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PREFACE

The first edition of this reference work, "Insect Sex Attractants," was published in 1965 by Wiley (Interscience). To date it is still the only book of its kind on the subject. However, the surge of interest in the insect sex pheromones as evidenced by the tremendous progress and by the phenomenal additional publications since 1965 has made it imperative to bring the entire subject up-to-date in this revised and expanded version.

In my earlier Preface I stated, "It is my sincere hope that this book will provide an incentive for greater discoveries in this fascinating field." An unprecedented increase in the number of species shown to produce sex pheromones (more than double the number known in 1965), in the number of species whose sex pheromones have been identified (37 now as compared to 3 in 1965), and the extensive literature in the field (about 1400 references as compared to 425 in 1965) indicate that this wish has been fulfilled.

The discovery that many sex pheromones are sexually excitatory rather than attractive has prompted me to substitute the more accurate and encompassing term "pheromones" for the term "attractants" in the title of this edition. Not only have all of the original chapters been extensively enlarged and revised, but a new chapter on test methods and responses has been added. This expanded review of the world literature should be extremely valuable to research and economic entomologists, insect physiologists, chemists, and ecologists.

Photographs and other illustrations are used with the kind permission of the copyright owners, with the source of each indicated. All listed references have been consulted directly. References which have appeared or were noted after the manuscript was prepared have been assigned

supplementary numbers, enabling me to include literature which appeared up to a few months prior to publication.

I acknowledge a debt of gratitude to my wife, Nettie, for painstakingly typing the bulk of the manuscript. A special note of thanks is due a number of experts on insect taxonomy at the National Museum of the Smithsonian Institution, Washington, D.C., for checking many of the insect names.

Martin Jacobson

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CHAPTER 1

INTRODUCTION

Insects have managed to persist in hostile surroundings because they have developed extraordinary adaptations or abilities, one of which is a highly specialized sense of smell. Because many insects depend on their sense of smell for survival, they can frequently be attracted to a trap by a chemical for detection purposes, to a toxicant that destroys them, or to a substance that makes them incapable of fertile mating (*599*).

Attractants may be classified as sex, food, or oviposition lures. The type of lure is inferred or deduced from insect behavior, and assignment is frequently uncertain. A chemical is probably a sex attractant if it brings to it an insect, which then assumes a mating position or attempts to mate with the chemical or with an object on which the chemical has been placed. This definition excludes a number of substances, mainly food attractants, which lure only one sex but do not elicit a sexual response. Sex attractants, usually released by a female to lure a male, are important, if not essential, links in the process by which the sexes locate each other for mating. Although odors released by female insects are usually for the purpose of attracting males from a distance, they may also serve to sexually excite the male before copulation and to evoke a courtship response. Sexual odors released by males are primarily for the purpose of sexually exciting the female, making her more receptive to the male's advances (aphrodisiacs). However, species

are known in which the males produce distance attractants for the female.

These chemical messengers are also called "assembling scents" (*663*) and "sex pheromones," from the Greek *pherein* (to carry) and *horman* (to excite, stimulate) (*647*). The term pheromone has been attacked by Kirschenblatt (*676*) as being etymologically incorrect, as it gives no clue to its exact derivation. Kirschenblatt (*674, 675*) previously proposed the term "telergones," from the Greek *tele* (afar) and *ergon* (action), to designate all biologically active substances secreted by animals into their environment which influence other organisms ("these substances are products of external secretion and differ principally by their importance from hormones, which display their physiological action within the organism producing them") (*674*). Micklem (*787*) cited the same objection to the term "pheromone" and suggested that it be changed to "pherormone." In replying to Micklem, Karlson and Lüscher (*649*) gave a new etymological explanation for their term, stating that the ending "mone" is regarded as a proper suffix used in such scientific terms as "hormones," "gamones," and "termones." "Pheromone" is now commonly used and widely accepted to include those substances secreted by an animal to influence the behavior of other animals of the same species (*1268*). Brown *et al.* (*213*) have recently proposed the term "allomone" to include those chemical substances produced by an organism which evoke a behavioral or physiological reaction in an organism of another species, and the term "kairomone" as a transspecific chemical messenger of benefit to the recipient rather than to the producer.

The use of sex pheromones by organisms other than insects has been conclusively demonstrated in algae (*805, 878*), nematodes (*484, 485*), spiders (*532*), crustaceans (*77, 323, 679, 1011*), fishes (*1187*), and mammals such as dogs (*354*), cattle (*354*), deer (*810*), mice (*158, 1129*), hamsters (*814*), and primates (*321, 784–786, 1237*). Indeed, it is possible that sex pheromones play a part in the courtship and reproduction of humans as well (*66, 306, 1177a*). Excellent reviews of this subject are those by Whitten (*1263*), Michael and Keverne (*784*), Bruce (*214, 215*), and Ralls (*906*).

General reviews on various aspects of the subject of insect pheromones may be found in references *112, 144–146, 151–154, 229, 244, 247, 305, 375, 375a, 422, 468, 479, 501, 521, 525, 529, 530, 545, 550, 574, 587, 594, 596, 599, 601, 636a, 639, 644, 669, 695, 700, 707, 713, 789, 807, 907, 932, 978, 979, 1092, 1156, 1188, 1254, 1268, 1272,* and *1292*. Brief reviews of insect sex pheromones are found in references *64, 78, 150, 192, 249, 316, 544, 590, 646, 650, 699, 738, 756, 797, 798, 811, 817,* and *850*. The assembling of various moths and butterflies has been reviewed by Poulton (*883*).

Reviews in references *37, 122, 128, 230, 592, 645, 703, 716, 812, 831a, 900* (140 references), *916, 1112,* and *1131* deal mainly with the chemistry

of insect sex pheromones; reference *1079* deals with their specificity (or lack of it), and references *249*, *254*, *440*, *449*, and *1269* are devoted to honeybee pheromones. Sex pheromones among the Lepidoptera are reviewed mainly in references *540*, *606*, and *757*, and those among the Coleoptera are discussed in references *78*, *223*, *774*, *997*, *1100*, *1133a*, *1206*, and *1286*.

CHAPTER II

OCCURRENCE OF SEX PHEROMONES IN THE FEMALE

As long ago as 1837, von Siebold (*1097*) recognized that a pair of appendages, sometimes colored, opening into the vagina of the females of some insect species may act as an attractant for males. He surmised that the odor emitted by a female insect probably functions to entice the male, while that emitted by a male may be used as a stimulus in copulation (aphrodisiac).

Acarina

Amblyomma americanum (L.), lone star tick
Amblyomma maculatum Koch, Gulf Coast tick
Dermacentor variabilis (Say), American dog tick

Females of these species produce a pheromone that attracts males of the respective species. Males respond only after reaching a state of maturity initiated by feeding (*138*).

Panonychus ulmi (Koch), European red mite

Males tend to aggregate around quiescent female deutonymphs to await the latter's eclosion (*899*).

Tetranychus urticae Koch, two-spotted spider mite

Males are attracted strongly to quiescent deutonymphs, remaining until emergence of the adult female, when mating occurs. They are also attracted to ether extracts of the deutonymphs (*307*, *308*).

ORTHOPTERA

Blaberus craniifer (Burmeister), giant death's head roach

Virgin females produce a volatile sex pheromone which attracts males and elicits antennal waving, alertness, and locomotion toward the females (*107*). It is also interspecifically effective in eliciting male courtship behavior in *Blaberus giganteus* and *Byrsotria fumigata*.

Blaberus giganteus L.

Virgin females may produce a volatile attractant for males, releasing courtship behavior (*107*).

Blatta orientalis L., oriental cockroach

Females appear to have a nonvolatile sex pheromone present on their body surface which facilitates sex recognition and releases male courtship behavior. The wing-raising display is less complex and variable than that of the male *Periplaneta americana* (*114*).

Blattella germanica L., German cockroach

Virgin females produce a substance attractive only to males. It is unattractive to males of *Blatta orientalis* and *Shelfordella tartara* (*1237*).

Byrsotria fumigata (Guérin)

Virgin females produce a volatile sex attractant which enables males to perceive them at a considerable distance and elicits alertness, antennal waving, and wing "pumping" (*106, 107, 110, 981*). A number of gynandromorphs are found to produce the female sex pheromone (*116*).

Leucophaea maderae (F.), Madeira cockroach

Smyth (*1117*) claims to have collected a volatile material from females that increases the incidence of courtship by males.

Mantis religiosa (L.), praying mantis

Caged virgin females can lure large numbers of males from a distance of up to 100 m between 8:30 AM and 1:00 PM (*658*).

Nauphoeta cinerea (Olivier), cockroach

The sex pheromone, if it exists, appears to be a nonvolatile substance on the surface of the female. Male display (raising of the wings) is readily evoked, even by unreceptive females (*107*).

Periplaneta americana (L.), American cockroach

Females emit an odorous attractant for the male. The substance adheres to paper or other materials with which the females come in contact (*985*). Virgin females, as well as filter papers exposed to them, cause male alertness, antennal movement, searching locomotion, and vigorous wing flutter (*107, 985*).

The wing-raising display, which is released much more readily in groups of males than in single males, is used as the single criterion of response in a bioassay method developed by Wharton *et al.* (*1258, 1259*). However,

Jacobson and Beroza (*600*) have shown that a number of organic compounds, including several that are repellent to males (such as amyl acetate), will elicit wing-raising, thus making it mandatory that an accurate bioassay show a combination of intense excitement, wing-raising, *and attempts to copulate with one another*. The mating urge is so powerful in this insect that males starved for 4 weeks in the laboratory and then given their choice of the female sex pheromone or food, invariably responded to the sex pheromone until they were near death (*764*).

The sex attractant is produced principally by virgin females and sporadically by mated females. Nymphs ordinarily do not produce the attractant, and a newly emerged female produces very little of the substance at first. During this nonproductive phase, the female does not attract the male, and mating does not occur. Maximum production is attained by the second week after eclosion. Carbon dioxide anesthetization and manual manipulation reduce the production of attractant somewhat (*1260*). Attractant synthesis is drastically depressed within 18 hours after copulation, which accounts for the sporadic production of the substance by mated females.

The female sex pheromone is effective in releasing courting behavior in males of other *Periplaneta* species and in males of *Blatta orientalis*, but not in *Eurycotis floridana*, *Leucophaea maderae*, or *Nauphoeta cinerea* (*107*). The sex pheromones of other species of *Periplaneta* also appear to be interspecifically effective within the genus (*114*, *980*).

Periplaneta australasiae (Fabr.), Australian cockroach

Periplaneta brunnea (Burmeister)

Females of these 2 species produce pheromones that attract and sexually excite males. The same behavior is elicited in males by exposure to filter papers over which females have crawled (*107*, *114*).

Periplaneta fuliginosa (Serville)

Virgin females apparently produce a chemical substance which acts as a releaser of courtship behavior in males, but this has not yet been proved (*107*, *114*).

HEMIPTERA

Dysdercus cingulatus Fabr., red cotton bug

A cardboard box (with pinhole perforations) containing virgin females was placed 15 inches from a group of males. The males were quickly attracted to the box, and vibrated their wings and raised their antennae. A corresponding box without females did not attract males, but a box in which a female had been confined 5 days earlier acted as an attractant (*837*).

Lygus hesperus Knight, lygus bug

Virgin females in field traps attracted males. Mating reduces the attractiveness of females for only a few days (*1153*).

Lygus lineolaris (Palisot de Beauvois), tarnished plant bug

Traps baited with field-collected females were attractive to males in the field (*1020*).

Rhodnius prolixus (Stal.)

A volatile substance produced by mating pairs, but not by females or males separately, sexually stimulates males. In the absence of females, the stimulated males attempt to mate with other males. Feeding is a prerequisite to pheromone production; males and females copulate only after a blood meal, and unfed males will not respond to the pheromone. Males are stimulated only in complete darkness (*83*).

HOMOPTERA

Aonidiella aurantii (Maskell), California red scale

Sexually mature virgin females, as well as their crushed bodies, are attractive to males within minutes of the latter's emergence. The pheromone is continuously present in the female, who may release or withhold it (*1018, 1173*). Females become unattractive within 24 hours after insemination (*1175*). Females reared in the laboratory on potatoes are as attractive as those reared on lemons, but they are slower to mature (*930*). Males of both a laboratory strain and a native strain collected from lemons at Corona, California, showed the same degree of copulatory response to a pheromone extract obtained from virgin females of the laboratory strain. Males of the laboratory strain in free flight showed better response to virgin females of the native strain than to those of the laboratory strain, but they were even more responsive to the pheromone extract (*1172*).

Matsucoccus resinosae Bean and Godwin, red pine scale

Males in large flight chambers were greatly attracted to virgin females held in screen cages and attempted to copulate with the screen. Ultraviolet light was attractive to males except in the presence of females. Virgin females in petri dishes spun a small amount of silky fluff on the posterior of their bodies. When removed, the fluff was very attractive to males, and they attempted to copulate with it. Copulation was also attempted with filter papers on which females had rested overnight (*350*).

Myzus persicae (Sulzer), green peach aphid

Although sex-pheromone production by the females had been suspected, it could not be demonstrated by the use of olfactometers and field traps baited with live males, females, or their extracts. Males sometimes congregate around a copulating pair. It was concluded that females may produce