacteria to New Monkeys* Washington, DC: Smithsonian, 2008.

Edwards, John S. "Sir Vincent Wigglesworth and the Coming Age of Insect Development." *International Journal of Developmental Biology* 42 (1998): 471-473.

Egerton, Frank N. "Changing Concepts of the Balance of Nature." *Quarterly Review of Biology* 48 (1973): 322-350.

Ehrlich, Anne E., and Paul R. Ehrlich. "Ehrlichs' Guide to the Apocalypse: Food." *The CoEvolution Quarterly* 2 (1974): 21-39.

Ehrlich, Anne, and Paul R. Ehrlich. "Coevolution and Pest Control." *The Mother Earth News* 50 (1978): 148-149.

Ehrlich, Paul R. "An Ecologist Standing up among Seated Social Scientists." *The CoEvolution Quarterly* 31 (1981): 24-37.

———. "Coevolution and Its Applicability to the Gaia Hypothesis." In *Scientists on Gaia*, edited by Stephen H. Schneider, 19-22. Cambridge: The MIT Press, 1991.

———. "Coevolution and the Biology of Communities." In *Biochemical Coevolution: Proceedings of the Twenty-Ninth Annual Biology Colloquium, April 26-27, 1968*, edited by Kenton L. Chambers. Corvallis: Oregon State University Press, 1970.

———. "Human Natures, Nature Conservation, and Environmental Ethics." *BioScience* 52, no. 1 (2002): 31-43.

———. *Human Natures: Genes, Cultures, and the Human Prospect*. Washington, DC: Island Press, 2000.

———. "Recombinant DNA, Paul Ehrlich, and Friends of the Earth." *The CoEvolution Quarterly* 17 (1978): 24-26.

———. *The Population Bomb*. New York: Ballantine Books, 1968.

———. "This Week's Citation Classic: Butterflies and Plants: A Study in Coevolution." *Citation Classics* 37 (1984): 16.

———. "We're Standing at the Edge of the World." *National Wildlife* October-November (1970): 16-17.

Ehrlich, Paul R., and L.C. Birch. "The 'Balance of Nature' and 'Population Control'." *The American Naturalist* 101 (1967): 97-107.

Ehrlich, Paul R., and John P. Holdren. "The Co-Evolutionary Race." *Saturday Review* (1970): 66.

Ehrlich, Paul R., and Peter H. Raven. "Butterflies and Plants." *Scientific American* 216, no. 6 (1967): 104-113.

———. "Butterflies and Plants: A Study in Coevolution." *Evolution* 18, no. 4 (1964): 586-608.

Eisner, Thomas. "Catnip: Its Raison D'être." *Science* 146, no. 369 (1964): 1318-1320.

Errera, Leo, Maistriau, and G. Clautriau. *Premières Recherches Sur La Localisation Et La Signification Des Alkaloids Dans Les Plantes*. Brussels: Henri Lamerin, 1887.

Feeny, Paul. "Biochemical Coevolution between Plants and Their Insect Herbivores." In *Coevolution of Animals and Plants: Symposium V; First International Congress of Systematic and Evolutionary Biology; Boulder, Colorado; August 1973*, edited by Lawrence E. Gilbert and Peter H. Raven, 3-19. Austin: University of Texas Press, 1975.

———. "Plant Apparency and Chemical Defense." In *Recent Advances in Phytochemistry, Volume 10: Biochemical Interaction between Plants and Insects*, edited by James W. Wallace and Richard L. Mansell, 1-40. New York: Plenum Press, 1976.

Feeny, Paul P. "Effect of Oak Leaf Tannins on Larval Growth of the Winter Moth *Operophtera Brumata*." *Journal of Insect Physiology* 14 (1968): 805-817.

———. "Inhibitory Effect of Oak Leaf Tannins on the Hydrolysis of Proteins by Trypsin." *Phytochemistry* 8 (1969): 2119-2126.

———. "Seasonal Changes in Oak Leaf Tannins and Nutrients as a Cause of Spring Feeding by Winter Moth Caterpillars." *Ecology* 51 (1970): 565-581.

———. "The Evolution of Chemical Ecology: Contributions from the Study of Herbivorous Insects." In *Herbivores: Their Interactions with Secondary Plant Metabolites, Second Edition*, 1-44. San Diego: Academic Press, 1992.

Fraenkel, Gottfried S. "A Hormone Causing Pupation in the Blowfly *Calliphora Erythrocephala*." *Proceedings of the Royal Society of London. Series B, Biological Sciences* 118, no. 807 (1935): 1-12.

———. "B(T), a New Vitamin of the B-Group and Its Relation to the Folic Acid Group, and Other Anti-Anaemia Factors." *Nature* 161, no. 4103 (1948): 981-983.

———. "Britain's Nutritional Requirements." In *Towards a Socialist Agriculture: Studies by a Group of Fabians*, edited by F.W. Bateson, 42-76. London: Victor Gollancz LTD, 1946.

———. "Effect and Distribution of Vitamin B(T)." *Archives of Biochemistry and Biophysics* 34, no. 2 (1951): 457-467.

———. "Evaluation of Our Thoughts on Secondary Plant Substances." *Entomologia Experimentalis et Applicata* 12, no. 5 (1969): 473-486.

———. "Insects and Plant Biochemistry: The Specificity of Food Plants for Insects." *Proceedings of the XIV International Congress of Zoology, Copenhagen* (1956).

———. "Isolation Procedures and Certain Properties of Vitamin B(T)." *Archives of Biochemistry* 34, no. 2 (1951): 468-477.

———. "Pupation of Flies Initiated by a Hormone." *Nature* 133 (1934): 834.

———. "The Importance of Folic Acid and Unidentified Members of the Vitamin B Complex in the Nutrition of Certain Insects." *The Biochemical Journal* 41 (1947): 469-475.

———. "The Nutritional Value of Green Plants for Insects." In *Symposia of the Ixth International Congress of Entomology (Amsterdam)*, 90-100. Amsterdam: DR W. Junk, Publishers, 1953.

———. "The Raison D'être of Secondary Plant Substances." *Science* 129 (1959): 1466-1470.

———. "This Week's Citation Classic: The Raison D'être of Secondary Plant Substances." *Citation Classics* 11 (1984): 288.

———. "Utilization and Digestion of Carbohydrates by the Adult Blowfly." *Journal of Experimental Biology* 17 (1939): 18-29.

Fraenkel, Gottfried S., and M. Blewett. "Deficiency of Riboflavin in White Flour." *Nature* 147, no. 3736 (1941): 716-717.

———. "The Basic Food Requirements of Several Insect." *Journal of Experimental Biology* 20 (1943): 28-34.

———. "The Vitamin B-Complex Requirements of Several Insects." *The Biochemical Journal* 37 (1943): 686-696.

Fraenkel, Gottfried S., and Donald L. Gunn. *The Orientation of Animals, Kineses, Taxes and Compass Reactions*. New York: Dover Publications, 1961.

Fraenkel, Gottfried S., J.A. Reid, and M. Blewett. "The Sterol Requirements of the Larva of the Beetle, *Dermestes Vulpinus* Fabr." *The Biochemical Journal* 35 (1941): 721-720.

Futuyma, Douglas J. "Reflections on Reflections: Ecology and Evolutionary Biology." *Journal of the History of Biology* 19, no. 2 (1986): 303-312.

Futuyma, Douglas J., and Montgomery Slatkin. "Introduction." In *Coevolution*, edited by Douglas J. Futuyma and Montgomery Slatkin, 1-13. Sunderland, MA: Sinauer Associated Inc., 1983.

Garb, Solomon. "Differential Growth-Inhibitors Produced by Plants." *The Botanical Review* 27 (1961): 422-439.

Gaudillière, Jean-Paul, and Hans-Jörg Rheinberger, eds. *From Molecular Genetics to Genomics: The Mapping Cultures of Twentieth-Century Genetics*, Routledge Studies in the History of Science, Technology, and Medicine. London: Routledge, 2004.

Gelperin, Alan, John G. Hildebrand, and Thomas Eisner. "Vincent Gaston Dethier." *National Academy of Sciencece Biographical Memoirs* 89 (2007): 76-95.

Gilbert, Lawrence E. "Editor's Note on the Second Edition." In *Coevolution of Animals and Plants, Second Edition*, edited by Lawrence E. Gilbert and Peter H. Raven, ix-xiii. Austin: University of Texas Press, 1980.

Gilbert, Lawrence E., and Peter H. Raven, eds. *Coevolution of Animals and Plants: Symposium V; First International Congress of Systematic and Evolutionary Biology; Boulder, Colorado; August 1973*. Austin: University of Texas Press, 1975.

———. "General Introduction." In *Coevolution of Animals and Plants: Symposium V; First International Congress of Systematic and Evolutionary Biology; Boulder, Colorado; August 1973*, edited by Lawrence E. Gilbert and Peter H. Raven, ix-xiii. Austin: University of Texas Press, 1975.

Giles-Vernick, Tamara. "Oral Histories as Methods and Sources." In *A Handbook for Social Science Field Research: Essays and Bibliographic Sources on Research Design and Methods*, edited by Ellen Perecman and Sara R. Curran, 85-102. Thousand Oaks: SAGE Publications, 2006.

Golinski, Jan. *Making Natural Knowledge: Constructivism and the History of Science (with a New Preface)*. Chicago: University of Chicago Press, 2005.

Goodman, Jordan. "Can It Ever Be Pure Science? Pharmaceuticals, the Pharmaceutical Industry and Biomedical Research in the Twentieth Century." In *The Invisible Industrialist: Manufactures and the Production of Scientific Knowledge*, edited by Jean-Paul Gaudillière and Ilana Löwy, 143-166. NY: St. Martin's Press, Inc., 1998.

———. "Plants, Cells and Bodies: The Molecular Biography of Colchicine, 1930-1975." In *Molecularizing Biology and Medicine: New Practices and Alliances, 1910s-1970s*, edited by Soraya de Chadarevian and Harmke Kamminga, 17-46. Amsterdam: Harwood Academic Publishers, 1998.

Gordon, H.T. "Citation Classics: Rapid Paper Chromatography of Carbohydrates and Related Compounds." *Current Contents*, no. 13 (1984): 18.

Gould, Stephen J. "The Hardening of the Modern Synthesis." In *Dimensions of Darwinism: Themes and Counterthemes in Twentieth-Century Evolutionary*

Theory, edited by Marjorie Grene, 71-93. Cambridge: Cambridge University Press, 1983.

Gould, Stephen Jay, and Richard C. Lewontin. "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme " *Proceedings of the Royal Society of London, Series B* 205, no. 1161 (1979): 581-598.

Hagen, Joel B. *An Entangled Bank: The Origins of Ecosystem Ecology*. New Brunswick: Rutgers University Press, 1992.

Hairston, Nelson G., Frederick E. Smith, and Lawrence B. Slobodkin. "Community Structure, Population Control, and Competition." *The American Naturalist* 94 (1960): 421-425.

Halsey, Richard W. "In Search of Allelopathy: An Eco-Historical View of the Investigation of Chemical Inhibition in California Coastal Sage Scrub and Chamise Chaparral." *Journal of the Torrey Botanical Society* 131 (2004): 343-367.

Hartmann, Thomas. "The Lost Origin of Chemical Ecology in the Late 19th Century." *Proceedings of the National Academy of Science* 105, no. 12 (2008): 4541-4546.

Harwood, Jonathan. "Biology in the Universities." In *Life and Earth Sciences since 1800*, edited by Peter and John V. Pickstone Bowler. Cambridge: Cambridge University Press, forthcoming.

———. "Geneticists and the Evolutionary Synthesis in Interwar Germany." *Annals of Science* 42 (1985): 279-301.

———. "Introduction to the Special Issue on Biology and Agriculture." *Journal of the History of Biology* 39 (2006): 237-239.

———. "Metaphysical Foundations of the Evolutionary Synthesis: A Historiographic Note." *Journal of the History of Biology* 27, no. 1 (1994): 1-20.

———. "National Styles in Science: Genetics in Germany and the United States between the World Wars." *Isis* 78, no. 3 (1987): 390-414.

———. *Styles of Scientific Thought: The German Genetics Community, 1900-1933*. Chicago: The University of Chicago Press, 1993.

Hausman, Bernice L. "Ovaries to Estrogen: Sex Hormones and Chemical Femininity in the 20th Century." *Journal of the Medical Humanities* 20, no. 3 (1999): 165-176.

Heinrich, Bernd. "The Role of Energetics in Bumblebee-Flower Interrelationships." In *Coevolution of Animals and Plants: Symposium V; First International Congress of Systematic and Evolutionary Biology; Boulder, Colorado; August 1973*, edited by Lawrence E. Gilbert and Peter H. Raven, 141-158. Austin: University of Texas Press, 1975.

Hesse, Mary B. "Models, Metaphors and Truth." In *Knowledge and Language: Metaphor and Knowledge*, edited by F.R. and J.J.A. Mooij Ankersmit, 49-66. Dordrecht: Kluwer Academic Publishers, 1993.

———. *Revolutions and Reconstructions in the Philosophy of Science*. Bloomington: Indiana University Press, 1980.

Holm, LeRoy. "Chemical Interactions between Plants on Agricultural Lands." 95-101. Washington, DC: National Academy of Sciences, 1971.

Horrocks, Sally M. "Nutrition Science and the Food and Pharmaceutical Industries in Inter-War Britain." In *Nutrition in Britain: Science, Scientists and Politics in the Twentieth Century*, edited by David F. Smith. London: Routledge, 1997.

Hungerford, H.B. "Relation of Entomology to the War Effort." *Transactions of the Kansas Academy of Science* 46 (1943): 303-308.

Hutchinson, G. Evelyn. "Concluding Remarks." *Cold Spring Harbor Symposia on Quantitative Biology* 22 (1958): 415-427.

———. "Homage to Santa Rosalia or Why Are There So Many Kinds of Animals?" *The American Naturalist* 93 (1959): 145-159. *Insect-Plant Interactions*. Washington, DC: National Academy of Sciences, 1969.

Janzen, Daniel H. "Coevolution of Mutualism between Ants and Acacias in Central America." *Evolution* 20, no. 3 (1966): 249-275.

———. "Community Structure of Secondary Compounds in Plants." *Pure and Applied Chemistry* 34 (1973): 529-538.

———. "Embryonic Field of Ecology, Review: Insect/Plant Relationships." *Science* 182, no. 4117 (1973): 1125-1126.

———. "Gardenification of Tropical Conserved Wildlands: Multitasking, Multicropping, and Multiusers." *Proceedings of the National Academy of Science* 96, no. 11 (1999): 5987-5994.

———. "Gardenification of Wildland Nature and the Human Footprint." *Science* 279, no. 5355 (1998): 1312-1313.

———. "Herbivores and the Number of Tree Species in Tropical Forests." *The American Naturalist* 104, no. 940 (1970): 501-528.

———. "How Many Babies Do Figs Pay for Babies?" *Biotropica* 11 (1979): 48-50.

———. "Interaction of the Bull's-Horn Acacia (Acacia Cornigera L.) with an Ant Inhabitant (Pseudomyrmex Ferruginea F. Smith) in Eastern Mexico." *The University of Kansas Science Bulletin* 47, no. 6 (1967): 315-558.

———. "New Horizons in the Biology of Plant Defenses." In *Herbivores: Their Interaction with Secondary Plant Metabolites*, edited by Gerald A. Rosenthal and Daniel H. Janzen, 331-350. New York: Academic Press, Inc., 1979.

———. "Promising Directions of Study in Tropical Animal-Plant Interactions." *Annals of the Missouri Botanical Garden* 64, no. 4 (1977): 706-736.

———. "Promising Directions of Study in Tropical Animal-Plant Interactions." *Annals of the Missouri Botanical Garden* 64 (1977): 706-736.

———. "Review: Insect Abundance. Fourth Synmposium of the Royal Entomological Society of London." *Science* 162, no. 3853 (1968): 557.

———. "The Interaction of the Bull's-Horn Acacia (Acacia Cornigera L.) with One of Its Ant Inhabitants (Pseudomyrmex Fulvescens Emery) in Eastern Mexico." Ph.D. Diss., University of California, 1965.

———. "What Are Dandelions and Aphids?" *The American Naturalist* 111, no. 979 (1977): 586-589.

———. "When Is It Coevolution?" *Evolution* 34, no. 3 (1980): 611-612.

Janzen, Daniel H., and Cornelius H. Muller. "Coevolution." *Science* 165 (1969): 416.

Jermy, Tibor. "Insect-Host-Plant Relationship--Co-Evolution or Sequential Evolution?" *Symposium Biologica Hungarica* 16 (1976): 109-113.

Johns, Timothy. *With Bitter Herbs They Shall Eat It: Chemical Ecology and the Origins of Human Diet and Medicine* Tucson: University of Arizona Press, 1990.

Kamminga, Harmke. "Vitamins and the Dynamics of Molecularization: Biochemistry, Policy and Industry in Britain, 1914-1939." In *Molecularizing Biology and Medicine: New Practices and Alliances, 1910s-1970s*, edited by Soraya de Chadarevian and Harmke Kamminga, 83-106. Amsterdam: Harwood Academic Publishers, 1998.

Kay, Lily E. "'Biochemists and Molecular Biologists: Laboratories, Networks, Disciplines': Comments." *Journal of the History of Biology* 29 (1996): 447-450.

———. "Life as Technology: Representing, Intervening, and Molecularizing." *Rivista di Storia Della Scienza* 1, Series II, no. 1 (1993): 85-103.

———. *Who Wrote the Book of Life? A History of the Genetic Code*. Edited by Timothy Lenoir and Hans Ulrich Gumbrecht, Writing Science. Stanford: Stanford University Press, 2000.

Keller, Evelyn Fox. *Making Sense of Life: Explaining Biological Development with Models, Metaphors, and Machines*. Cambridge: Harvard University Press, 2002.

———. *Refiguring Life: Metaphors of Twentieth-Century Biology*. New York: Columbia University Press, 1995.

Kimler, William C. "Advantage, Adaptiveness and Evolutionary Ecology." *Journal of the History of Biology* 19 (1986): 215-233.

———. "Mimicry: Views of Naturalists and Ecologists before the Modern Synthesis." In *Dimensions of Darwinism: Themes and Counterthemes in Twentieth-Century Evolutionary Theory*, edited by Marjorie Grene, 97-127. Cambridge: Cambridge University Press, 1983.

———. "Mimicry: Views of Naturalists and Ecologists before the Modern Synthesis." In *Dimensions of Darwinism*, edited by Marjorie Grene. Cambridge: Cambridge University Press, 1983.

Kimmelman, Barbara A. *A Progressive Era Discipline: Genetics at American Agricultural Colleges and Experiment Stations, 1900-1920. Dissertation, University of Pennsylvania*, 1987.

———. "Organisms and Interests in Scientific Research: R.A. Emerson's Claims for the Unique Contribution of Agricultural Genetics." In *The Right Tools for the Job: At Work in Twentieth-Century Life Sciences*, edited by Adele E. and Joan H. Fujimura Clarke, 198-232. Princeton: Princeton University Press, 1992.

———. "The American Breeders' Association: Genetics and Eugenics in an Agricultural Context, 1903-13." *Social Studies of Science* 13, no. 2 (1983): 163-204.

Kingsland, Sharon E. *Modeling Nature: Episodes in the History of Population Ecology, 2nd Ed.* Chicago: University of Chicago Press, 1995.

———. *The Evolution of American Ecology, 1890-2000*. Baltimore: Johns Hopkins University Press, 2005.

Kirk, Andrew. *Counterculture Green: The Whole Earth Catalog and American Environmentalism*. Lawrence: University Press of Kansas, 2007.

Kleinman, Kim. "His Own Synthesis: Corn, Edgar Anderson, and Evolutionary Theory in the 1940s." *Journal of the History of Biology* 32 (1999): 293-320.

Knorr, Karin D. "The Scientist as Analogical Reasoner: A Critique of the Metaphor Theory of Innovation." In *The Social Process of Scientific Investigation*, edited by Roger and Richard Whitley Krohn, 25-52. Dordrecht: Kluwer Academic Publishers, 1980.

Kohler, Robert E. *Landscapes and Labscapes: Exploring the Lab-Field Border in Biology*. Chicago: University of Chicago Press, 2002.

———. *Lords of the Fly: Drosophila Genetics and the Experimental Life*. Chicago: University of Chicago Press, 1994.

Kopec, S. "Studies on the Necessity of the Brain for the Inception of Insect Metamorphosis." *Biological Bulletin* 43 (1922): 323-342.

Lack, David. *Darwin's Finches*. Cambridge: The University Press, 1947.

———. "Evolutionary Ecology." *Journal of Animal Ecology* 34 (1965): 223-231.

Largent, Mark. "Darwin's Analogy between Artificial and Natural Selection in the Origin of Species." In *The Cambridge Companion to The "Origin of Species"*, edited by Michael Ruse and Robert J. Richards. Cambridge: Cambridge University Press, 2009.

Levins, Richard, and Richard C. Lewontin. "Introduction." In *The Dialectical Biologist*, edited by Richard Levins and Richard Lewontin. Cambridge: Harvard University Press, 1985.

Loehwing, W.F. "Root Interactions of Plants." *The Botanical Review* 3 (1937): 195-239.

Lovelock, James E. "Letter to the Editors: Gaia as Seen through the Atmosphere." *Atmospheric Environment* 6 (1972): 579-580.

Maasen, Sabine. "Who Is Afraid of Metaphors?" In *Biology as Society, Society as Biology: Metaphors*, edited by Sabine Maasen, Everett Mendelsohn, and Peter Weingart, 11-36. Dordrecht: Kluwer Academic Publishers, 1995.

Maasen, Sabine and Peter Weingart. *Metaphors and the Dynamics of Knowledge*. London: Routledge, 2000.

Maasen, Sabine, Everett Mendelsohn, and Peter Weingart. "Metaphors: Is There a Bridge over Troubled Waters?" In *Biology as Society, Society as Biology: Metaphors*, edited by Sabine Maasen, Everett Mendelsohn, and Peter Weingart, 1-10. Dordrecht: Kluwer Academic Publishers, 1995.

MacArthur, Robert, and Edward O. Wilson. *The Theory of Island Biogeography*. Princeton: Princeton University Press, 1967.

Maltz, Alesia. "The Role of Language in the Discovery and Acceptance of Vitamins." Ph.D. diss., University of Illinois at Urbana-Champaign 1990.

Margulis, Lynn, and Gregory Hinkle. "The Biota and Gaia: 150 Years of Support for Environmental Sciences." In *Scientists on Gaia*, edited by Stephen H. Schneider, 11-18. Cambridge: The MIT Press, 1991.

Margulis, Lynn, and James E. Lovelock. "The Atmosphere as Circulatory System of the Biosphere - the Gaia Hypothesis." *The CoEvolution Quarterly* 5 (1975): 31-40.

Mayhew, Madeleine. "The 1930s Nutrition Controversy." *Journal of Contemporary History* 23, no. 3 (1988): 445-464.

Mayr, Ernst. "Cause and Effect in Biology." *Science* 134 (1961): 1501-1506.

McKey, Doyle. "The Ecology of Coevolved Seed Dispersal Systems." In *Coevolution of Animals and Plants: Symposium V; First International Congress of Systematic and Evolutionary Biology; Boulder, Colorado; August 1973*, edited by Lawrence E. Gilbert and Peter H. Raven, 159-191. Austin: University of Texas Press, 1975.

Mellors, Robert E. "Obituary, M.C. Winternitz, M.D. (1885-1959)." *Cancer* 13, no. 1 (1960): 4.

Merchant, Carolyn. *The Death of Nature: Women, Ecology, and the Scientific Revolution*. San Francisco: Harper & Row, 1990.

Michener, Charles D. "A Method of Rearing Chigger Mites (Acarina, Trombiculinae)." *American Journal of Tropical Medicine* 26 (1946): 251-256.

———. "Comments." In *Conference on Insecticide Resistance and Insect Physiology*, 77. Washington, DC: National Academy of Sciences, National Research Council, 1952.

———. "The Professional Development of an Entomologist." *Annual Review of Entomology* 52 (2007): 1-15.

Mitman, Gregg. "When Pollen Became Poison: A Cultural Geography of Ragweed." In *The Moral Authority of Nature*, edited by Lorraine and Fernando Vidal Daston, 438-465. Chicago: The University of Chicago Press, 2004.

Mitter, Charles, and Daniel R. Brooks. "Phylogenetic Aspects of Coevolution." In *Coevolution*, edited by Douglas J. Futuyma and Montgomery Slatkin, 65-98. Sunderland, MA: Sinauer Associated Inc., 1983.

Mode, Charles J. "A Mathematical Model for the Co-Evolution of Obligate Parasites and Their Hosts." *Evolution* 12, no. 2 (1958): 158-165.

Molisch, Hans. *Der Einfluss Einer Pflanze Auf Die Andere, Allelopathie (the Influence of One Plant on Another, Allelopathy*. Jena: Verlag von Gustav Fischer, 1937.

Mukherjee, Subrata. "Fabian Socialism: One Hundred Years in the Life of a Doctrine." In *Essays on Fabian Socialism*, edited by M.M. Sankhdher and Subrata Mukherjee, 1-7. New Delhi: Deep and Deep Publications, 1991.

Muller, Cornelius H. "The Role of Allelopathy in the Evolution of Vegetation." In *Biochemical Coevolution: Proceedings of the Twenty-Ninth Annual Biology Colloquium, April 26-27, 1968*, edited by Kenton L. Chambers. Corvallis: Oregon State University Press, 1970.

———. "The Role of Chemical Inhibition (Allelopathy) in Vegetational Composition." *Bulletin of Torrey Botanical Club* 93 (1966): 333.

———. "This Week's Citation Classic: The Role of Chemical Inhibition (Allelopathy) in Vegetational Composition." *Current Contents* 45 (1982): 20.

———. "Volatile Growth Inhibitors Produced by Aromatic Shrubs." *Science* 143 (1964): 471-473.

Muller, Cornelius H., and Roger Del Moral. "Role of Animals in Suppression of Herbs by Shrubs." *Science* 173 (1971): 462-463.

Murdoch, William W. "'Community Structure, Population Control, and Competition'—a Critique." *The American Naturalist* 100 (1966): 219-226.

Nitecki, Matthew H., ed. *Coevolution*. Chicago: The University of Chicago Press, 1983.

Odum, Eugene. *Fundamentals of Ecology, 3rd Edition*. London: Saunders, 1971.

Olby, Robert. "The Molecular Revolution in Biology." In *Companion to the History of Modern Science*, edited by R.C. Olby et al. London: Routledge, 1990.

Orians, Gordon H. "Natural Selection and Ecological Theory." *The American Naturalist* 96 (1962): 257-263.

Oudshoorn, Nelly. "On the Making of Sex Hormones: Research Materials and the Production of Knowledge." *Social Studies of Science* 20, no. 1 (1990): 5-33.

Paech, Karl. *Biochemie Und Physiologie Der Sekundären Pflanzenstoffe*. Berlin: Springer, 1950.

Paine, Robert T. "Food Web Complexity and Species Diversity." *The American Naturalist* 100 (1966): 65-75.

Painter, Reginald H. *Insect Resistance in Crop Plants*. NY: Macmillan, 1951.

———. "The Role of Nutritional Factors in Host Plant Selection." In *Symposia of the Ixth International Congress of Entomology (Amsterdam)*, 101-105. Amsterdam: DR W. Junk, Publishers, 1953.

Painter, Reginald H., and J.H. Parker. *Resistance of Plants to Insects: A Bibliography*. Manhattan, KS: Kansas State College of Agriculture, 1932.

Palladino, Paolo. *Entomology, Ecology and Agriculture: The Making of Scientific Careers in North America, 1885-1985*. Amsterdam: Harwood Academic Publishers, 1996.

Pauly, Philip J. *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology*. New York: Oxford University Press, 1987.

———. *Fruits and Plains: The Horticultural Transformation of America*. Cambridge: Harvard University Press, 2007.

Perkins, John. "Insects, Food, and Hunger: The Paradox of Plenty for U.S. Entomology, 1920-1970." *Environmental Review* 7, no. 1 (1983).

Perkins, John H. *Insects, Experts, and the Insecticide Crisis: The Quest for New Pest Management Strategies*. New York: Plenum Press, 1982.

Pickering, Andrew. *The Mangle of Practice: Time, Agency, and Science*. Chicago: University of Chicago Press, 1995.

Poulton, Edward B. "Insect Adaptation as Evidence of Natural Selection." In *Evolution, Essays on Aspects of Evolutionary Biology*, edited by G.R. de Beer. London: Oxford University Press, 1938.

Prossert, C. Ladd, Stanley Friedman, and Judith H. Willis. "Gottfried Samuel Fraenkel." *Biographical Memoirs of the National Academy of Sciences* 59 (1990): 168-195.

Provine, William B. "The Development of Wright's Theory of Evolution: Systematics, Adaptation, and Drift." In *Dimensions of Darwinism: Themes and Counterthemes in Twentieth-Century Evolutionary Theory*, edited by Marjorie Grene, 43-70. Cambridge: Cambridge University Press, 1983.

Pugh, Patricia. *Educate, Agitate, Organize: 100 Years of Fabian Socialism*. Lodon: Methuen, 1984.

Rader, Karen. *Making Mice: Standardizing Animals for American Biomedical Research, 1900-1955*. Princeton: Princeton University Press, 2004.

Rasmussen, Nicolas. "Plant Hormones in War and Peace: Science, Industry, and Government in the Development of Herbicides in 1940s America." *Isis* 92, no. 2 (2001): 291-316.

Rehr, S.S., E.A. Bell, Daniel H. Janzen, and Paul P. Feeny. "Insecticidal Amino Acids in Legume Seeds." *Biochemical Systematics* 1 (1973): 63-67.

Rehr, S.S., Paul P. Feeny, and Daniel H. Janzen. "Chemical Defence in Central American Non-Ant-Acacais." *The Journal of Animal Ecology* 42, no. 2 (1973): 405-416.

Rehr, S.S., Daniel H. Janzen, and Paul P. Feeny. "L-Dopa in Legume Seeds: A Chemical Barrier to Insect Attack." *Science* 181, no. 4094 (1973): 81-82.

Reveal, James L. "The First Internation Congress of Systematic and Evolutionary Biology." *Taxon* 21, no. 4 (1972): 491-493.

Rhoades, David F., and Rex G. Cates. "Toward a General Theory of Plant Antiherbivore Chemistry." In *Recent Advances in Phytochemistry, Volume 10: Biochemical Interaction between Plants and Insects*, edited by James W. Wallace and Richard L. Mansell, 168-213. New York: Plenum Press, 1976.

Rosenfeld, Albert. "The Ultimate Weapon in an Ancient War." *Life* 45, no. 14 (1958): 105-108.

Rosenthal, Gerald A., and May Berenbaum, eds. *Herbivores: Their Interactions with Secondary Plant Metabolites, 2nd Ed.* San Diego: Academic Press, Inc., 1991.

Rosenthal, Gerald A., D.L. Dahlman, and Daniel H. Janzen. "A Novel Means for Dealing with L-Canavanine, a Toxic Metabolite." *Science* 192, no. 4236 (1976): 256-258.

Rosenthal, Gerald A., and Daniel H. Janzen, eds. *Herbivores: The Interactions with Secondary Plant Metabolites*. New York: Academic Press, Inc., 1979.

Rosenthal, Gerald A., Daniel H. Janzen, and D.L. Dahlman. "Degradation and Detoxification of Canavanine by a Specialized Seed Predator." *Science* 196 (1977): 658-660.

Rosenthal, Gerald A., and David Rhodes. "L-Canavanine Transport and Utilization in Developing Jack Bean, Canavalia Ensiformis (L.) Dc. [Leguminosae]." *Plant Physiology* 76, no. 2 (1984): 541-544.

Rumore, Gina. *A Natural Laboratory, a Nation Monument: Carving out a Place for Science in Glacier Bay, Alaska, 1879-1959, Ph.D. Dissertation*: University of Minnesota, 2009.

Ruse, Michael. "Adaptive Landscapes and Dynamic Equilibrium: The Spencerian Contribution to Twentieth-Century American Evolutionary Biology." In *Darwinian Heresies*, edited by Abigail Lustig, Robert J. Richards and Michael Ruse. Cambridge: Cambridge University Press, 2004.

———. *The Darwinian Revolution: Science Red in Tooth and Claw, 2nd Ed.* Chicago: University of Chicago Press, 1999.

Russell, Edmund. "Evolutionary History: Prospectus for a New Field." *Environmental History* 8, no. 2 (2003): 204-228.

———. "Introduction: The Garden in the Machine: Toward an Evolutionary History of Technology." In *Industrializing Organisms: Introducing Evolutionary History*, edited by Susan Schrepfer and Philip Scranton. London: Routledge, 2003.

Russell, Edmund P. "'Speaking of Annihilation': Mobilizing for War against Human and Insect Enemies, 1914-1945." *The Journal of American History* 82, no. 4 (1996): 1501-1529.

———. *War and Nature: Fighting Humans and Insects with Chemicals from World War I to Silent Spring*. Cambridge: Cambridge University Press, 2001.

Sapp, Jan. *Evolution by Association: A History of Symbiosis*. New York: Oxford University Press, 1994.

Sawyer, Richard C. . *To Make a Spotless Orange: Biological Control in California*. Ames: Iowa State University Press, 1996.

Schoonhoven, L. M. "After the Verschaffelt-Dethier Era: The Insect-Plant Field Comes of Age." *Entomologia Experimentalis et Applicata* 80 (1996): 1-5.

Shostak, Sara. "The Emergence of Toxicogenomics: A Case Study of Molecularization." *Social Studies of Science* 35, no. 3 (2005): 367-403.

Siddall, J.B. "Synthetic Studies on Insect Hormones." In *Insect-Plant Interactions*, 70-71. Washington, DC: National Academy of Sciences, 1969.

Smocovitis, Vassiliki Betty. "Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology." *Journal of the History of Biology* 25 (1992): 1-65.

Solbrig, Otto T. "Review, Costs and Benefits: Coevolution of Animals and Plants." *Systematic Botany* 1, no. 4 (1976): 393-394.

Sondheimer, Ernest, and John B. Simeone. "Preface." In *Chemical Ecology*, edited by Ernest Sondheimer and John B. Simeone. New York: Academic Press, 1970.

Sorensen, Willis Conner. *Brethren of the Net: American Entomology, 1840-1880, 2nd Ed*. Tuscaloosa: University of Alabama Press, 1995.

Stahl, Ernst. *Pflanzen Und Schnecken : Eine Biologische Studie Über Die Schutzmittel Der Pflanzen Gegen Schneckenfrass*. Jena: G. Fischer, 1888.

Stebbins, G. Ledyard. *The Ladyslipper and I, Autobiography of G. Ledyard Stebbins*. St. Louis: Missouri Botanical Garden Press, 2007.

Swain, Tony. *Chemical Plant Taxonomy*. London: Academic Press, 1963.

Terriere, L.C. "The Oxidation of Pesticides: The Comparative Approach." In *Enzymatic Oxidation of Toxicants*, edited by Ernest Hodgson, 175-193. Raleigh: North Caroline State University, 1968.

Thompson, John N. *The Coevolutionary Process*. Chicago: The University of Chicago Press, 1994.

Thorsteinson, A. J. "Host Selection in Phytophagous Insects." *Annual Review of Entomology* 5 (1960): 193-218.

———. "The Chemotactic Responses That Determine Host Specificity in an Oligophagous Insect (*Plutella Maculipennis* (Curt.) Lepidoptera)." *Canadian Journal of Zoology* 31, no. 1 (1953): 52-71.

———. "This Week's Citation Classic: Host Selection in Phytophagous Insects." *Citation Classics* 45 (1980): 254.

Tierney, John. "An Early Environmentist, Embracing New 'Heresies'." *New York Times*, 27 February 2007, D1 & D3.

Tinbergen, Niko. "On Aims and Methods of Ethology." *Zeitschrift fur Tierpsychologie* 20 (1963): 410-433.

Tonkin, Elizabeth. *Narrating Our Pasts: The Social Construction of Oral History*. Cambridge: Cambridge University Press, 1992.

Tukey, H.B. "Leaching of Substances from Plants." Washington, DC: National Academy of Sciences, 1971.

Turner, Fred. *From Counterculture to Cyberculture: Stewart Brand, the Whole Earth Network, and the Rise of Digital Utopianism*. Chicago: University of Chicago Press, 2008.

Turner, J.R.G. "Adaptation and Evolution in Heliconius: A Defense of Neodarwinism." *Annual Review of Ecology and Systematics* 12 (1981): 99-121.

Van Emden, H.F. "Aphids as Phytochemists." In *Phytochemical Ecology*, edited by J.B. Harborne. London: Academic Press, 1972.

Varley, G.C., G.R. Gradwell, and M.P. Hassell. *Insect Population Ecology: An Analytical Approach*. Berkeley: University of California Press, 1973.

Vaughan, Megan. "Reported Speech and Other Kinds of Testimony." In *African Words, African Voices: Critical Practices in Oral History*, edited by Luise White, Stephan F. Miescher, and David William Cohen, 53-77. Bloomington: Indiana University Press, 2001.

Verschaffelt, E. "The Cause Determining the Selection of Food in Some Herbivorous Insects." *Proceedings of the Royal Academy, Amsterdam* 13 (1910): 536-542.

Weiner, Charles. "Oral History of Science: A Mushrooming Cloud?" *Journal of American History* 75 (1988): 548-559.

Went, F.W. "Plants and the Chemical Environment." In *Chemical Ecology*, edited by Ernest Sondheimer and John B. Simeone, 71-82. New York: Academic Press, 1970.

Westman, Walter E., Robert K. Peet, and Gene E. Likens. "Robert H. Whittaker." *National Academy of Sciences Biographical Memoirs* 59 (1990): 424-444.

Wheeler, William Morton. *Ants: Their Structure, Development and Behavior*. New York: Columbia University Press, 1910.

White, Richard. *The Organic Machine: The Remaking of the Columbia River*. New York: Hill and Wang, 1995.

Whittaker, Robert H. "The Biochemical Ecology of Higher Plants." In *Chemical Ecology*, edited by Ernest Sondheimer and John B. Simeone, 43-70. New York: Academic Press, 1970.

———. "The Chemistry of Communities." Washington, DC: National Academy of Sciences, 1971.

Whittaker, Robert H. and Simon A. Levin, ed. *Niche: Theory and Application*. Stroudsberg, Pennsylvania: Dowden, Hutchinson & Ross, Inc., 1975.

Whittaker, Robert H., and Paul P. Feeny. "Allelochemics: Chemical Interactions between Species." *Science* 171 (1971): 757-770.

Wieland, Thomas. "Scientific Theory and Agricultural Practice: Plant Breeding in Germany from the Late 19th to the Early 20th Century." *Journal of the History of Biology* 39 (2006): 309-343.

Wigglesworth, Vincent B. "Factors Controlling Moulting and 'Metamorphosis' in an Insect." *Nature* 133 (1934): 725-726.

Williams, Carroll M. "Hormonal Interactions between Plants and Insects." In *Chemical Ecology*, edited by Ernest Sondheimer and John B. Simeone. New York: Academic Press, 1970.

———. "Perspectives in Insect-Plant Interactions." In *Insect-Plant Interactions*. Washington, DC: National Academy of Sciences, 1969.

Wilson, E.O. "Chemical Communication within Animal Species." In *Chemical Ecology*, edited by Ernest Sondheimer and John B. Simeone, 133-155. New York: Academic Press, 1970.

———. "Some Ecological Characteristics of Ants in New Guinea Rain Forests." *Ecology* 40, no. 3 (1959): 437-447.

Woods, Frank W. "Biological Antagonisms Due to Phytotoxic Root Exudates." *The Botanical Review* 26 (1960): 546-559.

Zangerl, Arthur, and May Berenbaum. "Increase in Toxicity of an Invasive Weed after Reassociation with Its Coevolved Herbivore." *Proceedings of the National Academy of Science* 102, no. 43 (2005): 15529-15532.

———. "Phenotype Matching in Wild Parsnip and Parsnip Webworms: Causes and Consequences." *Evolution* 57, no. 4 (2003): 806-815.

Zangerl, Arthur, M.C. Stanley, and May Berenbaum. "Selection for Chemical Trait Remixing in an Invasive Weed Aftee Reassociation with a Coevolved Specialist." *Proceedings of the National Academy of Science* 105, no. 12 (2008): 4547-4552.