Animal Communication by Pheromones

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Preface

Pheromones are chemicals, either odors or taste substances, that are released by organisms into the environment, where they serve as messages to others of the same species. Although humans exude a great variety of chemicals, they make little conscious use of this potential means for communication with one another. On the other hand, pheromones are widely used within much of the rest of the animal kingdom in a great variety of species, ranging from primitive protozoans to higher primates, as a primary means for transmitting information. Depending on the particular species involved and the situation in which it finds itself at the time, pheromones may be used for attracting a mating partner or for stimulating that partner to copulate, for directing others to suitable food or resting sites, for causing others to stay away when staying away is appropriate, or for a variety of other behavioral functions.

The scientific literature dealing with pheromones has expanded enormously during recent years as have the number of reviews which have proliferated in symposium volumes and in collections of chapters prepared by individual contributors. Although most of the review articles have dealt with insect pheromones, the importance of mammalian pheromones has received increased recognition in recent years, and a number of reviews concerning this group have also been published. However, with the exception of a book by Martin Jacobson entitled "Insect Sex Pheromones" (published by Academic Press in 1972), no single-authored monograph concerning pheromones has appeared.

I have felt for some time that the information concerning pheromone communication within the entire animal kingdom should be reviewed, digested, and presented in a cohesive manner. This book represents my attempt to perform this task. It is mainly directed toward an assessment of how the behavior of animals is controlled and influenced by pheromone communication. Attention to individual taxa, such as worms, insects, or fish, is minimized. Instead, an attempt has been made to generalize the diverse behaviors exhibited by animals when they are engaged in pheromone communication and to group together discussions of both primitive and advanced animals when they are using pheromone communication in a similar manner for such behavioral functions as sex, aggression, feeding, and recognition of other individuals. I have also attempted to draw attention to some of the interesting and specific pheromone behaviors that have evolved in particular animal species in relation to their particular ways of life.

Placing relatively simple invertebrates and complex vertebrates in the same generalized scheme involves the risk of making all these greatly diverse types of animals seem too much alike. However, despite this possibility, I felt this type of scheme of presentation valuable in achieving a mainly behavioral view of pheromone communication in the animal kingdom.

I wish to acknowledge a number of my colleagues who assisted me during the preparation of this book. J. S. Gaston prepared Figures 6, 8, 9, 10, 17, 18, and 26, and L. B. Bjostad prepared the schematic drawings of chemical molecules. P. A. Murray assisted in library research and in cataloging the literature. A. E. Colwell, J. F. Bollinger, and L. K. Gaston offered valuable advice concerning the substance of the manuscript. H. R. Bowman did all of the typing and the laborious collating of material. Finally, my children, Tom, Russell, Diane, and Hal, provided patience and encouragement during the years before and during preparation of this work; this book is dedicated to them.

H. H. Shorey

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1

Introduction

Most animals must communicate with others of their own species. The necessity for communication is obvious for animals, such as honeybees, rabbits, and man, that live in complex societies. Communication is the mechanism through which these social animals interact with each other and by which they are organized according to their relative statuses and functions.

Although the need is less obvious, communication is also essential in the lives of most animals that appear to live alone. However, for these solitary animals this communication often takes place only at certain critical times during their lives. For example, prior to mating in bisexual species, communication must be used to bring the two sexes—or at least their gametes—together. Once the two individuals have come together, additional communication is usually necessary to stimulate and guide the process of copulation or the union of gametes. A premating communication system may operate over a long range and be obvious to the human investigator, or it may operate only at very close range, perhaps following chance contact of the individuals, and be less obvious. Even in the latter situation, it appears unlikely that the entire sequence leading to mating occurs in any species without the occurrence of some communication between the animals involved.

As will be indicated throughout this book, many types of communication may be of vital importance in the lives of "solitary" animals, including the exchange of messages that keep them from coming together at inappropriate times. Thus, if a definition of sociality includes the communication of information among individuals of a given species, then almost all animals are social on a continuum from the "solitary" species to those that live in complex societies.

Considerable disagreement occurs concerning a precise definition of the term "communication" (115). I will adhere to a broad definition patterned after Wilson (710): Biological communication entails the release of one or more stimuli by one individual that alters the likelihood of reaction by another, with the reaction being of benefit to the stimulus emitter, the stimulus receiver, or both. A stimulus may act directly, eliciting an overt behavioral reaction in the receiving individual, or, it may only cause a change in the receiving animal's threshold of responsiveness to other stimuli.

A variety of stimulus modalities and associated sense organs may be used by communicating animals, the major ones being usually classified as chemical (olfactory or gustatory), mechanical (tactile or sonic), and radiational (light perception or visual). These major communication channels occur in widely diverse groups of animals, ranging from protozoans through the complex higher vertebrates. The chemical sense is very primitive (253, 710); it probably allowed primordial single-celled organisms to locate food in their environments and, as sexuality developed, to locate each other for exchange of genetic material. As discussed later (Chapter 11), the development of chemical communication among individual free-living cells was probably a necessary precursor to the evolution of metazoan animals, which consist of interacting groups of cells.

Chemical communication among animals of the same species is widespread and occurs throughout the animal kingdom. In fact, in many diverse groups of animals (with some notable exceptions, including the birds and higher primates), chemical communication appears to be the major channel for exchange of information. However, one must avoid overgeneralizing this point; various emphases on the other modalities of communication occur also. Since each species has evolved its mode of communication according to its individualistic way of life, channels for transfer of information between individuals of a given species are varied and could involve any one of the modalities of communication or even a mixture of these modalities.

This book is restricted to a consideration of chemical communication between individuals of the same species. The term "ectohormone," coined by Bethe (57) to describe these chemicals, is contradictory (329), with "ecto" meaning "external" and "hormone" referring to an "internal secretion." The chemicals are also often called "attractants" or, depending on their biological function, "sex attractants," "feeding attractants," etc. Such terms are too general in that they do not denote that the chemicals are used for communication between individuals of a given species. Also, although attraction of one animal to another may be the most obvious (to a human observer) result of chemical communication, a chemical that stimulates attraction may cause additional responses, such as copulatory behavior, once the animals are together.

In 1959, Karlson, Lüscher, and Butenandt (329, 330) proposed the term "pheromone" to represent a chemical(s) used for communication between individuals of a given species. The term is derived from the Greek "pherein" meaning "to transfer" and "hormon" meaning "to excite." Although "pheromone" was criticized early on etymological grounds, it has received wide acceptance and is now used throughout the world in the scientific literature (63). With incorporation of some minor modifications as proposed by Kalmus (324), a pheromone can be defined as a chemical or a mixture of chemicals that is released to the exterior by an organism and that causes one or more specific reactions in a receiving organism of the same species. Thus, if two or more chemicals are released together and cause a specific reaction, the chemical mixture must be regarded as a pheromone.

A more rigorous definition might require that a pheromone be synthesized *de novo* in specialized glands in the producing animal. To adhere to this rigor is difficult and may be unnecessarily restrictive. A continuum probably exists, from chemicals that are produced *de novo* and secreted from specialized glands, to chemicals that are metabolic byproducts of related substances that have been ingested, to chemicals that are metabolized within the animal to their biologically active state by symbionts such as intestinal bacteria, to chemicals that are ingested and released later in their original form. In most cases, the chemical identity of a pheromone and the biosynthetic mechanisms that led to the production of the pheromone are unknown. In the practical world, an investigator who observes that one or more unknown chemicals released by an animal cause a behavioral response in another animal of the same species calls the chemical message a pheromone.

Pheromones have been divided by Wilson (706) into two broad categories. A "releaser pheromone" triggers an almost immediate behavioral response in the receiving animal, with the response probably being mediated entirely by nervous system pathways. An overt response to the pheromone sometimes might not be seen. The response might entail only a change in the threshold of reactivity of the animal to some other environmental stimulus, such as the sight or sound of a potential mating partner. Thus, using a neurophysiological approach (at least for higher animals), we might more accurately say that a releaser pheromone stimulates specific chemosensory organs to relay action-potential-coded messages via their sensory neurons to the central nervous system. There the messages modify (increase or reduce) the likelihood that messages will leave the central nervous system via specific motor neurons, causing the animal to respond in a correspondingly specific way.

"Primer pheromones," constituting Wilson's second category, are probably also detected by chemosensory organs that relay appropriate messages to the central nervous system. However, the response is not a direct behavioral reaction. Instead, it entails a relatively enduring reorganization of the physiology of the receiving animal. Most known primer pheromones cause changes, presumably mediated by hormonal systems, in the developmental or reproductive processes of the receiving individuals. Examples of primer pheromones are male-produced chemicals that modify the reproductive state of female mice (105) and queen-produced chemicals that inhibit ovary development in worker honeybees (216). Primer pheromones will not be dealt with beyond this brief description, the focus of this book being on those relatively instantaneous changes in behavioral response (or responsiveness) stimulated by releaser pheromones.

Man's research interests tend to be anthropocentric, and most early investigations into animal communication were involved with those sensory modalities that are maximized in the human species, vision and audition. However, man has now become more aware that most of the rest of the animal kingdom appears to maximize chemical communication. A recent redirection of research interest has resulted in an explosive increase in our appreciation and knowledge concerning animal pheromones.

A practical factor has stimulated the entry of many investigators into the pheromone field and—of great importance—has provided an infusion of funds from agencies that sponsor research. Especially among the insects, certain pest species appear to be highly dependent on pheromone communication for their survival. Such pheromone communication systems include those that bring the two sexes together prior to mating and those that direct species mates to appropriate food or breeding sites (Chapter 5). After acquiring an intimate knowledge of the normal pheromone communication behavior in pest species, man can attempt to manipulate the behavior to his own advantage. He can modify a previously adaptive behavior, such as the orientation of an animal to a pheromone-emitting mate, into a nonadaptive one, such as entry into a trap baited with the same pheromone. Pheromones have been utilized for some time as bait in traps used for survey of the distribution and abundance of pest insects. To date, no practical pheromone-based system has been proved successful as a direct means for obtaining effective control of pests. However, considerable research is presently underway in this area and important breakthroughs enabling pheromonal control of insect behavior, and thus of pest insect populations, seem imminent (65).

Microanalytical chemistry is an area of research that has added considerable impetus to the pheromone field and has made possible the practical applications mentioned above. The first chemical identification of a pheromone used in the premating behavior of moths was that of the female silkworm. Identification of this pheromone was completed in 1959 (117) following many years of effort. The identification was based on about 12 mg of pheromone isolated from the abdominal glands of 500,000 female moths. The second identification, reported in 1966 (48) for the female cabbage looper moth, was based on about 5 mg of pheromone collected from 2500 female moths. Since that time, identifications of female moth sex pheromones have been reported at a rapidly increasing rate, totalling over 40 by 1976. With recent advances in instrumental techniques for characterizing small quantities of chemical, many identifications are now accomplished on a few hundred micrograms of pheromone.

The study of pheromones cuts across and utilizes the tools of many diverse disciplines, i.e., morphology, physiology, ecology, behavior, chemistry, and pest control. No encyclopedic attempt has been made in this text to include reference to every relevant research article. In those cases in which a large number of original articles document similar phenomena in related animal groups, only certain of the references are mentioned. Some aspects of pheromone communication are covered very briefly or not at all. The morphology of glands that produce pheromones and of sensory organs that perceive pheromones is mentioned ony briefly in Chapter 2. Chemical techniques are not discussed. However, the chemical structures of many animal pheromones are presented in the various chapters that deal with the use of these chemicals in animal communication. The use of pheromones in pest control is not mentioned at all, although considerable research effort is occurring in this area. Interested readers who desire additional information regarding these aspects are referred to a number of recent reviews (65, 66, 301, 309, 473, 479, 591, 602, 654).

This book is organized along behavioral lines, illustrating the various types of behavior stimulated by pheromones, the mechanisms by which the behaviors come about, and the adaptive advantages which accrue from the behaviors. Most of the behaviors may be separated into two general categories. First, a pheromone may cause locomotion and/or orientation (steering) responses that bring an animal toward or away from the pheromone source. These responses have the effect of causing animals to aggregate (Chapter 5) or disperse (Chapter 6). Second, a pheromone may stimulate or inhibit other responses such as sexual behavior (Chapter 8) or aggression (Chapter 7)—usually when the animal is close to the source of pheromone emission. Often, the same pheromone that causes animals to aggregate near its source also stimulates the additional close-range behavior. Likewise, a pheromone that causes animals to disperse may also inhibit other behaviors, such as aggression. Those pheromones that cause multiple behavioral reactions (i.e., aggregation followed by sexual behavior or aggression) are discussed more than once, appearing in each of the appropriate chapters. This organizational scheme is somewhat different from that employed by other authors who have categorized pheromones along more functional lines, such as those resulting in alarm behavior (all locomotory and close-range behaviors exhibited in response to pheromones released during times of danger) and sexual behavior (all locomotory and close-range behaviors exhibited in response to pheromones released by potential mating partners) (119, 706, 710).

2

The Pheromonal Communication System

A typical communication system consists of three components: a mechanism for emitting the message, a medium through which the message is transmitted from the point of initiation to that of reception, and a mechanism for receiving the message. In the case of pheromone communication, the emitting component is often a glandular organ associated with specialized devices that transfer the chemical molecules into the surrounding medium. The reception component is an olfactory (smell) or gustatory (taste) sensory organ. The medium may be air or water, depending largely on the way of life of the species involved and the medium in which it lives. However, in the case of those pheromones that are liberated onto the surface of one animal and that are perceived by gustation by a second animal that makes direct contact with the first, the medium becomes essentially nonexistent.

2.1 Emission of Pheromone

2.1.1 EMISSION FROM ANIMALS

Although the locations and morphological features of the pheromone-producing glands of most animal species remain unknown, these organs have been extensively studied in insects and mammals. In fact, the description by morphologists of the glandular structures found on a number of animal species has preceded the demonstration by behaviorists that the structures do indeed secrete pheromones.

The types and locations of pheromone glands found in insects and mammals are as varied as are the many communication functions attributable to the pheromones. Depending on the species, the glands may be found on the head, thorax, abdomen, or legs (Figs. 1, 2). In insects, the glands may also be found on the wings. Often, a single animal has a number of glands in a variety of locations.

Most pheromone glands of insects and mammals are composed of groups of modified epidermal cells. A gland may consist of a single layer

FIG. 1. Mature male marmoset monkeys, *Callithrix j. jacchus,* display their external genitalia, which are covered with scent glands. This behavior is a signal of aggressive threat and may provide visual as well as olfactory information to nearby males. (Courtesy of G. Epple.)

of cells on the exterior of the animal, or the gland may be complex and associated with internal reservoirs. Elaborate secondary devices associated with the gland may have the function of disseminating the pheromone into the surrounding medium. For instance, the pheromone glands on the tarsi of the black-tailed deer are associated with erectile tufts of hairs

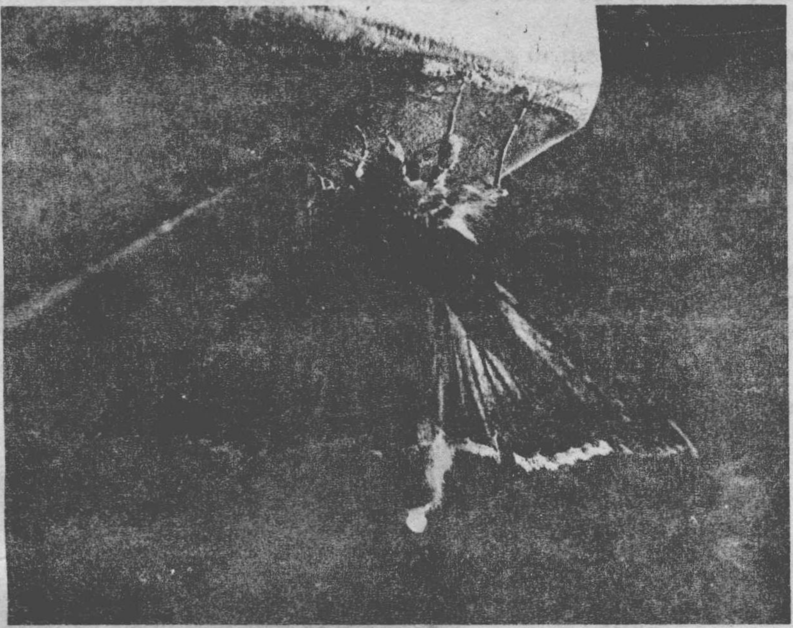

FIG. 2. Female cabbage looper moths cling to vertical surfaces or to the lower portion of horizontal surfaces when exposing the sex pheromone gland located at the end of their abdomens. (Courtesy of S. Gothilf.)

which greatly increase the surface area for evaporation of the pheromone molecules into the air (440). Similarly, male moths and butterflies frequently possess modified scales resembling hairs. The scales are enclosed in pouches which contain the pheromone glands. The pouches evaginate, erecting the pheromone-coated scales into the air at the time of premating communication between males and females (Fig. 3) (64). The ability to expose or erect pheromone-disseminating devices or to eject pheromone from reservoirs enables an animal to control the time of its pheromone emission.

2.1.2 EMISSION FROM OBJECTS

In many cases, the pheromone does not volatilize directly from the emitting animal. Instead, the emitter deposits the secretion on objects or on the substratum, establishing a scent mark. The deposited pheromone serves as the site for evaporation of the chemical into the air, and responses of other animals of the same species may be directed toward the marked area. Thus, scent marks have the advantage that the communicative process can occur even in the absence of the pheromone emitter,

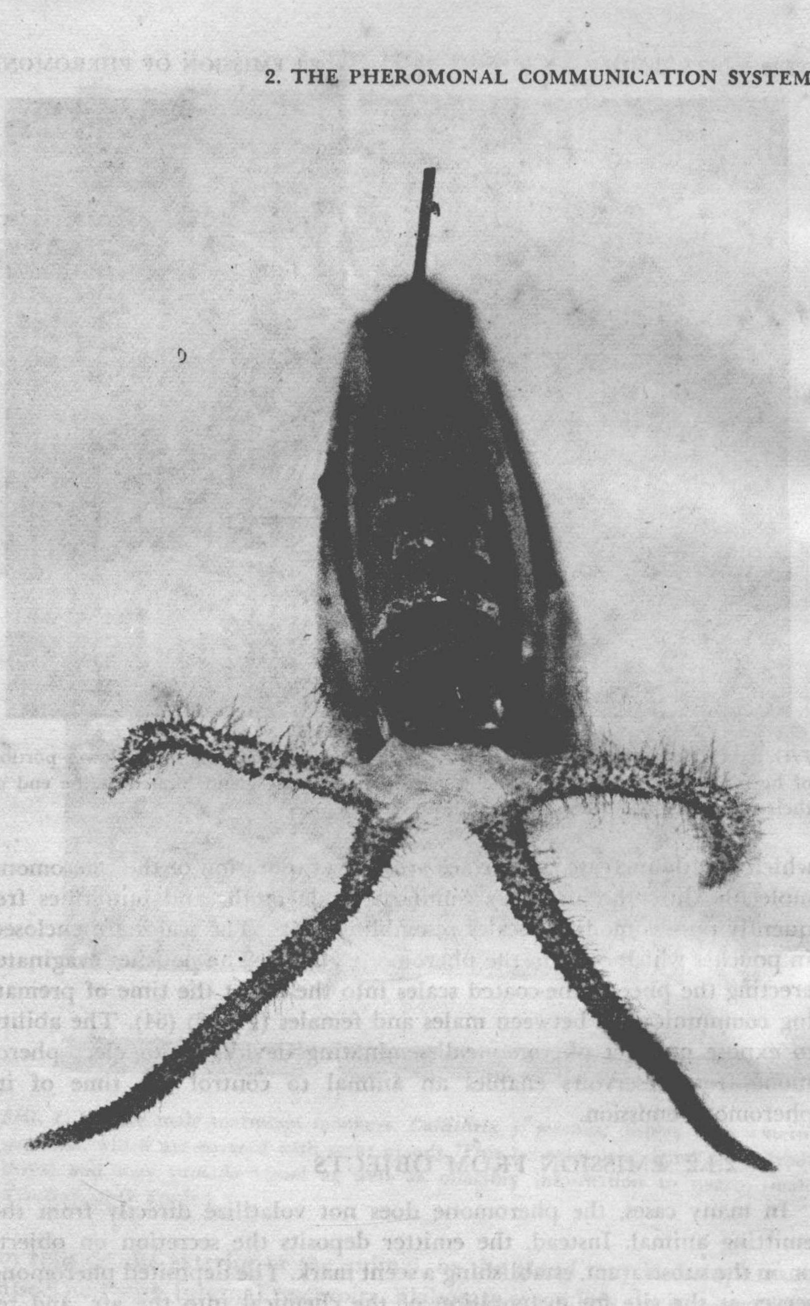

FIG. 3. A pinned museum specimen of the moth, *Creatonetus gangis,* showing the coremata that are inflated with air and extended from the terminal portion of the male abdomen during courtship and which may serve as devices for dissemination of pheromone. (Courtesy of M. C. Birch.)