Chemical Control of Insect Behavior

Theory and Application

Edited by H. H. Shorey
& John J. McKelvey, Jr.

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THEORY AND APPLICATION

EDITED BY

H. H. SHOREY

UNIVERSITY OF CALIFORNIA
RIVERSIDE

JOHN J. McKELVEY, JR.

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SERIES PREFACE

Environmental Science and Technology

The Environmental Science and Technology Series of Monographs, Textbooks, and Advances is devoted to the study of the quality of the environment and to the technology of its conservation. Environmental science therefore relates to the chemical, physical, and biological changes in the environment through contamination or modification, to the physical nature and biological behavior of air, water, soil, food, and waste as they are affected by man's agricultural, industrial, and social activities, and to the application of science and technology to the control and improvement of environmental quality.

The deterioration of environmental quality, which began when man first collected into villages and utilized fire, has existed as a serious problem under the ever-increasing impacts of exponentially increasing population and of industrializing society. Environmental contamination of air, water, soil, and food has become a threat to the continued existence of many plant and animal communities of the ecosystem and may ultimately threaten the very survival of the human race.

It seems clear that if we are to preserve for future generations some semblance of the biological order of the world of the past and hope to improve on the deteriorating standards of urban public health environmental science and technology must quickly come to play a dominant role in designing our social and industrial structure for tomorrow. Scientifically rigorous criteria of environmental quality must be developed. Based in part on these criteria, realistic standards must be established and our technological progress must be tailored to meet them. It is obvious that civilization will continue to require increasing amounts of fuel, transportation, industrial chemicals, fertilizers, pesticides, and countless other products and that it will continue to produce waste products of all descriptions. What is urgently needed is a total systems approach to modern civilization through which the pooled talents of scientists and engineers, in cooperation with social scientists and the medical profession, can be focused on the development of order and equilibrium to the presently disparate segments of the human environment. Most of the skills and tools that are needed are already in existence. Surely a technology that has created such manifold environmental problems is also capable of solving them. It is our hope that this Series in Environmental Sciences and Technology will not only serve to make this challenge more explicit to the established professional but that it also will help to stimulate the student toward the career opportunities in this vital area.

Robert L. Metcalf
James N. Pitts, Jr.
Werner Stumm

PREFACE

Man, in large part because of his own rampant increase in population, seems to be running a collision course with insects in competition for choice foods and fibers. If, within the years to come, he is to cope successfully with insects, he must gain as precise a knowledge as is possible of their behavioral systems and apply that knowledge in pest management programs. The promise of success in this area of investigation, combined with recent spectacular advances in chemical methodology, have encouraged entomologists, biochemists, physiologists, and scientists in related disciplines to accelerate their research on insect behavior. They have made remarkable progress not only in devising novel ways of combating insects but also in bringing about substantial improvements in the traditional ways of managing insect populations.

The behavior of insects in response to the chemicals in and around them ramifies the broad areas of research in entomology which The Rockefeller Foundation has chosen to support: developing biodegradable pesticides; examining juvenile hormones, antihormones, and the like for their potential usefulness in combating insects; studying the chemical and morphological resistance of plants to insect attack; and exploring the use of sex and other pheromones for insect control. For the research on pheromones, Dr. H.H. Shorey, Dr. R.M. Silverstein, Dr. D.L. Wood, and Dr. W.L. Roelofs, leaders of laboratories engaged in the multidisciplinary, multiuniversity programs under Rockefeller Foundation auspices, felt a need to summarize their findings, after 6 years of cooperative endeavor, and to compare notes, so to speak, with preeminent colleagues throughout the world. The Foundation Study and Conference Center in Bellagio, Italy, provided the venue for the 5-day conference in May 1975 that was organized to accomplish this objective and led to the publication of this book.

This book deals primarily with those chemicals that insects perceive by smell and which constitute their most important stimuli when they are at a distance from the source of chemical. Secondarily, it considers taste substances which are perceived by insects when in contact with the source. The book opens with an assessment of the physiological characteristics of the nervous system of insects that enable them to perceive such chemicals. It then considers how chemicals normally function to mediate insect behavior. Next, it treats of the diversity of chemicals that stimulate behavior. Finally, it evaluates how behavior-modifying chemicals can be used in pest management systems.

The authors of the chapters present the state of the art for the topics of their special competence. They have cautiously drawn conclusions about the significance and usefulness of the body of knowledge they have helped to amass on insect behavior, especially as this knowledge may apply to the control of insects in practical ways. But in each chapter readers will find a wealth of stimulating ideas reinforced by elegant research which makes them relevant to the development of insect control strategies. The book provides new concepts and guidelines that will assist researchers in insect sensory physiology, behavior, chemical ecology, and pest management.

We are grateful to the distinguished scientists who participated in the Bellagio Conference and who prepared the manuscripts for this work. We appreciate the support and the participation of the directors of the foundation's programs: Dr. Ralph W. Richardson in Quality of the Environment, and Dr. John A. Pino in Conquest of Hunger, and we owe a debt of gratitude to Dr. and Mrs. Olson, Director and Assistant Director of the Bellagio Conference Center for their role in facilitating the conference.

H.H. Shorey
John J. McKelvey, Jr.

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CONTENTS

CHAPTER 1

Interaction of Insects with their Chemical Environment

H.H. Shorey
Department of Entomology
University of California
Riverside, California

In the early evolution of animal communication, chemical messages were probably the first signals put to use (1). Today chemical communication appears to be the primary mode of information transfer in most groups of animals (2) (3). Even in so-called non social animals–such as protozoans, annelids, molluscs, nematodes, and many arthropods–chemical communication is used for such diverse functions as location of prey, avoidance of predators, and signaling to species mates prior to mating or during times of danger. The sophistication of this communication mode has reached its peak in those social insects and mammals that live as interacting groups of individuals in colonies or societies. Indeed, in many insects the great diversity of behavioral interactions and physiologic responses that can result when individuals receive chemical messages emitted by others of the same species may have been in large part the factor that allowed the evolution of high levels in sociality (4).

Man, unlike most other animals, is microosmatic, and minimizes his use of chemical communication with other organisms, both with individuals of his own species and with those of other species. Unfortunately, man is also anthropocentric in his research and, because he has little intuitive feel for chemical communication systems, until recently he has minimized his studies of this communication mode and maximized studies of visual and sonic communication among insects and other animals. This situation is being rectified rapidly: our knowledge of chemical communication among insects, for example, increased exponentially during the last decade. These advances are documented in the various chapters of this book.

The surge of interest in insect chemical communication systems is due to a number of interacting factors: an increased awareness of our vast ignorance of this vitally important aspect of insect biology; advances in microanalytical chemistry that have allowed identification of the minute quantities of chemicals involved; and an appreciation that the manipulation of the chemical communication systems of certain insects may be a valuable tool in pest management. Research scientists from many disciplines have now focused on and often specialize in studies of insect chemical communication. These disciplines include chemistry, morphology, physiology, ecology, behavior, and pest management. Without doubt, some of the advances in knowledge will provide guidelines and stimulation for research workers interested in exploring the chemical communication systems of noninsect groups.

The term *communication* has defied a definition that is satisfactory to most biological scientists. A broad definition is used here, patterned after Wilson (1): biological communication entails the release of one or more stimuli by one organism that alter the likelihood of reaction by another organism; the reaction is of benefit to the stimulus emitter, the stimulus receiver, or both.

Chemicals used in communication have not been satisfactorily defined either. Most investigators now use the terms *pheromone, allomone*, and *kairomone*, which are defined as follows:

1. A *pheromone* is a chemical or a mixture of chemicals that is released from one organism and that induces a response by another individual of the same species. The term was first coined by Karlson and Lüscher (5) and Karlson and Butenandt (6), and modifications to the definition were proposed by Kalmus (7). The most important modification is the omission of the implication in the original definition that a pheromone be synthesized *de novo* by the emitting organism. The chemicals may be either synthesized *de novo* or acquired intact by the organisms from their food or other aspects of the environment. This modification seems necessary because the biosynthetic pathways or the manner of acquisition of most chemicals regarded as pheromones are totally unknown.
2. An *allomone* is a chemical or a mixture of chemicals that is released from one organism and that induces a response by an individual of another species; the response is adaptively favorable to the emitter (8). Examples of allomones are the defensive secretions that are released by many insects and that are poisonous or repugnant to attacking predators. The "secondary substances" of plants (9-12) are also allomones. These substances, which usually have no other apparent role in the physiology of the plant, have presumably evolved as defense mechanisms against herbivorous insects and other animals.
3. A *kairomone* is a chemical or a mixture of chemicals that is released from one organism and that induces a response by an individual of another species; the response is adaptively favorable to the recipient (13). Blum (see Chapter 10) regards kairomones as pheromones or allomones that have evolutionarily backfired. The original development in the releasing individual of systems for the production and release of the chemicals presumably occurred in response to selective pressures favoring the releasing individual. Secondarily, individuals of other species evolved advantageous responses to the same chemical signals, often to the disadvantage of the releasing individual. For example, the secondary substances of plants, discussed

above as allomones conferring protection against herbivores, have in some cases been seized upon by certain herbivores that have evolved an ability to tolerate or even detoxify the chemicals and to use the chemicals as kairomonal stimulants for aggregation or feeding on the emitting plant species (see Chapter 2). Also, the various exudates from humans and other warm-blooded animals that attract blood-sucking insects serve as kairomones to the insects (see Chapters 7 and 18).

The responses induced by pheromones, allomones, or kairomones may be immediate behavioral reactions or long-lasting physiologic changes. The three classes encompass all chemicals used in communication between organisms. A fourth class of chemicals, discovered to be attractants or repellents through chemical screening, is not known to occur naturally. However, probably most chemicals in this latter class will eventually be found either to be naturally occurring chemicals that are reacted to by animals in their normal lives or to be sufficiently closely related to naturally occurring chemicals that they cause the same types of behavioral reactions as the natural chemicals.

Another way to categorize chemicals that modify animal behavior is in terms of the types of behavior they induce. Dethier et al. (14) erected the following six categories that encompass most behaviorally active chemicals:

1. A *locomotory stimulant* is a chemical that causes kinesis reactions (see Chapter 5) that, in the absence of orientation cues, often cause the animals to disperse from an area by increasing the speed of locomotion or appropriately affecting the rate of turning.
2. An *arrestant* is a chemical that causes kinesis reactions that, in the absence of orientation cues, often cause the animals to aggregate near the chemical source by decreasing the speed of locomotion or appropriately affecting the rate of turning.
3. An *attractant* is a chemical that causes animals to make oriented movements towards its source.
4. A *repellent* is a chemical that causes animals to make oriented movements away from its source.
5. A *feeding, mating, or ovipositional stimulant* is a chemical that elicits one of these behavioral reactions.
6. A *feeding, mating, or ovipositional deterrent* is a chemical that inhibits one of these behavioral reactions.

The same chemical may produce more than one of the foregoing reactions, and the classification of the reactions is in some respects oversimplified. For example, an attractant may induce much more elaborate behavioral reactions in animals than mere orientation to the source of a chemical gradient. A sensing of chemical cues, wind-direction cues, and visual cues from the environment may all be involved in the "attraction" of an animal to a distant odor source. Still, this classification is bound to produce some order in the field if it is adopted by most scientists. The term *attractant*, especially, has been very overworked and distorted by some writers: *sex attractant* is often used when *sex pheromone* will be more correct. A sex pheromone may be a locomotory stimulant, an attractant, an arrestant, and/or a sexual stimulant. Certainly *sex pheromone* is not synonymous with sex attractant (14) (15).

An insect does not think; it reacts. The reactions are usually triggered by external stimuli and modified by a host of environmental variables, internal physiologic variables, and some rudimentary learning. The reactions are often highly stereotyped and cause the insects to perform appropriate behaviors that enhance species survival when appropriate stimuli are encountered. Much of the sensory world of the insect involved in stimulation or inhibition of such behaviors as mating, feeding, and egg-laying is chemical. The reactions of the insects to these chemicals are so predictable that if man could learn enough about the attendant behaviors he could literally make the insects jump through a hoop.

It cannot be stressed too strongly that the key to devising efficient systems for the management of insect pests by chemically modifying their behavior is the acquisition of an intimate knowledge of the insects' own normal use of chemicals. This important factor is too often overlooked. Once a pheromone or other behaviorally active chemical is identified, there is a tendency to feel that the research is all over, and that the chemical can be used as a bait in traps or perhaps distributed through fields, causing insect control. Rather, the identification of the chemical should open the door to more necessary research to determine whether the normal behavior of insects can be interfered with and manipulated to our advantage.

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CHAPTER 2

Insect Chemosensory Responses to Plant and Animal Hosts

L.M. Schoonhoven
Department of Animal Physiology, Agricultural University
Wageningen, The Netherlands

Animal behavior is intimately related with the surrounding world. When we try to explain behavior, we must know which factors the animal selects through its sense organs in the complexity of the physical and biologic environment. In addition, we have to know according to which rules the sensory system codes the selected information it transmits as nerve potentials to the brain. The entomologist seeking to explain feeding and oviposition behavior of insects has to pay special attention to the chemical senses since they play a decisive role in many phases of behavior.

Ethology has provided important insight into the nature of environmental cues that elicit certain behavioral responses in the animal. The "sign stimulus," which releases a specific behavioral response, is often of a remarkably simple structure (1). This view seems to be true not only with visual stimuli but also with chemical signals. The pheromones of many insects are striking examples of sign stimuli, although recently cases have been found in which delicate mixtures of some compounds are involved, indicating that pheromones have a greater degree of complexity than hitherto had been presumed. *Pieris brassicae* caterpillars feeding on nonhost plants treated with sinigrin (2), and *Papilio ajax* larvae eating from filter paper treated with essential oils from their host plants (3) may be considered classical examples supporting the concept of a simple sign stimulus. In spite of substantial efforts, food selection in several other insects (e.g., Colorado potato beetle and the silkworm) could not be explained by the presence of simple sign stimuli. These cases may be due either to the fact that we have not discovered as yet the essential component or that the optimal stimulus consists of a

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