

14 Chemical Control of Behavior

THOMAS C. BAKER

University of California, Riverside, California, USA

1 Introduction	621
1.1 Information flow	622
1.2 Chemicals and insect movement	623
1.3 Theoretical considerations of chemical communication	623
2 Types of chemical communication	625
2.1 Mate-finding	625
2.2 Courtship	633
2.3 Host-finding (feeding, oviposition)	639
2.4 Host-finding (recruitment)	643
2.5 Self-defense	645
2.6 Defense of relatives	648
3 Orientation mechanisms	649
3.1 Direct reactions to odor	649
3.2 Indirect reactions to odor without wind	650
3.3 Indirect reactions to odor involving wind and visual cues	651
3.4 Integration of mechanisms by an insect flying in sex pheromone	654
3.5 The function of zig-zagging programs	657
3.6 Tonic vs. phasic pheromone stimulation	659
3.7 A new hypothesis	660
4 Chemical control of behaviors by man	661
4.1 Host-finding	661
4.2 Defense of relatives	662
4.3 Mate-finding	662
References	667

1 INTRODUCTION

The diversity of insect behaviors is staggering. Their repertoires are amazingly matched to their life histories and to the demands of the abiotic and biotic surroundings. Earlier chapters in this volume have described lucidly how behavior results from the integration of visual, auditory, tactile, olfactory, and gustatory sensory information from the environment with internal information from hormones and the central nervous system (CNS). It is the purpose of this chapter to review the types of behaviors elicited by cues from just one of

these modalities, chemicals, and to try to generalize about their effects. Certainly chemicals are powerful modifiers of insect behavior; so much so that entomologists now use them to suppress and monitor populations (see volume 12). We should not delude ourselves that such chemicals *completely* control insect behavior, notwithstanding the title of this chapter, but when compared to other stimuli across all the insect families, chemicals must be considered the most specific and influential mediators of behavior known. I would like to make some generalizations about how they affect insects.

1.1 Information flow

It may be helpful to depict information, in the form of chemicals, as being emitted from a source, travelling through an environmental channel, and reaching the receiver, the insect (Fig. 1, adapted from Shannon, C. and Weaver, W., 1949). Chemical communication, defined here in the broad sense as transmission of information between a source and receiver, will have occurred only when the signal reaches the receiving insect's CNS and has a chance of being integrated with the internal physiological state of the insect to result in a behavioral response. Before reaching the CNS, however, spurious information from the environment may be added to the channel. Such chemical noise is a factor in determining whether or not

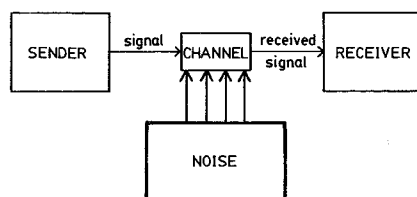


FIG. 1. Information flow that results in communication in an environment with noise. (Adapted from Shannon, C. and Weaver, W., 1949.)

information in the signal is integrated and communication occurs. The chemical signal:noise ratio must be high enough for the receiving individual's nervous system to discriminate the message contained in a stream of action potentials.

Hence, chemically mediated interactions among insects or among insects and other organisms in the environment can be viewed as "attempts" to either enhance or minimize the chemical signal:noise ratio. This ratio may be altered in three major ways: by changing either the quality or quantity of the chemical signal, or both. It is helpful, although somewhat subjective, to look at communication that occurs in nature based on whether the sender or receiver benefits (Alcock, J., 1982). Such an examination often reveals the type of selective forces occurring at the individual, not the group, level. In Table 1, I have categorized the major types of chemical communication occurring in insects according to the types of pressures placed on the signal:noise ratio by the sender and receiver. It is clear that in most cases the receiver "wants" the ratio to be high, and may go to great lengths physiologically to amplify the signal, using thousands of narrowly tuned receptors to filter out the background noise. The sender, on the other hand, very often does *not* "want" to send a signal

Table 1: Relationship between the signal : noise ratio and the types of behaviours in which chemical communication is used.

Behaviour	Sender	Receiver	Benefits of signal : noise ratio	How accomplished		
				Amplitude	Sensitivity	Specificity
Mate-Finding	adult insect	adult insect	high, benefits sender high, benefits receiver	low	high	high
Courtship	adult insect	adult insect	high, benefits sender high, benefits receiver	high	moderate	moderate
Host-finding (feeding, oviposition)	plant host tissues	insect	low, benefits sender high, benefits receiver	low	high	high
	flowers	insect	high, benefits sender high, benefits receiver	high	high	moderate
	insect host	insect	low, benefits sender high, benefits receiver	low	high	high
Host-finding (recruitment)	insect	insect's relative	high, benefits sender high, benefits receiver	high	low	high
Self-defense	insect	predator or parasite	high, benefits sender low, benefits receiver	high	low	low
	plant tissues	phytophagous insect	high, benefits sender low, benefits receiver	high	low	low
Defense of relatives (alarm)	insect	insect's relative	high, benefits sender high, benefits receiver	high	high	low
oviposition (deterrence)	adult female	adult female	high, benefits receiver	moderate?	moderate?	unknown

because the reactions of the receiver are detrimental. Therefore the sender allocates much effort to reducing the signal's amplitude and altering its quality so that it blends into the background noise and communication does not occur. I will examine the relationships in Table 1 in more detail later, when I address each type of behavior separately.

1.2 Chemicals and insect movement

I will discuss only the overt behavioral effects elicited by chemicals in this chapter, not the physiological, or primer effects. Overt "releaser" effects are manifested most often as changes in an insect's movements, which I prefer to view as resulting in three major types of outcomes: attraction, arrestment, and repellency. Here I take a broader view than Dethier, V. *et al.* (1960), who defined the effects of chemicals on behavior in terms of whether the movements take the insects toward or away from the source in a *directed* (steered) or non-directed fashion. For instance, a repellent was defined as a chemical that causes an insect to make a directed movement away from the chemical source. An attractant would cause a directed movement toward the source. In my view, whether or not the movements are *steered* toward or away from the source is irrelevant. What matters is the *outcome* of the movements in terms of the insect's displacement in space. After all, this is the evolutionary bottom line, how quickly and efficiently, not necessarily how directly, the insect can make it from point A to point B.

This distinction between movement reactions and the *end result* of those movements was pointed out quite clearly by Kennedy, J. (1978), and cannot be overemphasized. Thus the effects of a defensive chemical might be to make an attacker stop in its tracks (arrestment) or make it move away (repellency). Likewise, the effects of a sex pheromone may be viewed as causing first net movement toward the source (attraction) and then arrestment upon reaching the source. Although the question of how an insect steers in response to a chemical is critical to a complete understanding of the chemical's effects, it does not need to come into play in this generalized view of the overall *displacement* outcomes evoked by chemicals.

A more detailed examination of responses

reveals, for instance, that some lepidopteran courtship chemicals not only cause a female to become or remain arrested; they also evoke a change in her posture that allows the male access to her genital opening (Rutowski, R., 1977, 1980; Grula, J. *et al.*, 1980). Likewise, defensive chemicals that cause an attacker to become arrested may do so because they evoke an intense grooming response that is incompatible with continued movement toward the would-be victim (Eisner, T., 1970, 1972). Certainly it is imperative that the movement reactions used by insects to result in these displacement outcomes be fully explored (see section 3).

1.3 Theoretical considerations of chemical communication

Of all the communication modalities, chemical communication is the slowest. Once chemicals are emitted into the environment they linger, and are no longer under the control of the emitter. Communication by sound or light does not pose such problems and the temporal aspects of these signals can be tightly controlled by the emitter. Fade time (Bossert, W. and Wilson, E., 1963) and rise time of non-chemical signals are very short, and therefore are easily amplitude-modulated. In fact, the richness and specificity of auditory and visual signals are derived in insects mainly by amplitude modulation and not carrier frequency (Lloyd, J., 1966; Alexander, R., 1962; Bennet-Clark, H. *et al.*, 1980; Ewing, A., 1979; Hoy, R. *et al.*, 1977).

There are a few instances of amplitude-modulated chemical emissions that *may* have communicative value above and beyond that of the chemical blend itself (Conner, W. *et al.*, 1982; Baker, T. and Cardé, R., 1979a; Cardé, R. and Roelofs, W., 1973). The signal value of these pulsed signals needs to be proven, and these examples notwithstanding, the richness and diversity of chemical communication can be attributed to the diversity of chemical structures themselves. This was predicted 20 years ago by Bossert, W. and Wilson, E. (1963) when only a handful of pheromones had been identified. They predicted that most insect sex pheromones (which usually are species-specific) should be 10- to 18-carbon compounds because of the trade-off between the volatility necessary for sufficient long-distance transport, and the size of

the compounds, which directly affects the number of possible species-specific isomers and configurations. This prediction has been proven correct even though it was put forth at a time when "one-species, one-compound" was thought to be the rule for pheromone signals. Now that it has been shown that *blends* of pheromone compounds are the rule (see Borden, chapter 6; Tamaki, chapter 3), it is clear that signal specificity can be attained in so many structural ways, even without amplitude modulation. There is even one more way to find a specific, noise-free communication channel: by using a structure that is the mirror image of another. The evidence now favors a model for the transduction of chemical cues into action potentials that invokes chiral, "hand-in-glove" receptors (Amoore, J. *et al.*, 1967) rather than one which would involve infra-red vibration resonance (Wright, R., 1973; Callahan, P., 1975) (see Mayer, and Mankin, chapter 2). There is even evidence that the receptor sites for *cis*-11-tetradecenyl acetate on male red-banded leafroller moth antennae are chiral, even though the compound itself is not chiral (Chapman, O. *et al.*, 1978).

It is clear, then, that chemicals offer a richness of signals unmatched by other modalities, and this may account for their widespread use by insects for communication within their own species and with the rest of the biotic environment. The ubiquity and richness of signals can be a disadvantage, too, unless this large amount of potential noise is filtered out, possibly at considerable physiological cost, and at the cost of being ignorant of a large amount of the odorous environment. Once a more narrowly tuned path has been taken, and receptors have been devoted specifically to one set of signals, there may be no evolutionary turning back. Indeed the great diversity of insect species may have been due to such canalizing of insects with host plant chemicals, host insect volatiles, and with members of their own species (Ehrlich, P. and Raven, P., 1964).

What are some of the other advantages and disadvantages of chemical communication? The slow fade time of chemical signals allows marking of pathways, territories, or previous positions in the environment that would be impossible with other modalities (see Birch and Haynes, chapter 5). One's presence in a large area can be communicated long after one has departed. Hence, information con-

cerning profitable foraging routes, among other things, can be stored externally, in the environment, without the need to take up space in the CNS memory. The pheromonal "memory trace" in ants, for instance, is reinforced as long as food rewards are present, but is allowed to fade (disappear) with disuse and exhaustion of the food supply (Wilson, E., 1974). The topographical information is only available as long as the concentration is sufficiently high and above background noise such that it is above the response threshold of other worker ants. The area in which the chemical concentration is above threshold, i.e., the "active space" of the signal (Bossert, W. and Wilson, E., 1963) can be controlled by alterations in either the emission rate (deposition rate of trail pheromone) or the response threshold of the workers. The active space concept advanced by Bossert and Wilson in 1963 remains a valuable way of looking at chemical communication such as trail pheromones. Using mathematical formulae, it predicted the features that species-specific trail pheromones should have in order to produce sharp "edges" to the trail plus have a moderate fade time if not reinforced. These features included intermediate molecular weight compared to alarm or sex pheromones, moderate emission rate, and a high threshold, so that the concentration would fall quickly below threshold when the ants are more than a few mm from the source.

One reason that chemical communication can take place so slowly is that it must rely on evaporation and diffusion, except in the cases of some defensive chemicals that are forcibly ejected at close range onto their targets (Eisner, T., 1965). Thus, more so than light and sound, chemical signals are highly dependent upon the whims of the environmental channel through which communication must occur. The emissions may be transported by air currents in unwanted directions, or extremely high or low temperatures may change evaporation and diffusion rates. These changes may be especially disadvantageous for species trying to communicate by using a precise blend of two or more compounds having dissimilar vapor pressures. Cardé, R. *et al.* (1977) pointed out this problem after examining the sex pheromone systems of several sympatric species of tortricid moths. They noted that only the ratios of *geometric isomers* — those compounds having nearly identical

vapor pressures — were tightly and narrowly discriminated by males. Males had a higher tolerance, on the other hand, to a wider range of ratios in blends of compounds having different functional moieties (i.e. alcohols vs. acetates vs. aldehydes) or chain lengths. In other words, precise ratios of such vapor pressure-disparate compounds do not appear to be as important for communication as those of vapor pressure-similar compounds, because the ratios of emitted similar compounds should not vary as much with ambient temperature.

Both light and sound have high directionality, mainly because intensity can be compared simultaneously by receptors on different parts of the body. Light and, to some extent, sound, do not move well around objects and therefore produce intensity "shadows" that, when caused by the receiver's own body parts, can enhance the location of the signal's source by producing a steep gradient between receptors located on different sections of the body. The directionality, or polarization, of a chemical signal is usually only provided by the movement of the medium (the air) itself. This is because sufficiently steep gradients that allow either simultaneous intensity comparisons by two or more receptors or sequential ones by movements through space are not likely to occur at very great distances due to properties of diffusion. Trail pheromones have high lateral directionality because sharp lateral gradients are present and able to be sampled by the widely spaced antennae (Hangartner, W., 1967). An ant is never more than a few mm from the "source", the entire length of deposited trail. There is no evidence that a longitudinal gradient from source to nest or vice-versa is present that would give the trail directionality. Similarly, odor "plumes" may provide a rather narrow path with which moths may chemotactically stay in lateral contact, but without wind the "toward", or "away-from"-source polarity is not present in the chemicals alone.

Compared to light, there is a relative paucity of "reflected" chemical signals. Reflection of ambient light predominates in visual signalling, probably because, during daylight, background noise would swamp any synthesized light. Small sections of the ambient light spectrum can, however, be amplified by pigments that preferentially absorb some frequencies while reflecting others, or by cuticular structures that cause some frequencies to be

brilliantly enhanced at the expense of others (see Fuzeau-Braesch, chapter 12). The intensity of the concentrated, reflected light is sufficient to overcome the background frequencies. At night, a few insects have been able to find energetically feasible means of producing enough light to rise above background levels. Even so they have apparently had to skew their emission frequencies according to the predominant ambient frequencies (Lall, A. *et al.*, 1980). Ambient sound, because it is less predictable and abundant and because it is not easily concentrated, is not usually reflected for communication purposes. The resonance provided by special body parts and structures such as cricket burrows (Bennet-Clark, H., 1970; Forrest, T., 1982) may aid in amplifying and reflecting synthesized sounds but in general this modality does not lend itself well to reflection of ambient sounds.

The problems of directionality and signal:noise ratio may be the primary reasons for the synthesis of novel compounds for communication rather than reflection of available ones. Where good signal:noise ratios can be obtained, such as in the direct application of defensive chemicals at close range, the amplification and reflection of ambient compounds is found more commonly. The sawfly larva, *Neodiprion sertifer*, ingests and sequesters terpenes from its host conifer plants and then smears them on would-be parasite attackers (Eisner, T. *et al.*, 1974).

Other than these instances where defensive compounds are used, the ambient noise is used as a "passive" defense by many insects, as something to "blend into" rather than to amplify (see section 2.5 and Blum, chapter 4). Other examples of chemical signals virtually unchanged from the environment are found in some lepidopteran courtship pheromones, also used at close range. When reflection of ambient chemicals is used, it can follow a longer time-course than that of light or sound because of slow fade time, and chemicals can be stored and protected for a long time before retransmission because evaporation is minimal.

2 TYPES OF CHEMICAL COMMUNICATION

2.1 Mate-finding

In no other chemical communication system is the

signal:noise ratio greater, and the length of the active space longer, than in mate-finding systems. This is accomplished mostly by exceedingly low-response thresholds in the receivers, not by high emission rates. Mayer and Mankin (chapter 2) discussed how thousands of nearly identically tuned receptors are devoted by male moths to an incredibly narrow range of compounds. The substantial amount of background noise that must be present even in a temperate ecosystem with all its plant and insect volatiles, is filtered out.

Thousands of nearly identically tuned receptors would appear to offer much in the way of sensitivity to one specific chemical or blend, but at the cost of being able to discriminate only one odor from all the rest. However, the receptors' spectra are not identical, only similar, and so some discrimination over a narrow range of pheromone-like blends is possible. O'Connell, R. (1975) demonstrated that the sex pheromone receptor cells in male red-banded leaf-roller moths, although very similar, have slightly different tuning curves, which would allow discrimination among very similar blends. It would also account for the narrow behavioral response spectra in field trapping and laboratory bioassays (Baker, T. *et al.*, 1976) to ratios of two of this species' components. Behaviorally the moths appear oblivious to blends not involving these two compounds and this probably is a result of devoting all one's receptors to the important compounds and tuning out all the others. Only some "unnatural" synthetic pheromone analogs can stimulate the receptors enough to evoke responses, such as to an odd, 13-carbon pheromone analog, *cis*-11-13:Ac that appears to bind the sites of two components at once, those of *cis*-11-14:Ac and 12:Ac (Roelofs, W. and Cardé, R., 1977; Baker, T. and Roelofs, W., 1976).

In moths, convergence of the thousands of receptor axons takes place at the level of the olfactory lobe, and exiting to the brain are only a few hundred fibers (Boeckh, J. and Boeckh, V., 1979). The pheromone signal for *Antheraea polyphemus* is thereby amplified a measurable 10–100-fold over the levels at the individual sensilla.

Why have ultra-low thresholds been selected for in insects receiving sex pheromone signals, as exemplified by male moths? And why are sex pheromone emission rates so low compared to other types of

chemical communication? This emission rate difference is not small. For instance, nausute termite soldiers attacking an intruder can emit milligrams of sticky terpenoid secretion in a few seconds (Eisner, T. *et al.*, 1976). Female *Heliothis virescens*, on the other hand, emit only a few nanograms of sex pheromone each minute, and *Grapholita molesta* females only a few nanograms each hour (Pope, M. *et al.*, 1982; Baker, T. *et al.*, 1980). Thus, moth sex pheromone emission rates are many millions of times lower, and when taking into account the distance of communication (hundreds of meters compared to a few millimeters), the effective concentration for evoking a response may be trillions of times lower. Even for courtship pheromones, it is easy to extract microgram amounts from male moths and butterflies, whereas 10 ng or less of sex pheromone per female gland are usually the maximum for female moths. When the distance of communication is also considered, the emission concentration of sex pheromone compared to courtship again seems unnecessarily low. Why?

The answer may lie in sexual selection by the emitters for only the most discriminating, sensitive responders (Greenfield, M., 1981). By releasing lower amounts of pheromone, females may be selecting for "better" males who have the receptor equipment and vigor to respond from great distances to the minute amount of odor she produces. Trivers, R. (1972) and Thornhill, R. (1979a) considered the sex having the well-stocked, nutrient-rich gametes to be the one that has invested the most and, as such, to be the "limiting" resource. Female moths and female insects in general will usually be limiting because of their large, well-provisioned eggs. Presumably males initially became "tuned in" to any cues, including odors, that would help them locate these limiting resources. Over time, normalizing or stabilizing selection should have fashioned female-emitted chemicals that were blended to what the majority of males were sensitive to, and males that were tuned to what the majority of females were producing. Such males would have the maximal chance of flying into a potential mate's pheromone plume at above-threshold concentrations. At the same time, female "selectivity" for mates would have been operating by lowering the emission rates of an increasingly narrow blend of compounds. It would seem at first that females would risk luring no males at all by emitting

too little compound, especially at low population densities. But under most densities this has not been a problem, and there is still apparently much room for females to lower their rates further.

Males are sometimes the emitters of sex pheromones, and Thornhill, R. (1979a) and Trivers, R. (1972) predicted this should occur when the male is providing significant investment in the offspring, usually in the form of a nutritional investment of some sort that the female can use to manufacture eggs (Boggs, C. and Gilbert, L., 1979). The large orthopteran spermatophores or females feeding on male body parts are usually a part of a male-emitted auditory sexual signaling system. For chemical communication, the pheromonal signaling by male scorpion flies that have captured a prey item or manufactured a saliva ball on which females feed before producing eggs also lends support to this idea. The males' nutritional gifts make them the limiting resources to whose odors females must become sensitive if they are to arrive there before other females.

However appealing or correct this idea proves to be, one should not conclude that nutritional gifts are the only ones that can be limiting and zeroed in on by females. Sexual selection as proposed by Fisher, R. (1958) may account for the evolution of many male-based pheromone systems. In this model the male pheromone itself, plus the display associated with pheromone release, would be the "gift" (limiting resource) to females under situations where males' displays vary in quality, and where some males mate more often than others. Females' sons inheriting the pheromone display would be at a mating advantage in the next generation in the presence of the discriminating females in that generation (Baker, T. and Cardé, R., 1979a). An initial event such as incomplete reproductive isolation from female-emitted pheromone resulting in mating mistakes would have to have occurred, causing discriminating females to arise in the first place. Females might begin by discriminating for some species-specific male odor. Once this discrimination arose, sexual selection for increasing amounts of male odor and ever-more discriminating, choosy females could proceed in a "runaway" fashion (O'Donald, P., 1967) until a limit was reached due to natural selection, the physiological limits on emission rates, or the structures needed to produce such high rates.

In moths, such sexual selective pressures alone, without a special nutritional resource, may have been responsible for the male scent and hairpencil structures involved in close-range attraction of oriental fruit-moth females by displaying males (Baker, T. and Cardé, R., 1979a). Male hairpencils and brush organs in other species may have arisen under similar pressures (see section 2.2, and chapter 5 by Haynes and Birch). There are relatively few long-range olfactory signals emitted by male Lepidoptera and much research needs to be performed to deduce the relative roles of nutritional gifts, sexual selection for the display itself, and selection for "fit" males who have obtained defensive compounds (Conner, W. *et al.*, 1981). Male *Eldana saccharina* (African sugarcane borer) emit a pheromone from their hairpencils and attract



FIG. 2. Male African sugarcane borer (*Eldana saccharina*) everting brush organs on end of abdomen and emitting pheromone. Females respond to the male-emitted pheromone from several meters away by walking up and down plants until they locate the male (From Zagatti, P., 1981.)

females who walk to the males from many meters away (Fig. 2) (Zagatti, P., 1981). Do they provide a larger than usual spermatophore compared to other species, which the female can use for producing eggs? Research is under way on the oriental fruit-moth to determine the relative size of its spermatophore and quantity of accessory gland secretions passed to females.

It is possible that female-choice sexual selection could "run away" to the point where females are so choosy that the emission of a single male would rarely be enough to seduce a female. It might pay males to "pool" their displays to hasten the female's decision. Once this happened, individual males would be at a disadvantage and it would pay to be part of a group that emits sufficient odor and have at least some chance of being chosen by a female than none at all. Such a male "lek" system, or group of displaying males, is found in the aggregating and displaying males of *Estigmene acrea*, the saltmarsh caterpillar moth (Willis, M. and Birch, M., 1982).

The huge, bloated coremata are inflated by males hanging on foliage or other objects such as fences. The displaying males attract other males until the aggregation grows to large numbers (Fig. 3). Females are also attracted to these leks, whereupon one of the males mates with her. Whether males in these groups give extra-large nutritional gifts to females remains to be seen, but it is possible that the display behavior alone, and the mating advantage it confers on the female's sons in the next generations, may be all that is involved in the female's choice. For *E. acrea*, like *Grapholita molesta*, the female-based pheromone system is still functional. Female pheromone (Hill, A. and Roelofs, W., 1981) is emitted later in the evening, after male lekking has subsided. Females are still apparently enough of a limiting resource that a "dual" system of attraction is used.

A variety of male- and female-based mate-finding systems is exhibited by the bark beetles, family Scolytidae. The pheromone-host-tree blends of



FIG. 3. Artist's depiction of a lek formed by male *Estigmene acrea* moths, which hang on plants and inflate their coremata (δ_1). Both females (\varnothing) and males (δ_2) are observed to fly into these leks, the females ending up in copula (c) with some of the males, and the males landing and inflating their coremata to add to the aggregation of displaying males. Some males periodically withdraw their coremata (δ_3). (Drawing by Sam Gon, courtesy M. A. Willis and M. C. Birch; see Willis, M. and Birch, M., 1982.)

volatiles used by these species have heretofore been called "aggregation" pheromones, but as pointed out by Alcock, J. (1982), this label has fostered a possibly illusory impression of group cooperation by the beetles in "mass-attacking" the trees to overcome their defense of viscous terpenoid sap. When examined on the basis of selection pressures on individuals, these beetles' mating systems become even more interesting. For instance, the host- and mate-finding system of *Dendroctonus pseudotsugae*, researched so carefully over the years by Julius Rudinsky and his colleagues (Rudinsky, J. and Ryker, L., 1976, 1977), illustrates nicely that the stimuli and responses shaped by individual selection may have little to do with aggregation and more to do with selfish competition (Alcock, J., 1982).

Individual females locate a host tree and begin burrowing into the bark by eating it. On a relatively healthy tree with only a few females attacking it, there will be relatively large amounts of unaltered terpene-volatile resin exuded by the tree compared to the enzymatically altered terpenes emitted from the beetles' feces that make up the pheromone blend. Therefore relatively few other females (and males) in the area may be likely to be attracted to the tree at this stage because the chemical signal leaves doubt as to whether the tree's defenses are going to be overwhelmed. But if the tree is already weak with relatively low resin content (and terpene emissions) or if a healthy tree's supply of resin has been exhausted by further attack, the signal may shift to more predominantly pheromone compounds from the fecal pellets, and males will be attracted to the limiting, lucrative resource of a batch of unfertilized eggs in an already-excavated gallery in a favorable host environment for offspring. Other females likewise will be attracted because of the pheromone-proven existence of a favorable environment for offspring in that same tree.

Males that arrive at a gallery entrance emit a stridulatory chirp, and at this point a so-called "masking" compound is emitted as well, which keeps other males from being attracted to the gallery. As pointed out by Alcock, J. (1982) far from serving as a repellent or "masking" the pheromone blend "against the wishes" of approaching males (as implied by this term), sensing the odor and staying away may be entirely to the approacher's advantage and may have evolved in such a way as to

indicate an already-occupied gallery which would be a hopeless situation for mating.

Similarly, large amounts of the "masking" odor may indicate to approaching females that there is little space left in which her offspring can develop without incurring the fatal competition from the young of other females, who have a head start in size and development. This interpretation is quite different from the group-oriented picture of past reports, where the termination of "mass attack" by a group of beetles was thought to be orchestrated so that the (tree) resource would not be over-exploited to the group's detriment.

There seem to be many more examples of male-emitted pheromones in the bark beetles than in other insects, and this may be due to the substantial investment a burrowing male can make in his offspring relative to males of other insects. Females will have "learned" over evolutionary time to tune in to volatiles emitted by these males. In this case the "gift" is both a food and shelter resource, the gallery located in a good host tree. For instance males of the beetle, *Ips pini*, locate the tree and initiate the galleries. Future researchers on bark beetle pheromone systems will likely benefit by interpreting their results based on selection pressures on individuals. However, some of the beetle mate-finding systems may indeed have a group basis and benefit, and this should not be dismissed entirely. For instance, a few male-emitter systems may have evolved on a basis similar to lekking, although the fact that the signaling occurs on a resource "patch" would not precisely fit the concept of a lek (Brown, L., 1975). The pheromone components of bark beetles do not appear to be very different from the volatiles that to our noses make a walk in a coniferous forest such a pleasure. Perhaps lekking male beetles have opted to optimize the signal:noise ratio through the relative synthetic ease of only slightly modifying existing abundant terpenoids and raising their amplitude by group emissions to attract mates.

Emission systems based on groups of individuals would increase the active space compared to an individual signal. The active space concept introduced by Bossert, W. and Wilson, E. (1963) has provided a valuable framework on which to structure our thinking about chemical communication. For mate-finding systems, this concept has already been examined by Tamaki in chapter 3. Although it

has been a helpful concept, it has become clear that some aspects now need to be revised. The original calculations, with the subsequent predictions about communication distances, were based on the equations of Sutton, O. (1953) that dealt with time-averaged estimates of concentrations of gases transported by the wind. As such, one major change that needs to be made in these equations when they are used for behavior is to make the concentration instantaneous, not time-averaged, because behavior may be elicited by a virtually instantaneous exposure to molecules. This change would not affect the overall scheme of a behaviorally active concentration that depends on Q , the emission rate, and K , the behavioral threshold in the receiver (Bossert, W. and Wilson, E., 1963). But it would affect the precise numerical relationships outlined by Bossert and Wilson, perhaps making experimentally measured active space dimensions differ from the expected values, calculated according to a given wind speed, the emission rate and thresholds of the insects (Elkinton, J. and Cardé, R., 1983). Instantaneous rather than time-averaged concentrations may indeed be responsible for behavioral response, and the filamentous nature of odor plumes (Wright, R., 1958) makes it much more likely that a parcel of air could contain an above-threshold concentration of pheromone than if the insect were taking an overall average and then responding. Thus, one way the equations might be made more accurate for behavior would be to incorporate instead *peak* concentrations, or *average peak* concentration at a given distance.

Another shortcoming of these equations is that they were based on a system having no upper threshold, and we know it is possible to exceed a concentration at which a behavioral response is elicited. This is illustrated in the oriental fruit-moth male response to its female-emitted sex pheromone (Fig. 4).

At very low concentrations in a laboratory wind tunnel or at great distances from the source in the field above-threshold concentrations are present to cause the behavioral movements that result in "upwind flight" or displacement toward the source. Thus the "active distance" for upwind flight, on average extends to past 80 m for 1000 μg -loaded septa, 30 m for 100 μg -loaded septa, and 12 m for 10 μg -loaded septa. However, upwind flight, on

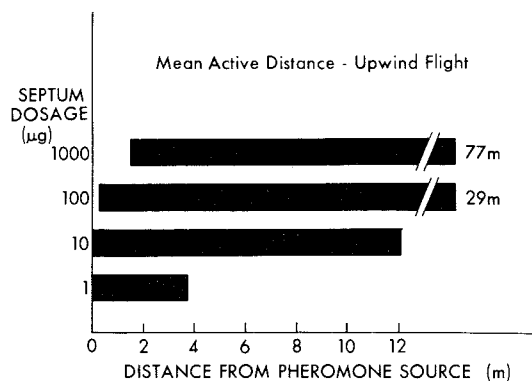


FIG 4 The mean active distances for upwind flight of *Grapholita molesta* males measured in response to four different sex pheromone dosages on a rubber septum dispenser. Note that at the two highest dosages the active space does not extend all the way to the source due to arrestment of upwind flight, even though males began flying upwind from farther away to these dosages. (From Baker, T. and Roelofs, W., 1981).

average, stops 1.5 m from the source for 1000 μg , and 0.2 m from the source for 100 μg , but extends all the way to the source for 10 μg (Baker, T. and Roelofs, W., 1981). In the laboratory wind tunnel these same distances for in-flight arrestment are found. Thus, there exists a concentration above which this behavior is no longer elicited but at which arrestment occurs within the plume (no displacement toward or away from the source), and then the moth leaves the plume by flying out and upward. Thus active space does not extend all the way to the source at higher septum loadings, and this is why one does not capture as many moths to the correct blend of components at 1000 μg compared to 10 μg . Female oriental fruit-moths emit pheromone at a rate similar to 10 μg septa ($1-2 \text{ ng h}^{-1}$). Premature arrestment of upwind flight has been observed for many other species (Tamaki, chapter 3) and it is likely that for lepidopterous sex pheromone systems, at least, the active space concept must be modified for behaviorally active compounds to take into account upper, as well as lower, thresholds (Baker, T. and Roelofs, W., 1981).

It is also important when measuring active spaces to specify precisely the behavioral response whose threshold is being measured. For instance, oriental fruit-moths may begin walking, on average, at slightly greater distance (lower concentrations) than they begin flying upwind. Thus the active space for walking without wing fanning extends farther

than for upwind flight. By the same token, the upper threshold for walking may be lower than that for upwind flight, resulting in the disappearance of walking at greater distances from the source than those at which upwind flight is terminated.

For mate-finding systems, environmentally modulated variations in the active distances over which responders fly upwind may be more a result of changes in K , the behavioral threshold, than in Q , the emission rate (Bossert, W. and Wilson, E., 1963). Certainly, the diel variations in trap captures of moths in traps containing continuously emitting sources attest to that. But when the distances over which behavioral responses are elicited are actually measured, the dramatic variations are seen more clearly. For instance, walking in male oriental fruit moths was elicited to 1000 μg septa on some warmer days at distances of 140 m, well over the average of 80 m. On the other hand, on cooler days, especially those below a critical threshold of 16°, walking only occurred at ca. 25 m and on these days no upwind flights were observed at all. The males' thresholds were apparently changed dramatically by changes in temperature. Apart from these immediate changes to exogenous factors, the oriental fruit-moth threshold also fluctuates according to an endogenous circadian rhythm whose phase is set by photoperiodic cues. This makes wing fanning while walking behavior less likely to be elicited at particular time periods by a given concentration of pheromone, even under unvarying light conditions (Baker, T. and Cardé, R., 1979b).

The active spaces for other insects' mate-finding systems differ from the oriental fruit-moth. One must be careful, though, in examining the literature for such values, to make certain that the maximum distances of attraction were not merely the maximum distances that were tested. Another cautious note must be sounded for data that are taken from capture-mark-release-recapture studies. For instance, it was quite impressive that marked *Antheraea polyphemus* males were recaptured in sex pheromone traps more than 2 linear miles from their point of release (Kochansky, J. *et al.*, 1975). The length of the active space cannot be derived from these results, because as the authors point out, it is not clear at what point males began responding to the sex pheromone plume. The study did show that it is possible the active space could have extended for 2 miles.

Long "active distances" are possible when molecular transport by wind not only keeps the molecules concentrated in a long narrow plume, but also makes anemotaxis possible, which increases the efficiency and accuracy of the orientation (section 3). Some mate-finding systems may not be able to take advantage of wind because there is too little of it. For instance, almond moth males (*Ephestia cautella*) begin to change their wandering "searching" flight pattern and begin approaching calling females at about 1.5 m in the relatively stagnant air of grain storage (Hagstrum, D. and Davis, L., 1982). Male American cockroaches (*Periplaneta americana*) walking in still air make correct sharp turns toward the source when they are 41–80 cm away (Bell, W. and Tobin, T., 1981). Therefore, the length of the active space for "correct turn" behavior is at least 80 cm. The pheromone beyond this distance causes increased locomotory velocity but with few turns toward the source. When sufficient air currents are present (the wind detection threshold is 0.015–0.03 m s^{-1} ; Bell, W. and Kramer, E., 1979) the males can use them to orient to a sex pheromone source at least 2 m away (Tobin, T. *et al.*, 1981) (section 3).

In the Lepidoptera, a relatively few enzymes might be responsible for the great diversity of sex pheromones. Roelofs, W. and Brown, R. (1982) have hypothesized that one enzyme in particular, Δ -11-desaturase (Bjostad, L. and Roelofs, W., 1983), is the only one needed to explain most of the great variety of tortricid and noctuid pheromones. The major variable would be whether it acted before or after a chain-shortening step or a chain-elongation step, also enzyme-performed. Conjugated, di-unsaturated pheromone molecules would result from the Δ -11-desaturase acting both before and after chain-length alterations. The beauty of this system is that it explains how a small number of enzymes would be responsible for most of the known pheromones and only the order of their reaction would need to be altered to create a new signal. For new pheromone signals to evolve, new enzymes would not need to come into play; only a change in their order of performance plus corresponding changes in receptor enzymes in males.

Sex pheromone isomer production (*cis:trans* ratios) may be governed by very simple Mendelian

inheritance (Klun, J. and Maini, S., 1979) (chapter 3 by Tamaki). But of course many other steps are involved in their manufacture and transport. For the red-banded leafroller moth, the long-chain fatty acyl moieties that eventually become pheromone molecules are housed and transported primarily on triglycerides, but also on choline phosphatides and ethanolamine phosphatides (Bjostad, L. *et al.*, 1981; Bjostad, L. and Roelofs, W., 1983). The fatty acyl groups only at the *Sn*-2 position on choline phosphatides and at the *Sn*-1, *Sn*-2, and *Sn*-3 positions on triglycerides are apparently cleaved and converted to the corresponding pheromone components, *cis*- and *trans*-11-tetradecenyl acetate. The *cis:trans* ratio is apparently determined by the relative numbers of *cis* or *trans* molecules in these positions that happen to be plucked out by the enzyme.

How narrowly are males tuned to particular ratios of sex pheromone components? Are there behavioral phenotypes in the population that respond preferentially to one ratio? This cannot be determined by ordinary field trapping experiments because males are only given one chance to "choose" a particular ratio in a series. They are then trapped and unable to undo a "mistake". Thus the distribution of males in traps emitting a spectrum of blends, far from reflecting a series of discrete male response types or preferences, may merely reflect the probability of "mistakes" being made around a mean "preferred" ratio to which the receptors are tuned. Another way of looking at the distribution is that it reflects the breadth of tuning in the male population.

There is evidence that male oriental fruit-moths captured to off-ratios on either side of the optimal one actually made mistakes, and when given another chance, prefer optimal ratio. Males were allowed to fly up to septa emitting three different ratios of the sex pheromone components *cis*-8-dodecenyl acetate and *trans*-8-dodecenyl acetate, and upon landing and approaching closer than 4 cm, they marked themselves with a fluorescent powder color-coded for that ratio (Cardé, R. *et al.*, 1976). After an evening of unencumbered self-marking, the powders were replaced with sticky traps, and marked males in the area were recaptured to the same three blend ratios. The males were then examined under ultraviolet lamps for the presence

of colored powder on their bodies. A recapture distribution that would have indicated the existence of behavioral phenotypes specific for each type of ratio would have been one in which yellow-colored males (11% *trans*) were recaptured in greater than expected proportions to 11% *trans*, and blue-colored males (3% *trans*) and red males (8% *trans*) recaptured in greater than expected proportions in traps containing 3 and 8% *trans*, respectively. This distribution was not found in the observed recapture pattern, however. More males were recaptured to 8% *trans* regardless of their previous marking history.

More work needs to be performed to determine the malleability of a communication channel to shifting selection pressures and to see whether or not these pressures on the male or female can result in changes in the emissions and response ends of the channel. Preliminary evidence (Roelofs, W., *et al.* 1983) indicates that red-banded leafroller females selected for their higher than average or lower than average *trans* isomer content, when mated to normal-ratio-responding males, produced daughters that emitted significantly higher and lower than average amounts of *trans*, respectively. Interestingly, when the rare 10% of males that flew upwind to the source to an off-ratio (20% *trans*), were selected for mating to normal-ratio females, their daughters had significantly higher ratios of *trans* than normal. Furthermore, their sons now responded very readily to the 20% *trans* off-ratio. Nearly 100% of the sons flew upwind to, and touched, the 20% *trans* source. These results are yet another indication that emission and reception of sex pheromone signals are very closely genetically linked.

The fact that such a pheromone component ratio can be shifted in the laboratory brings up the possibility that under pressure in the field, blend ratio shifts can occur. This might be due to an increase in background levels of that blend due to a new species moving into the area, or possibly due to man-made interference. This latter possibility has increased in recent years with the introduction of mating disruptant formulations that emit the exact blend emitted by females of the target species. Recently Haynes, K. *et al.* (1983) examined airborne emissions from females of the pink bollworm moth (*Pectinophora gossypiella*) to see whether such shifts had occurred during the past 4 or 5 years of

mating disruption pressure in southern California. They found no evidence of changes in the average ratio of *Z,Z* to *Z,E* isomers of 7,11-hexadecadienyl acetate used by females or in the rate of pheromone emitted. The latter was expected to have increased if "resistance" to the disruptants had developed. Likewise a ratio shift might have been detected in a resistant population. It was not. Monitoring populations for resistance to pheromones should prove valuable in detecting the onset of resistance in a population put under pressure from high background levels of the very chemicals the individuals use for communication.

2.2 Courtship

Chemicals and other cues used in mate-finding intergrade into those involved in insect courtship. For instance, the total blend of three female-emitted sex pheromone components is necessary to elicit optimal levels of hair-pencil displays in male oriental fruit-moths, but visual cues from the female help increase the displays (Baker, T. and Cardé, R., 1979a). The fact that the sexes now have located each other and are close enough to touch allows new, additional compounds to come into play that might otherwise have been useless at long range due to volatility factors, among others. The gradients of these compounds will be very steep at close range and the relatively small active spaces will have sharp boundaries due to high thresholds in the responders. The steepest possible gradients, approaching all-or-nothing levels, are found in the "contact" pheromones involved in much of courtship. Other odor cues used in courtship are more volatile and act at distances of a few cm or more. At these short distances the signal:noise ratio is high due to high emission rates rather than low thresholds.

Electronantennogram (EAG) results have shown, for instance, that female moths do have antennal receptors that respond to male courtship pheromone, but the maximum amplitude that can be elicited is only *ca.* 1–2 mV (Nishida, R. *et al.*, 1982; Grant, G., 1970, 1971), indicating that there are likely fewer receptors available for courtship pheromone detection on female antennae than on male antennae devoted to sex pheromone reception. Male EAGs can reach 10 mV or more (Roelofs, W., 1977).

The active space of courtship pheromones is usually short, therefore, and the responses are elicited only at a range of a few cm or by actual contact. The usual responses are short-range attraction, arrestment, or arrestment coupled with changes in posture or body orientation. When a male German cockroach's antennae touch the female, the pheromone, 3,11-dimethyl-2-nonacosanone, causes the male to turn 180° and face away while raising its wings (Nishida, R. *et al.*, 1979; Schal, C. *et al.*, 1983). The female is then attracted over a short range by a yet-to-be-identified pheromone to the male's abdominal tergites, where she commences feeding on secretions and he couples with her. If the female is not attracted, the residual effects of contact with the pheromone cause a "local search" by the male for the female, which consists of high angular velocity coupled with low linear velocity of movement that initially keep him arrested in one small location where he had first contacted the female's pheromone (Schal, C. *et al.*, 1983).

A courtship pheromone is emitted by males of the pierid butterfly, *Eurema lisa*, from patches of specialized scales on the hind wings. When the female's antennae touch the scales, or are near them, she remains quiescent and at the same time bends her abdomen downward so that the genital opening projects out beyond the margins of her hind wings, making it available for clasping by the male's abdomen (Rutowski, R., 1977). A similar response, quiescence coupled with "acceptance" posture, is taken by females of *Colias eurytheme* and *Colias philodice* (Grula, J. *et al.*, 1980; Rutowski, R., 1980). The pheromone blends are mixtures of hydrocarbons and long-chain esters whose volatility is lower than most sex pheromones. Here again the active space is quite small, often requiring contact. EAGs reveal low mV response from the female antennae, indicative of a moderate-to-high threshold. The emission rate is apparently controlled by the forewings, which cover these scales under normal circumstances, helping keep the emission low by providing a small volume into which the compounds can evaporate. Equilibrium vapor pressure would be reached with fairly low numbers of molecules having entered the vapor phase. When the wings are extended during courtship, there would be a sharp increase in the numbers of molecules available to adsorb onto the female's antennae.

Other modifications of wings, such as the costal folds of phycitine and tortricid moths, provide a similar way to rapidly increase emissions to high levels (Grant, G. *et al.*, 1975; Grant, G. and Brady, U., 1975; Grant, G., 1978). A large surface area for evaporation is suddenly created when hair-like scales are everted from within the folds during wing vibration. The phycitine courtship pheromones, which variously elicit quiescence, female postural changes, and 180° changes in body orientation (Grant, G. *et al.*, 1975; Grant, G. and Brady, U., 1975; Grant, G., 1976; Krasnov, S., 1981) act over a range of a few cm. This active space is probably aided at the emission end by the wind generated during wing vibration, transporting the molecules directly to the female.

In the oriental fruit-moth a 45–90 cm s^{-1} wind is generated that propels the relatively volatile courtship pheromone toward the female (Fig. 5) (Baker, T. and Cardé, R., 1979a). A blend of two compounds, *trans*-ethyl cinnamate and methyl-2-epijasmonate, accounts for most of the behavioral response, the attraction of females (Baker, T. *et al.*, 1982). Here, the emissions are kept minimal by having the scent scales housed in abdominal pouches and then sud-

denly everting and splaying them to rapidly enlarge their collective surface area and the subsequent emission rate of pheromone. The individual scales comprising the hairpencils, like those of other species, are hollow with a honeycombed, porous construction optimally suited for conducting the secretion from the gland cells and for maximal surface area (Fig. 6) (George, J. and Mullins, J., 1980).

The addition of wind allows the signal to have additional directionality and females may be able to use anemotaxis to orient to the male's abdominal tip. In general, though, anemotactic orientation in response to courtship pheromones appears to be rare, not only because overt orientation responses are rare themselves, but because of the close range involved. At these short distances *direct* rather than indirect chemo-orientation responses (Bell, W. and Tobin, T., 1982) may be more important considering the sharp gradients that exist at that range. Also, other indirect orientation responses to the odor (orientation to cues in other modalities that are triggered by the presence of the odor) may be more immediate, and informative, than wind.

The landing and arrestment of female queen

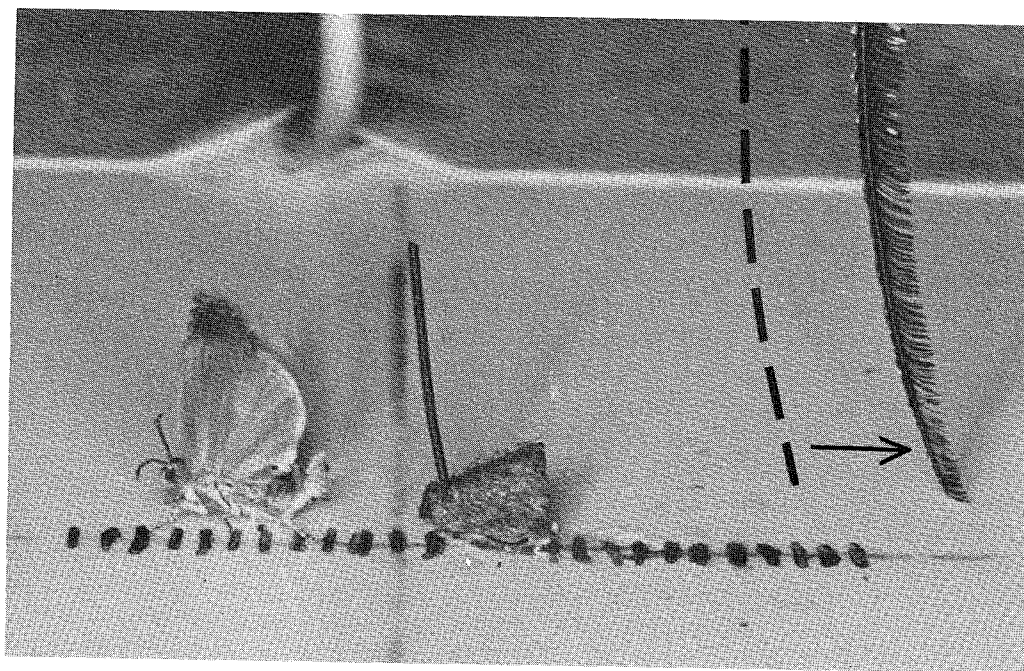


FIG. 5. Wind of 45–90 cm s^{-1} is generated by *Grapholita molesta* males during their hairpencil display. Here a feather-anemometer is deflected from its resting position (dashed line) by a male displaying at a sex pheromone-emitting model female. Distance between each marking near model and male is 1 mm (From Baker, T. and Cardé, R., 1979a)

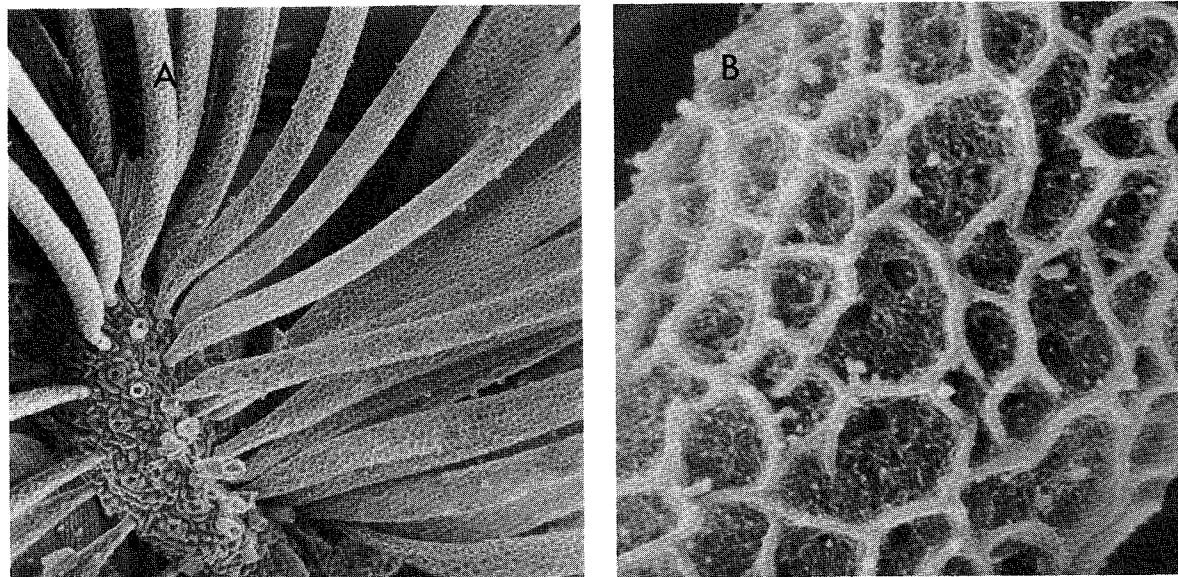


FIG 6 A: Scanning electron micrograph ($\times 800$) of *Grapholita molesta* hairpencils (modified scales or hairs) everted from their pouch. Note that many have been fractured near the base, and their hollow interiors can be seen. B: Greater magnification ($\times 14,400$) of a portion of one of the scales showing honeycombed ridges, which provide great evaporative surface area, and pores which likely facilitate transport of courtship pheromone from within the scale's hollow interior to its surface. (From George, J. and Mullins, J., 1980.)

butterflies, *Danaus gilippus* after contact with the male's courtship pheromone, danaidone (Pliske, T. and Eisner, T., 1969; Meinwald, J. *et al.*, 1969), is an interesting case of indirect responses to odor. The pheromone is disseminated through the air on pieces of cuticular dust coated with a diol sticker by the splaying apart of hairpencils, and the dust adheres to the female's antennae. Hence the chemical message is delivered by means of a type of *contact* chemoreception. The input from such a chemical signal should be unvarying, and so the alighting and arrestment by the female and her "receptive" posture must be the result of indirect visual responses to foliage plus an internal motor program.

The playing out of an internally stored program of movements, rather than orientation continually guided by feedback from the chemical itself or from indirect cues, is illustrated well by the movements and 180° turns performed during courtship by male German cockroaches (Schal, C. *et al.*, 1983). The postural changes adopted by responding female pierids (Gruha, J. *et al.*, 1980; Rutowski, R., 1977) must also be the result of an internal motor program not guided by external feedback. A steep gradient can have a direct effect on orientation though, as

when male German cockroaches preferentially turn through the shortest route to face 180° away from the position of the antenna that had been briefly touched by female pheromone.

It is too early to tell how species-specific courtship pheromones are, although it appears that thus far they are not as specific as sex pheromones. For instance, danaidone has been found in the male scent brushes of a variety of danuids in the genera *Danaus*, *Amauris* and *Lycorea* (Boppré, M., 1978; Meinwald, J. and Meinwald, Y., 1966; Meinwald, J. *et al.*, 1969, 1971, 1974; Edgar, J. *et al.*, 1971, 1973; Schneider, D. *et al.*, 1975). In addition, hydroxydanaidal has been identified from the coremata of three species of arctiid moths, *Utethesia ornatix* (Conner, W. *et al.*, 1981) and two species of *Cretonotos* (Schneider, D. *et al.*, 1982). In *Utethesia* hydroxydanaidal is employed at close range. After males orient to and locate the female by means of her sex pheromone, they inflate their large scent-disseminating coremata near her antennae, whereupon she remains quiescent and permits copulation. In *Cretonotos* there are no reports as yet as to how the pheromone functions, but from the information given (Schneider, D. *et al.*, 1982), it would not be surprising that male

lek formation and attraction of females occurs in a manner similar to that reported by Willis, M. and Birch, M. for *Estigmene acrea* (1982). Individual *Creatonotos* males are reported to hang on plants or wires and inflate their coremata similar to *E. acrea* males starting an aggregation.

Benzyl alcohol and benzaldehyde have been identified in large quantities from the male scent brushes of a large number of noctuid moths (Birch, M., 1974). Yet far from being the common, non-specific courtship pheromones of a variety of species, they may in fact be pheromone *components* of more complex, species-specific blends. Without knowing the other components of tortricine moth female sex pheromones and working only from compounds identified from gland extracts, one might erroneously conclude that *cis*-11-14:Ac is a very general non-specific tortricine sex pheromone — *until* one places it in traps in the field and finds that, by itself, it captures very few males. *cis*-11-14:Ac is found in nearly every tortricine female sex pheromone gland, and is *part* of the sex pheromone *blend* in nearly all these species, often as the major component (Roelofs, W. and Brown, R., 1982), but it is not the sex pheromone. Thus at this point we should be cautious in concluding anything about the specificity of the purported noctuid courtship pheromone components benzyl alcohol and benzaldehyde. The fact that they are present in very large quantities in the gland does not necessarily mean they are pheromone components, either. Mellein is found in extracts of oriental fruit-moth hairpencils in great quantities, yet its behavioral effects are minimal compared to the combination of *trans*-ethyl cinnamate and methyl-2-epijasmone (Baker, T. *et al.*, 1982).

It would not be surprising, though, if courtship pheromones turned out to be less species-specific than sex pheromones. For one thing, the most important species-discriminating step may have already occurred at long range through visual (Silberglied, R. and Taylor, O., 1978), auditory, or olfactory cues. When mistakes are made through the long-range cues, *then* courtship cues may be important in species discrimination (Grula, J. *et al.*, 1980). Female moths, for instance, might discriminate for an odor that is emitted by males of their species from the intersegmental membranes of the abdominal tip when the claspers are everted

during a copulatory attempt. This would help reduce mating mistakes between the males of the female's species and those of a second species she sometimes attracts (Baker, T. and Cardé, R., 1979a). Sexual selection could then exaggerate both the male's clasper extension and her "choosiness" (see below). A female of yet a third species might attract males of her own species plus occasionally those of a fourth species due to the lack of complete sex pheromone specificity. If the male-produced clasper odor was identical to that of the first species, females of the third species would still be able to discriminate for this odor, because they never would encounter species No. 1 males. Sexual selection could amplify and increase the concentration of this odor in species No. 3 just as in species No. 1 once the process was triggered. Courtship signals do not travel very far; the channel's signal : noise ratio is high, due mainly to the high concentration at close range, and noise is not a problem. Therefore the same signal can be used effectively by many different species without a need for further specific tuning of blends.

The use of courtship pheromones at high close-range concentrations also permits compounds found in flowers and plants to be used that normally might have been drowned out by background noise if used at greater distances. Male euglossine bees, for instance, appear to gather floral odors from flowers and apparently use them in their courtship displays. The methyl-2-epijasmone used by oriental fruit-moths in their displays is found in lemon peels and probably in other fruits, and the methyl *cis*-jasmonate is a constituent of jasmine oil and known as "queen of aroma" when blended into many man-made perfumes. The closely related *cis*-jasmone is found in male *Amauris ochlea* hairpencils (Petty, R. *et al.*, 1977) and 2-phenyl-ethanol, or oil of rose, has been isolated from the hairpencils of many noctuid moths. The behavioral activity of these latter compounds has not been verified. Danaidone, danaidal, and hydroxy-danaidal are found in large quantities in a wide variety of butterflies' and moths' hairpencil secretions, and an alkaloid precursor is ingested from plants by larvae or adults. Adult males are attracted to dead or withered plants such as *Heliotropium* or *Senecio* and first dissolve the alkaloid crystals with their saliva, then re-imbibe the solution (Pliske, T., 1975a; Boppré, M., 1981; Edgar, J., 1975). The danaidone

or danaidal can apparently be cleaved in one step from the other portion of the molecule, and it is apparently the volatile esterifying acids of the alkaloids on the plants that attract males to the exudate. For the moths *Utethesia ornatix* and *Cretonotus*, hydroxydanaidal in its alkaloid precursor form is apparently ingested by larvae from their host plant and sequestered until adulthood when hydroxydanaidal is cleaved and used during courtship. Male *Cretonotus* larvae, if deprived of the hydroxydanaidal precursor during development, metamorphose into adults with small, stunted coremata (Schneider, D. *et al.*, 1982). The consequences of possessing withered coremata is not clear, but it is possible that such males would be at a mating disadvantage. Preliminary data show that when male larvae of the oriental fruit-moth are reared on lima bean diet rather than their normal diet of fruit, their hairpencils lack the *trans*-ethyl cinnamate and jasmonates that are important in attracting females during the hairpencil display (Baker, T. *et al.*, 1982; Nishida, R. *et al.*, 1982).

Finally, the most extensively researched case is that of the queen butterfly *Danaus gilippus*. When larvae were reared in enclosures containing their own larval food plant, *Asclepias*, but the adult males lacked access to other plants, the males were considerably less successful at mating than wild males. Pliske, T. and Eisner, T. (1969) were able to demonstrate that the males lacked danaidone, and that when their hairpencils were artificially coated with a mixture of the cuticular dust, the diol sticker, and danaidone, mating competence was restored in these males. Combinations of dust and diol lacking danaidone did not restore mating ability. Presumably these males were able to induce arrestment and the acceptance posture in females, behaviors which had been well-described in wild males and females (Brower, L., *et al.*, 1965; Pliske, T. and Eisner, T., 1969). The males lacked danaidone because their cages kept them from visiting the pyrolizadine alkaloid-exuding plants in the area.

It remains to be seen how many other courtship pheromones have floral, herbal, or plant-like bases to them; but it seems clear at this point that these pheromones are more closely related to plant products and odors than are sex pheromones, and it is likely that at least part of the reason is that plant-odor background noise does not interfere

during courtship because large amounts of odor are used at very close range.

How did courtship pheromones and displays evolve? As discussed in section 1, an important force likely was sexual selection by the sex that has a substantial investment in a courtship resource. The resource might be a nutritional "gift" to aid in development of the embryo, or it might be the odorous display itself, which confers a mating advantage to individuals that possess it in subsequent generations. Certainly there are enough cases which demonstrate males with impaired hairpencils or courtship pheromone production are at a mating disadvantage (Birch, M., 1970; Pliske, T. and Eisner, T., 1969; Conner, W. *et al.*, 1981; Baker, T. and Cardé, R., 1979a; Grant, G. and Brady, U., 1975). Another possible evolutionary mechanism has been proposed (Conner, W. *et al.*, 1981) that invokes the defensive value imparted by compounds such as the alkaloids ingested by *Utethesia ornatix* males, or the benzaldehyde possessed by males of several moth species. Females presumably would assess the amount of these defensive compounds or their metabolites to ensure that their offspring would also have the ability to acquire large quantities of these materials and be well protected. This scenario is one step more complex than it needs to be, however. Females may discriminate for *any* odor that males already possess, although it would not be disadvantageous that the display compound is linked to chemicals that *also* provide defense and "fitness" in offspring having the propensity for acquiring them.

The fact that some male ithomiines apparently use their hairpencil products including a lactone (Edgar, J. *et al.*, 1976) to "repel" other males and defend territories does not mean that the chemicals have inherent repellent qualities, i.e. qualities that are obnoxious and cause displacement away from the source against the "will" of the receiver. As pointed out by J. Alcock for bark beetles that are "inhibited" by so-called "masking" compounds, it must also benefit the receivers to move away after sensing such a signal. This was proposed for ithomiine males by Pliske, T. (1975b): a fruitless courtship of another male can be broken off in the pursuit flight stage when the pursued male's pheromone is detected. Likewise the report that benzaldehyde emitted from armyworm male hairpencils is "repellent" to other males does not mean that this

compound is a good defensive compound. The other males must benefit by staying away, possibly because the presence of the compound along with sex pheromone means that going to the source and attempting to mate is futile. By the time the male arrives there, the benzaldehyde-emitter will have already succeeded in copulating. More work needs to be done on the role of compounds such as benzaldehyde and benzyl alcohol during courtship. It is unclear what effect they have on females, although there is some indication that they can reduce locomotion (Clearwater, J., 1972). The male-male "inhibitory" function (Hirai, K. *et al.*, 1978) in groups of males housed in long tubes could have been due to other factors, such as adsorption of female pheromone on the males located upwind so that the downwind males, far from being inhibited by male-produced odors, simply did

not receive enough female pheromone to stimulate them adequately. Adsorption of pheromone onto moths' bodies has been documented (Baker, T. *et al.*, 1980) and can be significant.

In another species, courtship pheromone causes other males to be attracted to the source of the emissions. In the oriental fruit-moth the hairpencil pheromone plays an important part in the "alternative" mating strategies undertaken by males that arrive late after a first male has already begun his courtship display. Late arrivals are attracted to, and touch the end of, the displaying male's abdomen, similar to the attraction of females (Fig. 7) (Baker, T., 1983). Like females, the touch delivered by males causes a misdirected copulatory attempt at the displayer (Baker, T. and Cardé, R., 1979a; Baker, T., 1983), which disrupts the first male's courtship and

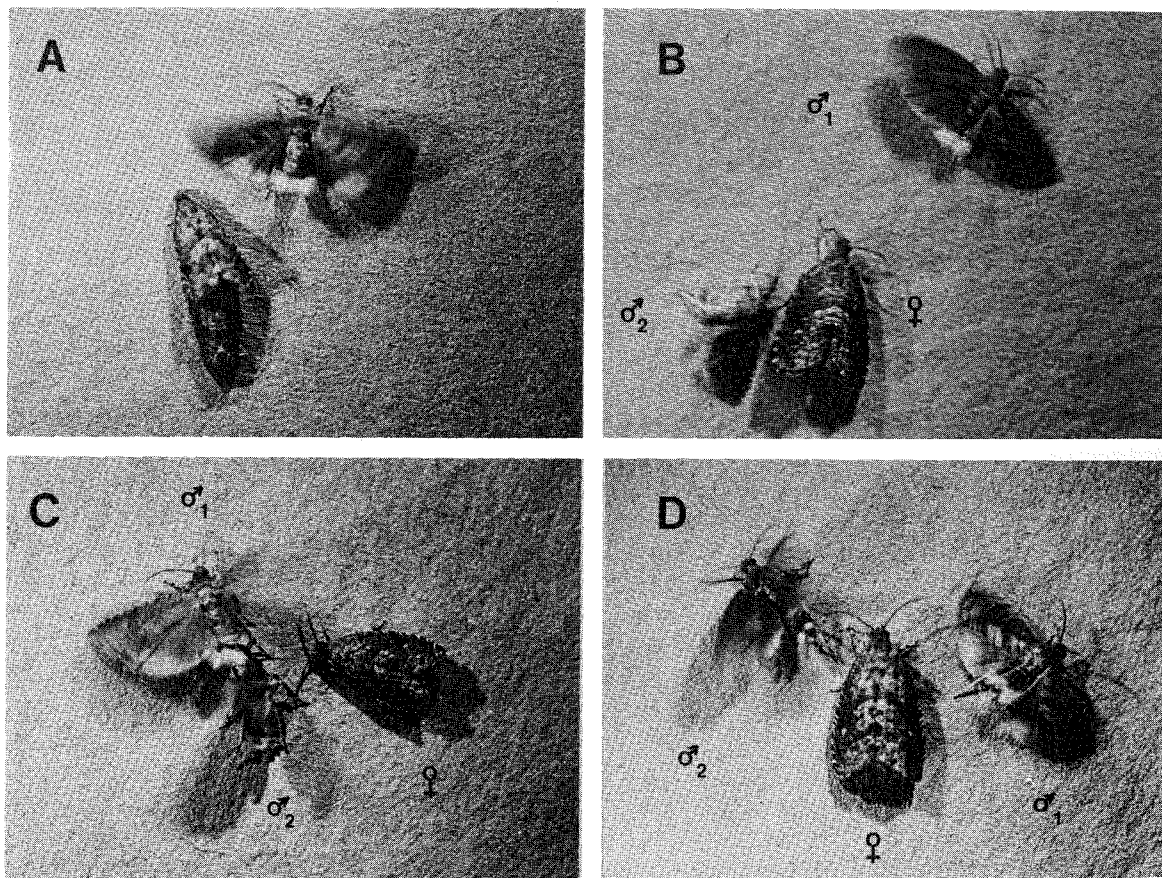


FIG. 7. Alternative courtship "strategies" performed by competing *Grapholita molesta* males. **A:** Late-arriving male displaying his hairpencils at a pair in copula; **B:** late-arriving male (σ_2), without displaying, attempting copulation with a female who was being attracted toward the first-arriving male's display (σ_1); **C:** late-arriving male (σ_2) about to touch the abdomen of a displaying first-arrival (σ_1), eliciting a misdirected copulatory attempt by σ_1 toward σ_2 ; **D:** two males displaying simultaneously toward a female, who eventually touches the abdomen of σ_1 (From Baker, T., 1983.)

buys precious time for the late male who then often succeeds in mating with the female. Another tactic practiced by late arrivals is to "sneak" a copulatory attempt with a female who is in the process of being attracted to the first male's display (Fig. 7). The late arrival does not display first, but immediately approaches and bends his abdomen toward the female's. Attempting copulation without displaying is extremely unusual in courtships involving a single male and female, and a male never mates successfully unless he first displays. But in this particular competitive situation, the presence of courtship pheromone from the displaying first-arrival apparently not only triggers the unusual immediate copulatory attempt without display, but also makes the female receptive to such an attempt. The second male therefore sneaks in under the barrage of courtship pheromone provided by the already-displaying male, and this tactic is successful nearly 50% of the time. Other tactics include displaying simultaneously alongside the first arrival (Fig. 7), during which time a female may "choose" the second male over the first. Finally if males arrive *after* copulation by the first male, they often nevertheless display at the coupled female (Fig. 7) and a small percentage of the time the female breaks away from the male and mates with the second male.

Attraction of males to other males' displays occurs in other groups. For instance, male bittacid scorpion flies are sometimes attracted to pheromone-releasing males that have captured a prey item which is to be presented to a female. The attracted male, however, behaves like a female, adopting the typical "wings-down" female posture which induces the first male to present the prey to him (her) (Thornhill, R., 1979b). This pseudo-female "strategy", as for oriental fruit-moths, following attraction to the male emitter, increases mating success under these competitive circumstances. Attraction of males to other males' emission occurs during the formation of leks as in *Estigmene acrea* (Fig. 3). Lek formation is known in tephritid flies (Prokopy, R., 1980) and in some *Drosophila* (Spieth, H., 1968). Much work needs to be done to understand male-male attraction and lek formation in the Diptera, but already it appears that there are many interesting olfactory-mediated courtship and male mating strategies in this group.

The alternative courtship strategies in oriental

fruit-moth males do not appear to be genetically fixed in each individual. The male may behave as a pseudo-female one moment and then try to sneak a copulation during another. This is in contrast to the apparently hard-wired alternative courtship behaviors of some male crickets in auditory mate-finding systems. "Silent" males, which have a genetic predisposition to sing less often, wait near singing males (also genetically so predisposed) and may intercept and mate with the females attracted to the singing males (Cade, W., 1981). The "sneaking" of copulations here, unlike in oriental fruit-moths, is therefore apparently more likely in some individuals than others.

For olfactory-mediated courtship in insects, the whole area of alternative behaviors and strategies needs further intensive study. This body of knowledge will add to the already large one that exists for vertebrate mating systems (Gould, J., 1982; Alcock, J., 1979).

2.3 Host-finding (feeding, oviposition)

Host plants or host insects often emit chemicals which are used by phytophagous insects or insect predators and parasites to locate the hosts. One may or may not choose to label this as communication, but nevertheless information flows from the sender to a receiver through an environmental channel containing chemical noise. Once the receiving insect locates the host, other gustational and contact chemoreception cues come into play to determine whether the host that was located is accepted for feeding or oviposition. I will not deal with host acceptance and feeding cues in this chapter, but rather will focus on olfactory cues that allow host-finding to occur.

The "sender" is usually under selective pressure to minimize the signal:noise ratio so that information flow does not occur. This may be especially true, for instance, for plants that are ephemeral in space and time and that have a relatively narrow range of toxic chemical defenses. Feeny, P. (1976), in his plant apparency hypothesis, compared such unapparent plants to more permanent, perennial plants such as trees located in dense homogeneous stands. The latter are more apparent and predictable in time and space and have more general chemical defenses such as terpenes, phenols, and tannins

for the wider range of attackers that are likely to find them. He predicted that for apparent plants specific chemical and other cues used for host location should be less important because the host is ubiquitous. For unapparent plants with a few specific toxic defensive compounds, insects that have evolved detoxifying mechanisms may now use these specific chemical cues to zero in on and locate the host plant from a distance. Certainly this hypothesis needs testing and revising, which will take much time, but in the meantime it is noteworthy that some of the most specific, behaviorally active chemical host stimuli from plants have been found in the Brassicaceae, and Solanaceae, families that include many agricultural plants that under natural conditions would be classified as "unapparent" (Feeny, P., 1976). These plants formerly would have existed intermixed with a wide variety of plants from other families in fairly recently disturbed, non-climax ecosystems. Finding a brassicaceous host plant in natural conditions might require a lot of searching, and olfactory cues could be quite important from a long distance.

For instance, females of the onion fly, *Hylemia antiqua*, use olfactory cues to locate susceptible onions for oviposition. A single volatile from onions, *n*-propyl disulfide, has been shown to attract flies in great numbers (Dindonis, L. and Miller, J., 1980a), but a blend of *n*-propyl disulfide plus other volatiles, or a rotting onion alone, attracts even more flies (Dindonis, L. and Miller, J., 1981). Fresh onions, interestingly, attract no more flies than *n*-propyl disulfide alone, and it appears that micro-organisms are responsible for producing some of the extra volatiles that make rotting onions more attractive (Dindonis, L. and Miller, J., 1981). Without the interaction with onion-derived chemicals the micro-organisms were unable to produce attractive volatiles. Displacement toward the source of volatiles occurs as a result of movements that are likely at least partly anemotactically-mediated, as demonstrated by Dindonis, L. and Miller, J. (1980b), who used wind-vane traps that swing freely to always keep the same side downwind. The distribution of flies captured on the cylindrical screen surface (Fig 8) indicated that the flies' approach clearly was from downwind and at ground level. Observations of flies approaching sources in a wind tunnel hinted that they remained motionless

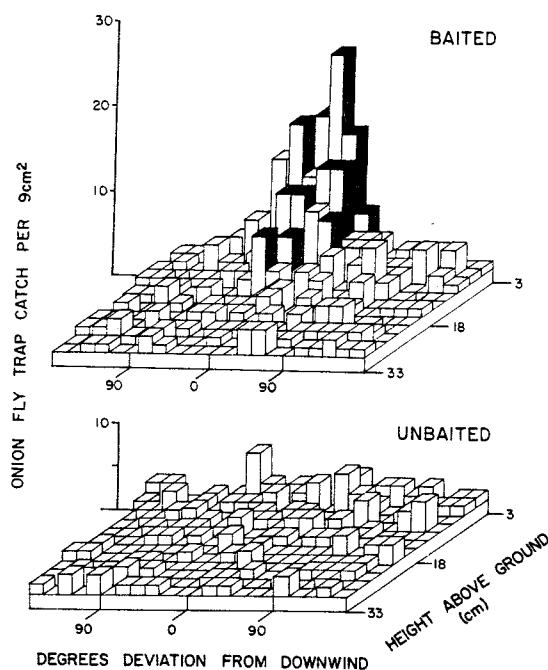


FIG. 8. Mean distribution of captured onion flies, *Hylemia antiqua*, on the surface of special rotating sticky traps that always keep one surface facing downwind. The flies responding to onion volatiles (top graph) approached the traps from downwind and near the ground, in contrast to those blundering onto the sticky surfaces of unbaited traps (bottom graph). (From Dindonis, L. and Miller, J., 1980b.)

for long periods of time, then suddenly flew in short hops along the ground to the buried onion source.

As exemplified by the onion fly, it is clear that in general olfactory-mediated location of plant hosts is accomplished by responses to blends of compounds, not a single compound alone. Another example is host plant location by the Colorado potato beetle (Visser, J. and Avé, D., 1978). Curiously the volatiles emitted by potato leaves that induce positive anemotaxis by adult beetles are apparently not related to the numerous alkaloids contained in the solanaceous host. Rather the blend is composed of what Visser, J. and Avé, D. (1978) call general "green leaf" volatiles emitted by numerous varieties of plants. The blend emitted by potato leaves is composed mainly of *trans*-2-hexen-1-ol, hexan-1-ol, *cis*-3-hexen-1-ol, *trans*-2-hexenal, and linalool (Visser, J. *et al.*, 1979). In contrast to this solanaceous plant, the predominant volatiles of several brassicaceous plants are *cis*-3-hexenyl acetate, *cis*-3-hexen-1-ol and hexyl acetate, with

trans-2-hexenal being absent. In the Colorado potato beetle, if the blend of potato volatiles is altered by the singular addition of synthetic *trans*-2-hexen-1-ol, *trans*-2-hexenal, *trans*-3-hexen-1-ol, or *cis*-2-hexen-1-ol, there is no longer any positive anemotaxis to the source by beetles (Visser, J. and Avé, D., 1978). Thus the blend quality is important to orientation, and different blends of green odor from different plant species or families may elicit species-specific host-finding behavior. There were many plants in the Solanaceae that attracted Colorado potato beetles but those in the Brassicaceae and other families were either neutral or repellent (Visser, J. and Nielsen, J., 1977). It will be interesting to see how many polyphagous versus oligophagous insects use similar "green odor" blends in locating host plants. It is not clear how specific these cues would be, or how great the active space would be, especially considering the background levels of green odor generated by the nearly-identical volatiles from green leaves everywhere.

Parasitoids or predators searching for prey also utilize olfactory cues to locate hosts. Some researchers would consider insects that attack specific parts of plants such as fruits and seeds, to be parasitic (Price, P., 1975). This seems logical, and often the insects use the fruit or seeds' specific odors to locate them. For instance the apple maggot fly, *Rhagoletis pomonella*, flies upwind in a wind tunnel to a combination of airborne-extracted volatiles recently identified from whole apples (Fein, B. *et al.*, 1982). A blend of hexyl acetate, *trans*-2-hexen-1-yl acetate, butyl hexanoate, propyl hexanoate, hexyl propanoate, butyl hexanoate, hexyl butanoate, and butyl-2-methylbutanoate attracted as many flies in the wind tunnel as the natural extract. This mixture also attracts many more flies to traps than do blank controls. None of the synthetic compounds alone evoked optimal attraction. Interestingly both males and females were equally attracted, the females presumably so that they may oviposit in the apples. As part of a mixed mating strategy, males wait on apples for females to arrive, so that they may inseminate them, and a marking pheromone deposited by females helps arrest males on the apple (Prokopy, R. and Bush, G., 1972). In this regard the above mixture of volatiles may help males locate the fruit. The mixture is likely different from the volatiles emitted from leaves, and therefore

would provide a high signal:noise ratio for the flies.

Chemically-mediated attraction to other plant parts also occurs. For instance, flowers produce distinctive odors, at least to the human nose. But to insects these also play a major role in locating these sources of carbohydrates and protein. Perhaps nowhere is the coevolution of plants and insects more clearly delineated than in flower-insect relationships. The fields of pollination ecology and behavior have been investigated more thoroughly for vision than for other modalities. Visual cues have evolved to provide loud, clear signals from these plant parts that preferentially reflect only the electromagnetic wavelengths that stand out against the background's ambient wavelengths (Price, P., 1975). An assortment of patterns helps guide insects to the nectar source and effect pollination.

Odors do play a role in location of flowers, even for bees, which are highly visual. Von Frisch, K. (1967) demonstrated that bees associate a particular odor with the nectar reward, and that the floral odor is carried back to the hive on the worker's body where recruits learn it during the recruiter's dance. The odor aids in location and recognition of the particular type of flower that has abundant nectar and pollen at that time. Under agricultural conditions with large monocultures, or when there is an abundant source of nectar from one type of flower close to the hive, the floral odor alone may be enough for bees to fly upwind and locate the field of flowers (Wenner, A. *et al.*, 1969; Gould, J., 1975). Certainly more work needs to be performed to isolate and identify the components of each species' floral odor that evokes behavioral responses in the particular insect species that parasitizes its flowers. Dodson, C. *et al.* (1969) identified 60 different compounds in the fragrances of several orchid species, each species having its own characteristic blend. Male euglossine bees are known to be attracted to these species, and apparently gather the fragrances for later use in lekking behavior. While collecting the components, the most common of which is cineole, the bees pollinate the orchids, which have a variety of elaborate mechanisms for depositing and removing the specialized pollen packets, or pollinia (Dressler, R., 1968).

The coevolution of odor and insect can be quite tight. For instance, each species of orchid in the

genus *Ophrys* produces an odor that apparently mimics a species-specific sex pheromone of one of a variety of hymenopterous species. Male wasps and bees orient upwind to the flower and, after landing, attempt to copulate with it (Kullenberg, B. and Bergström, G., 1973, 1976). Visual signals that seem to mimic the female body of each species also aid in inducing males to attempt copulation, and again the flowers use a variety of mechanisms to stick pollinia to the courting males' bodies or remove them. Such a narrow species-specific chemical signal represents the ultimate in insect-flower coevolution. As in other flowers, the narrowing of the chemical signal would minimize usurpation of the floral resources by other species of insects who might be attracted and take the nectar or pollen but fail to consistently visit other flowers of the same species or otherwise pollinate the flowers properly. The cost of such narrow tuning, of course, is the reliance on only one insect species for pollination, and lack of offspring if that species should leave the area. But, as for flowers of other species with less restricted insect pollinator-visitors, a unique blend of floral chemical components allows the insect pollinator species to exploit the resources of that species when they are available.

Another very narrowly tuned host-finding system also apparently involves a sex pheromone; but in this instance predation, not nectar or pollen-feeding, is the motive. The bolas spider, *Mastophora dizzideani*, from Columbia apparently emits a blend of chemicals that mimics the sex pheromone of at least one species of armyworm moth. Fall armyworm moths, *Spodoptera frugiperda* (only males), were seen orienting toward the spider from downwind, and when they got close the spider ensnared them by swinging a sticky ball toward them on the end of a silk thread (Eberhard, W., 1977). This technique resulted in a success rate of about 10%; 8 out of 82 males Eberhard observed orienting within 1 m downwind of the spider were captured. Small numbers of other noctuid species (*Leucania* sp.) were also attracted, and it is not clear whether they use the same blend as *Spodoptera frugiperda* or whether other species with a similar blend, abundant at a different time of the year to *S. frugiperda*, can also be attracted by the spider. Possibly the spider can alter its emission to attract other species utilizing a different blend when other species are

more abundant. Certainly more work needs to be done, but it is clear that the spider is able to utilize a clear chemical signal that already has a high signal : noise ratio and large active space to locate its hosts, except it makes its hosts do the traveling!

As covered by Vinson (chapter 9, this volume), chemical signals play an important role in host-finding by other predators and parasites but they are not nearly as spectacular as the bolas spider. Nevertheless, it is clear that other insect species do sometimes take advantage of their insect hosts' communication channels. The clerid beetle predator, *Enoclerus lecontei*, is attracted to the pheromone emitted by *Ips confusus* bark beetles as they excavate galleries on their host trees. The synthetic pheromone compounds alone attract significant numbers of these predators (Wood, D. et al., 1968). Similarly, the synthetic pheromone blend of *Dendroctonus brevicomis* attracts the trogositid predator, *Temnochila chlorodia* (Bedard, W. et al., 1980). The synthetic blend of *Ips typographus* attracts the clerid species *Thanasimus formicarius* and *Thanasimus femoralis*. Interestingly *T. formicarius* responds more to ipsenol and ipsdienol, one or both of which are emitted by all *Ips* species in Europe, which explains why this species attacks all *Ips* beetles there. *T. femoralis* responds optimally to *cis*-verbenol, emitted by only a few *Ips* species, including *I. typographus* (Bakke, A. and Kvamme, T., 1981). Devoting enough receptors and neuronal circuitry to detect the pheromone from a decent distance would involve considerable trade-offs, such as becoming less sensitive to other chemical cues in the environment. Therefore the coevolution of host and predator again is canalized down an olfactory-mediated evolutionary road that becomes increasingly narrow, and for which there is apparently little opportunity to turn back.

The mechanisms by which insects orient to their hosts through olfaction are just beginning to be understood, but in many cases they appear to be similar to those used by insects orienting to sex pheromones. The end-results of the movement reactions to host odor are displacement toward the host (attraction) followed by arrestment at or near the host. In many cases attraction is aided by anemotaxis. Arrestment very often involves an inverse orthokinesis; that is, the parasite moves more slowly when the concentration of the host's odor is

high (Waage, J., 1978). A chemotactic (steered) response such as longitudinal klinotaxis may help the parasite turn back into an area where host odor is present if it begins to move away from the host. An example of these mechanisms acting to localize a parasite at its host is provided by *Nemeritis canescens*. When the mandibular gland secretion of its host, *Plodia interpunctella* larvae, is present, linear velocity of movement is very low as is angular velocity (Waage, J., 1978). When the odor is lost, linear velocity increases dramatically, as does angular velocity and the parasite "scans" a much larger area very quickly. When the odor is lost at the boundaries of the "patch" of odor, an apparently self-steered, 160° turn is made which tends to bring it back into the odor "patch" (Waage, J., 1978). Thus arrestment over the host is a result of several mechanisms acting together.

Finally, some compounds result in displacement away from a potential host. These oviposition "deterrents" or repellents are sometimes deposited by a female after oviposition and result in other females not ovipositing in that host. After inserting an egg in a host hawthorn fruit females of the apple maggot fly, *Rhagoletis pomonella*, smear yet-to-be-identified compounds on the surface of fruit, and the effect thus far appears to be that it causes secondary arrivals to maintain a higher rate of locomotion plus induces flight to other trees in the area (Roitberg, B. *et al.*, 1982). Arrestment is prevented and the end-result is movement away from the marked fruit and that patch (tree) harboring the fruit. The pheromone is not inherently obnoxious or irritating because females need to "learn", often through just a single ovipositioned reinforcement, to leave fruits that are thus marked (Roitberg, B. and Prokopy, R., 1981). Again, similar to the "masking" of bark beetle pheromones by first-arriving males and the inhibition of late-arriving *Spodoptera* males' approaches by a first-arrival's scent, the "deterrency" of the pheromone occurs at the individual, not population, level. It seems best to view the lack of multiple ovipositions of a single fruit not as an attempt by the flies to evenly exploit the available resources, but as a response by an individual late-arriving female to a threat to her egg. Her offspring may be at a disadvantage in an already-infested fruit, and early detection and reaction to such a fruit is to the late-arrivals' advantage. The

"deterrency" is self-imposed, and advantageous to the individual, not necessarily to the population.

2.4 Host-finding (recruitment)

Individual insects can help others locate food sources by leaving chemical deposits or by stationing themselves at the source and emitting an odor (described in detail by Haynes and Birch, chapter 5). The major feature of this type of communication system is that in all cases the recruited insects are closely related to the recruiter — the one emitting the signal. In this respect alone, recruitment pheromones differ from all the others discussed thus far. Bark beetles' pheromones do result in recruitment to a potential host tree, but that may be only a side-effect of the pheromone's primary purpose, to bring individual males and females together for mating. Recruitment pheromones' sole purpose, on the other hand, is to alert relatives as to location of food or nest resources. There are no other known secondary functions.

The apparently altruistic motive to this type of communication is nicely explained by theories of kinship (Dawkins, R., 1976; Hamilton, W., 1964) which predicts that helping one's brothers and sisters, sons and daughters, or other close relatives should pay off evolutionarily because a good proportion of one's own genes reside in their bodies. The special type of haplo-diploid kinship that exists in many social hymenopterans does not need to be invoked for this type of cooperation (Evans, H., 1977) in finding food sources. Certainly the extra-strong sister-sister relationships that exist in these hymenopterans might make sister-sister recruitment more likely than between brothers and sisters (Wilson, E., 1974). However the trail-recruitment of nest-mates (tent-mates) by larval Lepidoptera of *Archips cerasivoranus*, *Malacosoma disstria* and *Malacosoma americanum* (Fitzgerald, T. and Edgerly, J., 1979; Fitzgerald, T. and Gallagher, E., 1976), or the trail-recruitment of workers and soldiers in the many species of termites (Wilson, E., 1974) are every bit as efficient as in the Hymenoptera. Male and female Lepidoptera and Isoptera have no special kinship, only the "usual" diplo-diploid kind.

As discussed by Haynes and Birch (chapter 5) and Blum (chapter 4) there are many types of chemical recruitment systems. They may be divided into the

following:

- (1) trail-recruitment, in which the chemicals are applied in such a way that the recruit is never more than a few mm from the deposited "trail". This would always provide the sharpest possible gradient, because the recruit would never be far from the chemical source and allow the most accurate (tropotactic) chemo-orientation to be used to maintain lateral contact with the trail.
- (2) Trail-recruitment where the pheromone is deposited with large gaps between, that might force sequential (klinotactic) chemo-orientation to be used by the recruiter, or even anemotaxis. The trail-recruitment system of some species of *Trigona* stingless bees is an example of this type of system (Lindauer, M., 1961; Haynes and Birch, chapter 5) although it is not clear whether the bees orient to the point source deposits through anemotaxis or chemotaxis or both.
- (3) "Calling" recruitment by a recruiter who stations itself at the food source and releases a scent.
- (4) Tandem running, in which a recruiter leads a single recruit out to the food source by means of a pheromone on its body.

Trail-recruitment systems are found in a variety of ant species. In some species the trail pheromone alone is sufficient to both alert and activate worker ants as well as guide them toward the food. This "mass recruitment" system, considered to be the most advanced form of recruitment (Wilson, E., 1974), is used by several *Solenopsis* species (Wilson, E., 1962a,b; Hangartner, W., 1969) and by two *Novomessor* species (Hölldobler, B. *et al.*, 1978). Many other species, however, use trails for orientation but rely on behavioural displays such as food offerings, mouth opening, antennation, running, or release of attractive secretions to alert and activate recruits to the presence of the chemical trail. Then, as in mass recruitment, they follow the trail to the food source independent of the recruiter (Szlep, R. and Jacobi, T., 1967; Möglich, M. and Hölldobler, B., 1975; Hölldobler, B. and Wilson, E., 1978; Cammaerts, M.-C., 1980; Robertson, P. *et al.*, 1980). Each recruiter generally activates about 5-20 workers.

A form of chemical recruitment considered to be more primitive than trail-recruitment is tandem running (Wilson, E., 1974). Here a single

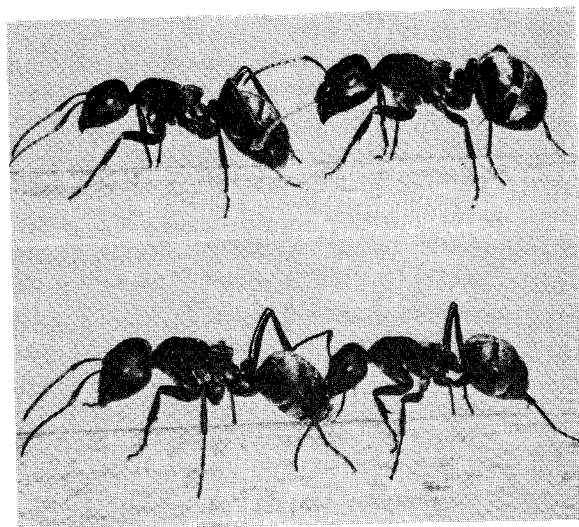


FIG. 9. Recruitment by tandem running in *Camponotus sericeus*. The leader ant orients according to a trail pheromone it has previously discharged from the hindgut, and the follower is stimulated to maintain contact with the leader by a surface pheromone on the leader's gaster. Tactile stimuli help keep the follower aligned. (From Hölldobler, B. *et al.*, 1974)

recruited ant maintains tactile contact with the recruiter which leads the recruit to the food source (Fig. 9). Cuticular surface pheromones (Hölldobler, B. *et al.*, 1974; Möglich, M. and Maschwitz, U., 1974) and pygidial gland pheromones (Hölldobler, B. and Traniello, J., 1980) have been shown to be important in evoking continued following of the leader ant. Odor trails, when present, provide only orientation cues for the leader, as in *Camponotus sericeus* (Hölldobler, B. *et al.*, 1974) and *Leptothorax* sp. (Möglich, M. and Maschwitz, U., 1974). Mixed forms of recruitment appear to be utilized by some ant species such as *Leptothorax unifasciatus*, in which tandem running is used in the early stages of recruitment to a food find, and trail-following predominates in the later stages after trails have become established (Lane, A., 1977). In another species, *Camponotus paria*, contact between the leader and follower is not necessary, but the leader deposits a short-lived trail that is followed by the single recruit (Wilson, E., 1974).

How "accurate" are chemical trail-recruitment systems, compared to, say, dance-language sun-compass systems used by bees? As mentioned earlier, trail deposition might be viewed as a kind of a "cheat-sheet" for ants, who do not apparently have the memory capacity of honeybees. This information storage, a chemical memory trace external to the CNS, may actually convey more information at great distances from the source than the honeybee dance-recruitment system. Wilson, E. (1974) used information-theory analysis on the two types of recruitment and found that angular errors, or accuracy of orientation, decrease in magnitude farther from the nest in a typical trail-recruitment system. The recruit's side-to-side errors stay the same all along the trail with respect to the trail itself because the ant is never far from the pheromone "source" and the sharp gradient it provides.

Trail pheromone specificity was discussed in detail by Haynes and Birch (this volume). I will end this discussion in chemical recruitment by saying that, in general, these systems are usually at least species-specific. It would not be surprising if future research will show some degree of colony-specificity to some of these systems as well, inasmuch as they likely arose to benefit relatives, not the species.

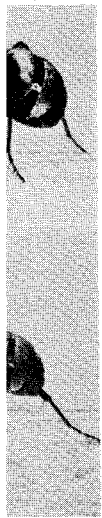
2.5 Self-defense

There are at least three major ways for an insect to defend itself against attack by parasite or predator by means of chemicals. One is to blend into the chemical background noise so that information does not flow to the attacker and "communication" does not occur. The result is that an attack is not evoked. The second way is to emit a chemical that changes the attacker's behavior *rapidly*. For instance, an irritating chemical may change a predator's behavior from locomotion to grooming. Since grooming is incompatible with locomotion, arrestment is the end-result and the would-be insect prey can then lower its signal: noise ratio by moving rapidly away to effectively reduce its amplitude. A third way, which will not be discussed here, is used when an attack has occurred and the predator has the animal in its grasp. A toxic compound can be produced that causes the predator to become ill, or to associate the odor with a previous bad experience and drop the prey. This type of chemical defense is

usually coupled with strong visual signals that function as an early-warning system to keep an attack from occurring. Such an association of chemical and visual signals, in most evolutionary models, requires that the predator be capable of associative learning.

Chemical crypsis, blending into the chemical background, is accomplished in two ways: reducing the concentration of one's emissions, and altering the quality of one's emissions so that they match those that predominate in the environment. Of course, the visual equivalent of the last strategy is to paint oneself with pigments that absorb and reflect the same light frequencies as the substrate the insect normally finds itself on. It is likely that when not communicating with members of their own species, most phytophagous insects keep the amplitude of volatile emissions to a minimum. Indeed most of the body is covered with heavy molecular weight waxes that have low volatility and low emission rates. When potential attackers are nearby, however, even these compounds will have a relatively higher amplitude and the "active space" for attraction of, and attack by, a predator could be exceeded. The blend quality may then be altered to more closely match the background chemicals. An example is provided by larvae of the green lacewing, *Chrysopa slossonae*, worked out in detail by Eisner, T. *et al.* (1978). The larvae are predators on woolly alder aphids, and the aphids are attended by ants that collect their honeydew. The lacewing larvae, however, can come under attack by the ants guarding the aphids. To blend into the waxy background noise both visually and chemically, they steal wax from the aphids and cover their bodies with it. When the lacewings were experimentally denuded it became clear that they were much more likely to be attacked and removed from the area by ants than when they were covered with wax. Even when the covered larvae were discovered and attacked, the wax then provided a more active type of defense by eliciting cleaning behavior when the ant's mouthparts became filled with wax. This defensive behavior is a high priority for the lacewings, as evidenced by the large time-allotment they give to covering themselves with wax compared to feeding and resting.

The termitophilous staphylinid beetle, *Trichopsenius frosti*, also avoids evoking attack from its termite hosts, *Reticulitermes flavipes*, by matching its ensemble of cuticular hydrocarbons to those of the termites (Howard, R. *et al.*, 1980). Over



nponotus
a trail
hindgut,
with the
r. Tactile
lobler, B.

with the
od source
ildobler,
Masch-
romones
(0) have
g contin-
or trails,
cues for
ildobler,
ax sp.
(1974).
e utilized
vax uni-
used in
ood find,
he later
tablished
nponotus
wer is not
ived trail
ilson, E.,

evolutionary time, the beetles had an extra problem to surmount, however, because termite reproductives have a slightly different array of compounds than the workers. The beetles solved this problem by developing a blend that was intermediate between that of the workers and reproductives, with the proportion of branched to normal components being closer to that of reproductives, and the proportion of saturated to unsaturated components more closely matched to the workers' blend. In other words, the beetles became an "average" termite in terms of their body odor. The most remarkable feature of this defense is that these odors are not simply acquired by adsorption of the termite's own hydrocarbons onto their cuticle. Howard, R. *et al.* (1980) found that the beetles *synthesize* these compounds from acetate starting material to form the precise blend of "average termite" compounds. This is powerful evidence of the strong selective forces operating on this defensive system to tune it to reduce the signal: noise ratio. A similar example is provided by the beetles, *Myrmecaphodius excavaticollis*, which inhabit nests of its ant hosts, *Solenopsis* spp. (Vander Meer, R. and Wojcik, D., 1982). The beetles' body hydrocarbons also match those of their hosts, except that they apparently acquire them through adsorption of ambient chemicals, not synthesis. They are therefore capable of shedding the compound acquired from one host and picking up a new set as they move in with a new *Solenopsis* host species.

Insect-produced chemicals that deter or repel attackers are primarily known through the work of Eisner and his colleagues (Eisner, T., 1970, 1972; Eisner, T. and Meinwald, J., 1966). The arrays of compounds used and behaviors involved are too numerous to review here, but some examples will illustrate how attackers can be arrested or repelled by these chemical defenses.

Making an attacker switch over from attack behavior to grooming behavior is a widely used means of arresting a predator. The potential prey must deliver a chemical signal that arrives quickly at the target and rapidly sends stimuli through the sensory nervous system that suddenly tips the behavioral hierarchy's balance in favor of grooming rather than locomotion (see Hansell, chapter 1). The stimuli are too intense for the CNS to ignore and, as in the use of tear gas by humans, the poten-

tial victim can escape while cleaning and grooming occur in the attacker. Such chemicals are often forcefully ejected to speed their delivery, plus the amplitude of the signal is optimized by accurately focusing the entire secretion solely on the target. Often spreader-sticker compounds are included to speed penetration and increase amplitude by involving a greater number of cuticular receptors (Eisner, T., 1970). This is illustrated by the defensive secretion of the whipscorpion, *Mastigoproctus giganteus*, which ejects onto the cuticle of its attackers an irritating spray composed of 84% aqueous acetic acid plus 5% caprylic acid. The spray's activity is enhanced by the caprylic acid spreader-penetrant which results in a broader area of contact for the acetic acid (Eisner, T. *et al.*, 1961).

Probably no better example exists of forcible ejection of a defensive secretion than that provided by the bombardier beetle. Eisner, Schildknecht, and colleagues have worked out the mechanics and chemistry of this system over the years (Aneshansley, D. *et al.*, 1969; Eisner, T., 1958; Schildknecht, H. and Holoubek, K., 1961; Schildknecht, H. *et al.*, 1968). When the beetle is disturbed, its turret-like nozzle on its abdominal tip can be aimed in the direction of the attacker to accurately deliver a blast of boiling-hot quinones onto its body. The chemical reactions that result in the hot, irritating spray are quite complex, and require that the precursors be housed separately so that the beetle avoids irritating itself with its own quinones. Two glands with storage sacs for the reactants are separated by cuticular barriers until the moment the defensive secretion is needed. One sac contains hydroquinones and hydrogen peroxide, and the other holds peroxidases and catalases. When the quinones are needed, the contents of the first sac are forced into the second, and are mixed in the second chamber or "reaction chamber". The result is an explosive reaction that generates heat and quinones, and the secretion is discharged from the chamber at 100°. The quinones are the active components that arrest ant attackers and other predators by inducing them to release their hold on the beetle and begin recovering by cleaning and grooming, which allows the beetle to walk away.

Another interesting example of an ejected irritating spray is that produced by the stick insect, *Anisomorpha buprestoides*. The secretion, composed

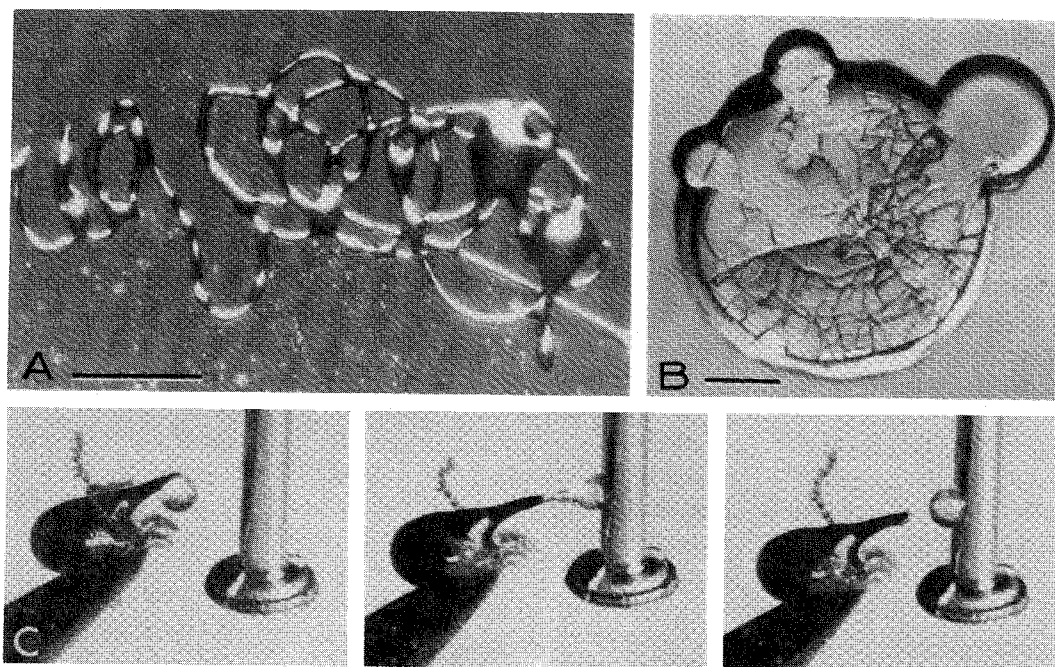


FIG. 10. Discharge of defensive chemicals from *Nasutitermes exitiosus* snout. A: The natural pattern of discharge from a soldier onto a glass slide shows that the chemical is sprayed in a pattern of loops (by quick head movements) which increases the coverage; B: a droplet of secretion that was allowed to stand in air for 2 days, then compressed to show a liquid core under an outer crust; C: head of a soldier squeezed with forceps to eject defensive fluid for analysis and experimentation (From Eisner, T. *et al.*, 1976.)

mostly of anisomorphal, a terpene dialdehyde, is sprayed from openings on the insect's thorax. Eisner, T. (1965) demonstrated that the phasmid will often discharge its spray at avian predators even before they touch the insect during their approach. When the spray hits its eyes and face, the bird stops to clean them, and the insect walks away. Of course, vertebrate predators have the capacity to learn quickly and the birds usually do not attack the stick insect again in the near future. Two species of ants and a beetle were also repelled by the spray, which the phasmid aimed and ejected accurately at them when they hit one of its legs.

It is not clear how long-lived the effects are of such sprays aimed at arthropod predators. However, some of them are often both irritating and gummy. Nausute termite soldiers of the species *Nasutitermes exitiosus*, are walking squirt-guns of sticky defensive terpenoid secretions, and virtually their entire head is devoted to storing these compounds (Eisner, T. *et al.*, 1976) (Fig. 10). The viscous secretion not only entangles attackers such as ants, but irritating components elicit grooming behavior and cause them to become arrested. The

major chemicals responsible for arresting and repelling arthropod attackers, such as ants, were monoterpenoids such as α -pinene and β -pinene (Eisner, T. *et al.*, 1976). The secretion also functions as an alarm pheromone, attracting other soldiers to the area, but tactile cues are needed to cause the attracted soldiers to discharge their spray.

Prestwich and his colleagues have determined the chemistry of termite defensive secretions for many species in both the lower and higher termites (for review see Prestwich, G., 1979). Some of the chemicals are toxic when contacted or inhaled by arthropod attackers. There is a rich diversity of compounds, among which are represented monoterpenes, sesquiterpenes and diterpenes, macrocyclic lactones, various ketones, vinyl ketones, other acetate-derived compounds, mucopolysaccharides and *n*-alkanes (Prestwich, G., 1979; Prestwich, G. and Collins, M., 1981). There is also a wide variety of cephalic weaponry for applying these chemicals (Prestwich, G., 1979). The defensive chemistry of termites, which varies among families, appears to provide an evolutionary picture of the termites and allows hypotheses to be formed as to the biochemical

shifts that have occurred over evolutionary time (Prestwich, G. and Collins, M., 1982).

Apparently non-irritating, but sticky, secretions can be effective at arresting a predator. For instance, female black widow spiders produce copious amounts of a viscous silk from their abdomens when attacked (Vetter, R., 1980). In a head-standing posture on the ground or while hanging upside-down on her web, she uses her hind legs to stretch out the threads as they come out and also to apply the silk to the attacker's body, such as onto the muzzle of a mouse. Immediately the mouse begins intense grooming trying to remove the secretion that has stuck its whiskers together. Similar gummy secretions are emitted by onychophorans, millipedes, and other arthropods, and like those of the black widow have also been shown to have significant defensive value (Eisner, T., 1970, 1972).

2.6 Defense of relatives

Individuals in many insect species emit chemicals when they are being attacked that induce "alarm" responses in any conspecifics nearby. That the emission of such alarm pheromones often occurs as, or just before, the insect is killed, or that it may bring the emitter under more danger than if it had merely fled, brings forth the question of how these signals could have evolved. Certainly alarm pheromones often are part of a defensive secretion emitted to thwart an attacker. But when one understands that in every case where alarm behavior has been observed the responders are actually close relatives of the emitters, it is clear that kinship selection likely has made possible the evolution of this type of chemical communication. In this way, as in trail-recruitment systems, the "altruistic" individual who releases the signal in fact is not sacrificing anything at all. It actually benefits because the greater-than-average proportion of its genes which resides in its relatives will be more likely to be perpetuated as a result of its behavior (Dawkins, R., 1976).

Alarm pheromone systems are reviewed by Blum in this volume and he has also reviewed alarm systems of the social Hymenoptera (Blum, M., 1974, 1979). Alarm pheromone systems of non-eusocial insects have recently been reviewed by Nault, L. and Phelan, P. (1983), and an excellent review of ant alarm pheromone systems is found in Parry, K. and

Morgan, E. (1979). Some of the features alarm systems have in common will be examined here.

As predicted by Bossert, W. and Wilson, E. (1963) the alarm pheromone systems described thus far utilize volatile chemicals, usually more volatile than trail and sex pheromones. Secondly, these same compounds or blends of compounds appear to be used by a number of closely related species. Specificity of the signals appears to be lower than sex pheromones, perhaps because the active space is so small that only the intended receivers nearby will be affected. Also, there would appear to be little disadvantage to any outsiders perceiving the signal.

The alarm pheromone systems of aphids exhibit these characteristics, and have been well worked out by Nault and his colleagues (Nault, L. and Montgomery, M., 1977, 1979; Nault, L. and Phelan, P., 1983). Most of the species use (*E*)- β -farnesene, a fairly volatile terpenoid, as their alarm pheromone. This compound is found in 18 genera in three subfamilies. In each species the response to the pheromone is somewhat different, however. Nymphs may have a different response from adults; alates may behave differently from non-alates. When attacked, or in the grasp of a predator, the aphid typically exudes drops of liquid from two tubercle-like organs in the end of its abdomen. Although the cornicle secretion may have originated as a defensive secretion, the triglycerides and fatty acids which are the predominant components are not very effective at protecting aphids from predation (Goff, A. and Nault, L., 1974). The main function of these heavier molecules may be to serve as a substrate for the emission of the more volatile alarm pheromone molecules (Nault, L. and Phelan, P., 1983). The typical response to pheromone of nearby individuals is to fall from the host plant, although in some species those individuals farther away from the emitter and exposed to lower concentrations will merely walk away (Montgomery, M. and Nault, L., 1977). Some species only walk, regardless of concentration, and others continue feeding while jerking their bodies (Montgomery, M. and Nault, L., 1977; Nault, L. *et al.*, 1976). Thus for species which both drop and walk, there appear to be smaller active spaces for dropping than for walking, the former being elicited only by the higher concentrations that can occur closer to the emitter. Many species in which walking or jerking, not dropping, is the only response to

pheromone, are tended by ants, and the ants are attracted to the source of the alarm pheromone (Nault, L. *et al.*, 1976). For ant-attended aphids, arrestment has been selected for because the ants will dispose of the attacker and movement away from the cluster may result in loss of this protection.

For those aphids that have dropped from the plant, the pheromone appears to cause a prolonged change. They have a higher linear velocity and walk in fairly straighter paths without orienting to nearby vertical objects (Phelan, P. *et al.*, 1976). Those merely knocked from the plant by an experimenter have a low velocity of movement, execute many turns, and orient toward the nearest vertical silhouette, which tends to result in a high rate of return to the plant from which they fell (Phelan, P. *et al.*, 1976).

The alarm pheromones of social Hymenoptera are best-known in the ants. It has become increasingly clear that these pheromones are complex blends of chemicals, not individual compounds acting alone (Blum, M., 1979). Typically the contents of the various glands, mandibular, Dufour's, poison, etc., are characterized by chemists and several of the myriad compounds are found to evoke the behavioral response, "alarm", in workers. The uncertain definition of what constitutes an alarm response has added to the difficulty of analyzing just how species-specific and powerful these pheromones are (Parry, K. and Morgan, E., 1979). In contrast to the commonly imprecise descriptions of the response which usually include increased "excitation" and velocity of movement, alarm behavior may also include increased rates of turning, displacement toward or away from the source, opening of the mandibles, biting, digging, stinging, trail-laying and other behaviors (Parry, K. and Morgan, E., 1979). Several compounds have, however, been identified from glands that, compared to other analogs, are the most powerful elicitors of alarm behavior, which has also been carefully described.

One such compound is 4-methylheptan-3-one, which has been identified from the mandibular glands of at least six species of *Pogonomyrmex*, and shown to evoke alarm behavior in *Pogonomyrmex barbatus* and *Pogonomyrmex badius* (Parry, K. and Morgan, E., 1979; McGurk, D. *et al.*, 1966; Wilson, E., 1958). Low concentrations of this compound result in alarm-attraction of nearby workers whereas high concentrations result in alarm-

"frenzy" as well as digging behavior (Wilson, E., 1958). This same compound has also been identified as a mandibular gland alarm pheromone in *A. texana* and is present in the mandibular glands of at least six other *Atta* species (Blum, M. *et al.*, 1968). Again, in *A. texana* low concentrations alarm and attract workers and high concentrations alarm and repel them. Interestingly the (S)-(+ enantiomer of this chiral compound is about 100 times more active than the (R)-(- enantiomer (Riley, R. *et al.*, 1974) in *A. texana* and about 200 times more active than (-) in *A. cephalotes*. Thus, even though each species can discriminate the optical isomers of this compound, they both apparently use the (+) enantiomer as the major alarm pheromone component. Either species-specificity comes from secondary components blended with the major one, or there is little or no specificity. Wilson, E. (1974) concluded that alarm pheromones are not likely to be species-specific because there have been no evolutionary pressures on them to become so.

3 ORIENTATION MECHANISMS

The reactions to chemicals that modulate insects' behaviors often result in displacement toward or away from the emission source. Even when no displacement occurs, however, movements may be made by the insect in order to remain in the same location, as in an insect flying in wind that must measure its airspeed and drift in order to keep station while in an odor plume (Marsh, D. *et al.*, 1978). Although the evolutionary "bottom line" as far as the insect is concerned is its displacement, the insect's steering and velocity of movement are the means by which the displacement outcomes are achieved. In the following section I will examine some of the mechanisms currently thought to be used by insects to displace in odor fields. Although each possible mechanism will be examined separately, it should be stressed that more than one can be used at any time and two or three reactions might be integrated to form one resultant movement (Kennedy, J., 1983; Bell, W. and Tobin, T., 1982).

3.1 Direct reactions to odor

One useful way to look at responses to odor is to

determine whether or not the insect is able to sample an existing gradient and detect differences in odor concentration. If it can, and can steer in response to this difference, the response may be called a *direct* response (Bell, W. and Tobin, T., 1982). This would be in contrast to an *indirect* response in which the odor triggers steering to another stimulus such as wind, or activates a stored motor program, and does not itself guide the animal (Bell, W. and Tobin, T., 1982).

An odor gradient may be sufficiently steep to allow for direct response if the insect has two or more receptors spaced far enough apart such that a simultaneous comparison of concentrations can be made. Alternatively, a direct response can be made during sequential sampling (Bell, W. and Tobin, T., 1982; Kennedy, J., 1983). The shallower the gradient the faster the insect must move and the longer its memory must be of the concentration at previous points along its path. Traditionally, simultaneous sampling of concentration has been called *tropotaxis* and sequential sampling *klinotaxis*, but regardless of the terms, these mechanisms have been recognized for a long time (Fraenkel, G. and Gunn, D., 1940; Kennedy, J., 1977, 1978).

A good example of direct response mediated by simultaneous sampling of the gradient is presented by the ant, *Lasius fuliginosus*, which zig-zags along its pheromone trail. If the antennae are experimentally glued in a crossed position, with every excursion from the trail the ant turns in the wrong direction, away from the trail instead of toward it, proving that each turn is due to the sampled gradient (Hangartner, W., 1967). From experiments with honeybees (Martin, H., 1965) and *Bombyx mori* (Kramer, E., 1975), both of which can respond by turning to ca. 2-fold differences in odor concentration between antennae, one might expect for *L. fuliginosus* that the chemical concentration of one antenna must be double that on the other in order for the ant to turn back toward the trail.

Male American cockroaches, *Periplaneta americana*, can make a "correct" turn toward a pheromone source in still air when they get close enough to it to detect a concentration difference, apparently simultaneously across their antennae (Hawkins, W., 1978; Bell, W. and Tobin, T., 1982). Before arriving to within about 70 cm of the source in a circular arena, the cockroaches exhibit increased

velocity of movement in response to pheromone and a certain degree of apparently random turning.

The change from simultaneous to sequential sampling can be induced experimentally in honeybees by fixing the antennae so that they no longer diverge and cannot simultaneously sample a concentration difference. They then tend to swing their head more from side to side, apparently to sample the lateral gradient through time at different positions, transverse to the body axis (Martin, H., 1965). American cockroach males do the same thing. When one antenna is removed the remaining one sweeps greater distances from side to side for sequential samples of concentration (Rust, M. *et al.*, 1976; Bell, W. and Tobin, T., 1982). Whether the entire body moves side to side or just the mobile receptors, it is apparent that when the animal encounters shallower gradients the simultaneous comparisons will eventually be insufficient to detect differences, and movements to and fro from more widely spaced areas will need to be made for the differences to have a chance of being significant.

There are not very many other examples of such classical transverse klinotactic responses to concentration (see Kennedy, J., 1978, 1983; Bell, W. and Tobin, T., 1982). Most of such sampling is performed *along* the insect's resultant path, not *across* it, and the response to a change in concentration may be a turn directly back along the concentration gradient, or else a change in the movement pattern. Such longitudinal klinotaxis was not originally recognized by Fraenkel, G. and Gunn, D., (1940), but was pointed out by Kennedy, J. (1978). It would first appear that the turn back along the gradient is more of a *direct* response to odor but the change in movement may also be a *self-steered* change in the pattern or severity of turning that is difficult to distinguish from what has classically been described as klinokinesis (Fraenkel, G. and Gunn, D., 1940; Kennedy, J., 1978). This type of reaction may be described as another type of *indirect* response to concentration.

3.2 Indirect reactions to odor without wind

Indirect reactions to odor include those in which responses to cues from other modalities are switched on. For instance, odor may trigger anemotaxis, a response to wind, which will be discussed in the next section. In addition, the response to the concen-

tration
direct
modali
change
necessa
is not s
maneu
and exc
modali
modula
to fall
klinoki
Kenned
response
response
difficult
complic
program
disorga
loops c
Linear
orthok
which c

One
is the
response
pherom
et al.,
made v
tion if
tenna is
antenn
so. The
is recei
This se
accordi
real gra
of the t
the leg
follow,
them, v
(Schal,

Ano
wasp, I
female
is pres
back to
pling is
and the

tration difference that has been sampled can be indirect in a way not related to cues from other modalities (Kennedy, J., 1983). The concentration change may trigger a *self-steered* maneuver that necessarily bears some relation to the gradient, but is not steered by it (Kennedy, J., 1978, 1983). The maneuver pattern may be centrally programmed and executed with or without feedback from other modalities in the environment. These reactions, modulated but not steered by concentration, appear to fall into the class of reactions classically called klinokineses (Fraenkel, G. and Gunn, D., 1940; Kennedy, J., 1977, 1978). In some instances such responses may be integrated with another indirect response to odor, anemotaxis, and it is often difficult to pick these two reactions apart. Another complicating factor is that even without wind, the program of movements may range from being very disorganized-looking to being quite patterned, with loops or zig-zags (Bell, W. and Tobin, T., 1982). Linear velocity of movement (classically called the orthokinetic component) may also be integrated, which can result in striking changes in displacement.

One good example of an indirect response to odor is the response of male German cockroaches responding to antennal contact with female sex pheromone (Bell, W. and Schal, C., 1980; Schal, C. *et al.*, 1983). First a single 180° rotational turn is made with respect to the cockroach's initial direction if both antennae are touched, but if one antenna is touched the male turns 180° away from that antenna's position, turning the shortest route to do so. Then after a short time if no further stimulation is received a second turn of *ca.* 180° is performed. This second turn, like the first, must be self-steered according to an internal turn program, because no real gradient remains to guide it. The performance of the turn program is aided by proprioception from the legs and antennae. Even more 180° turns may follow, but the male begins to move more between them, which results in wider areas being sampled (Schal, C. *et al.*, 1983).

Another example without wind is provided by the wasp, *Nemeritis canescens* (see section 2.3). As the female walks from an area where the host odor is present into clear air, it performs a 160° turn back toward the "patch" of host odor. The sampling is performed along its path of displacement, and the response is to perform an about-face, taking

her back into the patch. The about-face appears to be self-steered, triggered by the drop in concentration but not steered by the gradient (Waage, J., 1978). Mosquitoes flying from one side of a choice chamber into a column of air permeated with a repellent or having suboptimal humidity or temperature will turn back nearly immediately and re-enter the original column of air (Daykin, P. and Kellogg, F., 1965; Daykin, P. *et al.*, 1965).

Tenebrio molitor also exhibits similar self-steered movements when the humidity is suddenly raised (Havukkala, I., 1980). A turning-back reaction, based presumably on an internal program and its previous walking direction, results in a 165° turn, on average, in the 2 s immediately following the humidity increase.

In a sense, a change in linear velocity with odor concentration, classically known as orthokinesis (Fraenkel, G. and Gunn, D., 1940), may be considered to be an indirect response. The rate of locomotion is not steered by the gradient, only modulated by it, possibly according to an internal mechanism, and thus may fall into the category of indirect responses along with klinokinesis. The two kineses in combination can, without any other mechanisms, result in significant displacement toward the source, as demonstrated by Rohlf, F. and Davenport, D. (1969) in computer simulations.

Performance of more elaborate, organized programs of movements may occur as part of an indirect response. Zig-zags or counterturns (Kennedy, J., 1983; Tobin, T., 1981) are a primary example. Just as in less well-patterned self-steered movements, the zig-zagging program that was switched on by odor can also be modulated by its concentration, and the width and frequency of the zig-zags may be greater or smaller depending on the ambient concentration. Oriental fruit-moth males (Baker, T. *et al.*, 1984) exhibit zig-zag movements in zero wind when pheromone is present and not when it is absent. This will be discussed in more detail in section 3.4.

3.3 Indirect reactions to odor involving wind and visual cues

Another set of indirect reactions to concentration involves those to other stimuli in the environment. For instance, odor may trigger orientation to visual

objects nearby, such as dark vertical silhouettes, as occurs in bark beetles and gypsy moths responding to sex pheromone (Shorey, H., 1973). In the gypsy moth, pheromone-baited traps placed on thick tree trunks captured significantly more males than those on thin trunks (Cardé, R. *et al.*, 1977).

But perhaps the most widely used indirect response to odor involving another stimulus is anemotaxis, or steering with respect to the wind's direction. For walking insects, sensing the wind's direction and walking at some angle to it or directly upwind is not difficult, because pressure differences on sensory hairs, antennae or body parts can be detected since the animal is anchored to the ground by tarsal contact. An example of odor-conditioned anemotaxis in a walking insect is that exhibited by the American cockroach to its sex pheromone (Bell, W. and Kramer, E., 1980). When pheromone is absent in wind, at other than very low wind velocities, the cockroaches exhibit negative anemotaxis, displacing downwind. When a low concentration of pheromone is introduced, however, their tracks are almost always in the general upwind direction, although with increasing concentrations the tracks become straighter upwind (Fig. 11).

Even in relatively uniform, wide plumes, there are side-to-side oscillations though, (Tobin, T., 1981), and such movements may be indicative of an additional, indirect response discussed earlier, an internal program or movement pattern triggered by the odor (Tobin, T., 1981; Bell, W. and Tobin, T., 1982). In addition, a direct response may occur, a tropotaxis, by the animal's long antennae which can simultaneously sample the clean air outside the plume area (Tobin, T., 1981; Kennedy, J., 1983). Coupled with odor-conditioned anemotaxis, this steering to maintain contact with the plume could contribute to location of the pheromone source (Bell, W. and Kramer, E., 1980; Tobin, T., 1981).

In the silkmoth *Bombyx mori*, a similar anemotactic response was observed in a relatively homogeneous pheromone field (Kramer, E., 1975). The males walked generally upwind, but reversed their course periodically while still within the field. The result was a zig-zag walking track with displacement upwind, and the zig-zags were again apparently part of an internal program triggered by the presence of pheromone and superimposed on an anemotactic response.

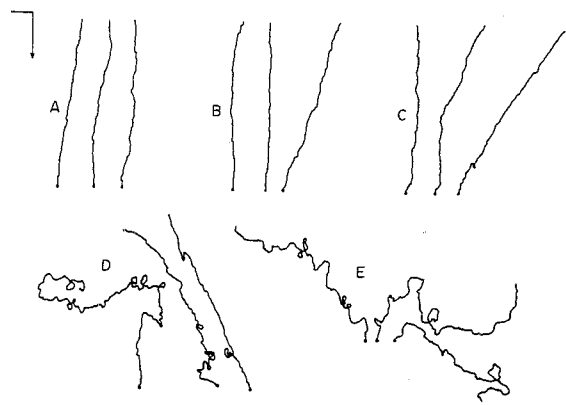


FIG. 11. Tracks of American cockroach males recorded from a servosphere device. Wind containing sex pheromone is from top, indicated by arrow. In A and B, the two highest concentrations of pheromone elicit nearly straight upwind walking by males, whereas the two lowest concentrations in D and E evoke more circuitous movements, not always upwind. (From Bell, W. and Kramer, E., 1980)

Flying insects have a much more difficult task in integrating anemotaxis into their response to odor, contrary to W. Bell and T. Tobin's (1982) statement that the only thing different about chemo-orientation for flying compared to walking insects is that there is a third dimension. Flying insects cannot detect wind very well by pressure differences alone because with no ground contact they are displaced along with the wind. Hot-air balloonists swept along at great speeds commonly report how calm the air around them seems; almost motionless at times. Like the balloonist, however, if the insect can obtain a *visual* fix point or frame of reference, it can determine in which direction it is drifting. Unlike the balloonist the insect can then compensate for its drift by thrust and steering movements. Thus odor-modulated anemotaxis in a flying insect involves the odor triggering a response to the apparent motion of the visual field (Kennedy, J., 1977, 1978, 1983).

This response to visual drift information by flying insects, called the optomotor response, has been well-documented (Kennedy, J., 1940; Kennedy, J. and Marsh, D., 1974; Marsh, D. *et al.*, 1978; Miller, J. and Roelofs, W., 1978; David, C., 1982a,b). When a ground pattern is rotated in the downwind direction, moths flying in pheromone plumes in wind can be displaced downwind *while still facing generally upwind* in the plume because the rate of apparent image movement across the eyes exceeds the preferred rate and the insect reduces its airspeed

(Marsh, D. *et al.*, 1978). Conversely the animal can be made to *increase* its airspeed, work harder, and fly right past a pheromone source when the pattern is rotated in the upwind direction. The moth flies faster upwind to attain the preferred rate of general front-to-back image movement (Marsh, D. *et al.*, 1978).

If the ground pattern predominates as the major visual input, increasing the moth's height of flight above the pattern should require the moth to fly at higher airspeeds in order to attain the same velocity of image movement as when it was at a lower altitude. In fact faster flight at increasing flight heights happens to some degree in male oriental fruit-moths displacing upwind in their pheromone plume. At greater heights it takes a faster-rotating ground pattern to reduce their airspeed to the same degree as at lesser heights (Kuenen, L. and Baker, T., 1982a). Also, velocity of flight up the plume is faster at greater heights above a *stationary* floor than at lesser heights. Because other factors such as competition between fixed objects in the room and the floor pattern could contribute to the higher velocities with increasing height, these observations are not definitive: they do suggest height-induced changes in angular velocity of image movement influence flight speed. Recent work with *Drosophila* flying upwind to banana odor in a striped "barber's pole" visual field surrounding the flies demonstrated more clearly that angular velocity of image movement, as controlled by distance from the visual pattern, was the predominant factor influencing airspeed (David, C., 1982b). Other visual parameters that were varied were wavelength of the striped pattern, its pitch, and its frequency. These played less pronounced roles in modulating the flies' airspeeds.

The amount of drift allowed by flying insects seems to vary with concentration. As pointed out by Kennedy, J. (1940) and Marsh, D. *et al.* (1978) an insect flying at any angle but 0° (directly upwind) or 180° (directly downwind) with respect to the wind will experience some degree of transverse image movement across its eyes, the visual equivalent of a sideways skid (Fig. 12). The difference between the moth's course angle and its track angle is its drift angle, which could possibly be measured visually by the angle of transverse image movement across the eyes. Kennedy, J. and Marsh, D. (1974) and Marsh, D. *et al.* (1978) showed that when a pheromone source is removed and the male flies out of the front

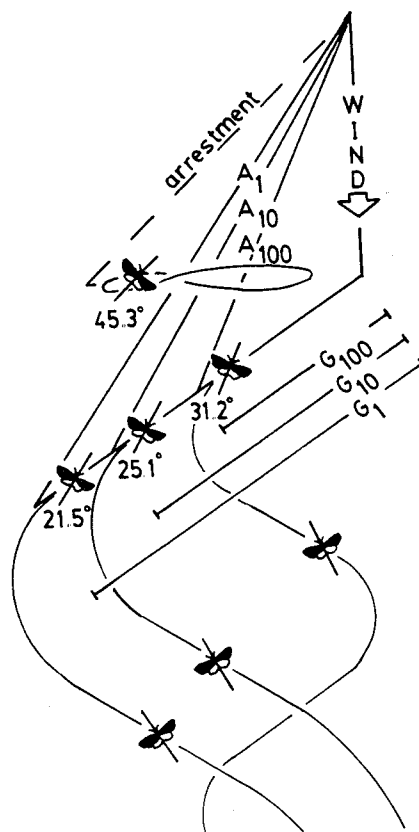


FIG. 12. The relationship between oriental fruit-moths' course, track, and drift angles in wind as they flew toward sources impregnated with 1, 10, and 100 μg of sex pheromone in a laboratory wind tunnel (from Marsh, D. *et al.*, 1978). Video-recordings were made from above in plan view. As the concentration increased from 1 to 100 μg , groundspeeds decreased, as illustrated by the lengths of lines G_1 , G_{10} , G_{100} . Airspeeds (A_1 , A_{10} , A_{100}) similarly decreased with higher concentrations. On average, moths' track angles with respect to the wind were nearly identical along the relatively straight "inter-reversal" portions of the zig-zag track (depicted by the straight line common to the three flying moths along G_1 , G_{10} , G_{100}) but to attain that track angle, the course angles of moths flying to increasingly high concentrations were higher (pointed more upwind) as illustrated by the body axis lines of the moths along G_1 , G_{10} , G_{100} . (Although "course angle" is for illustrative purposes here used synonymously with "body axis angle", "thrust direction angle" is a more precise way of defining course.) Due to the differences between course and track, the angle of transverse image drift is more severe (31°) at 100 μg than at 1 or 10 μg (21° and 25°). During the in-plume 90° cross-tunnel casting flight characteristic of arrestment, the males allowed even more severe transverse image drift of 45° . At higher concentrations the zig-zags during upwind flight were narrower and more frequent, as shown. At zero wind velocity course and track angles are identical and the drift angle is therefore zero. (After Marsh, D. *et al.*, 1978, from Kuenen, L. and Baker, T., 1982b.)

end of the plume in wind, experiencing a concentration drop, the straight legs of the tracks become oriented at nearly 90° crosswind. The drift angle, the difference between the course and track, must now have increased. Kuenen, L. and Baker, T. (1983) obtained similar results with the oriental fruit-moth. In wind, when males flew out of the front end of the plume, the straight legs of the zig-zag track became nearly 90° cross-tunnel. The concentration decrease also produced a concurrent increase in linear velocity and a decrease in turning frequency, causing wider zig-zags. Thus the males appeared to allow the drift angle to increase during the concentration-induced cross-tunnel casting.

Marsh *et al.* showed that the track angle is kept constant under varying wind velocities, and Kuenen, L. and Baker, T. (1982b) showed that up to a point moths kept the track angle constant with increasing pheromone concentrations (Fig. 12). But after flying closer to the strongest point source, the concentration became high enough to cause in-flight *arrestment* within the plume and, the key feature of the movements that changed was the track angle accomplished mainly by changing the course angle, not the airspeed or ground speed (Fig. 12). The other movement parameters, such as turning frequency, linear velocity, angular velocity, etc., remained no different from those values during the attraction to the high concentration that immediately preceded the arrestment. During arrestment the average course angle increased to 45° , as did the drift angle, to produce the 90° cross-wind track within the plume. The high and low concentrations produced high and low frequencies of zig-zag turns (see next section) by modulating the internal self-steered movement pattern, but during casting flight in the plume (arrestment) or casting after flight out of the plume, the increased drift angle due to the change in course was the main change in steering that caused arrestment with either narrow (in plume) or wide 90° cross-wind oscillations of track (Kuenen, L. and Baker, T., 1982b).

3.4 Integration of mechanisms by an insect flying in sex pheromone

Recent evidence indicates that the oriental fruit-moth and other moths integrate several indirect responses to pheromone (optomotor anemotaxis, a

self-steered zig-zag program, linear velocity of movement) in order to locate a sex pheromone source in wind. What is the evidence for a self-steered program of zig-zags modulated by pheromone concentration? First, in our laboratory's flight tunnel, males initiating flight in a pheromone plume in wind and then flying in still air when the wind was stopped were able to continue zig-zagging up the plume to locate the pheromone source a significant percentage of the time (Fig. 13) (Baker, T. and Kuenen, L., 1982). Proof that the narrow zig-zags in zero wind were modulated by the pheromone came from a second experiment in which the source was removed while wind was on in order to create a truncated plume. The wind was then stopped, and the moths that had started upwind in the plume now found themselves first in zero wind in the plume and then flying out of the plume's front end into clean air. At this point their zig-zags became wider and steered more cross-tunnel, and the turning frequency became lower with a slight increase in the linear velocity. Since no wind was blowing, the change in the zig-zag pattern could not have been steered anemotactically but rather was evidence for a concentration-dependent program of movements self-steered by the moth. Whether the movements in still air were aided by visual feedback from the environment, such as flow-field oscillations, or were performed solely through proprioceptive feedback is not known at this point and deserves further study. Preliminary evidence (Kuenen and Baker, unpublished data) indicates that in still air the moths do respond to a moving floor pattern. However, this is not proof that they use feedback from the *stationary* pattern to perform their movements in still air because the pattern's *movement* is the visual equivalent of wind drift, and it is already known that insects compensate to a moving pattern in zero wind (Kennedy, J. and Marsh, D., 1974; Kennedy, J., 1940).

These experiments confirmed and extended the results of Farkas, S. and Shorey, H. (1972), who first showed that male moths could continue to a pheromone source in still air once having started toward it while wind was on. However, they not only overextended their findings to declare that only chemotaxis, not anemotaxis, was used even with wind present, but they also proposed that the type of chemotaxis used was one in which all movements were *directly* steered by a gradient. As pointed out

FIG. 13. plume a to remain of each of view end of the zig-zagging stationary.

by Kennedy to the g because filamentc however, that avo (Wright, Baker, T.

Other c zags con oriental f of pre-ex exposure no pre-ex stationary teristic si wind on stationary

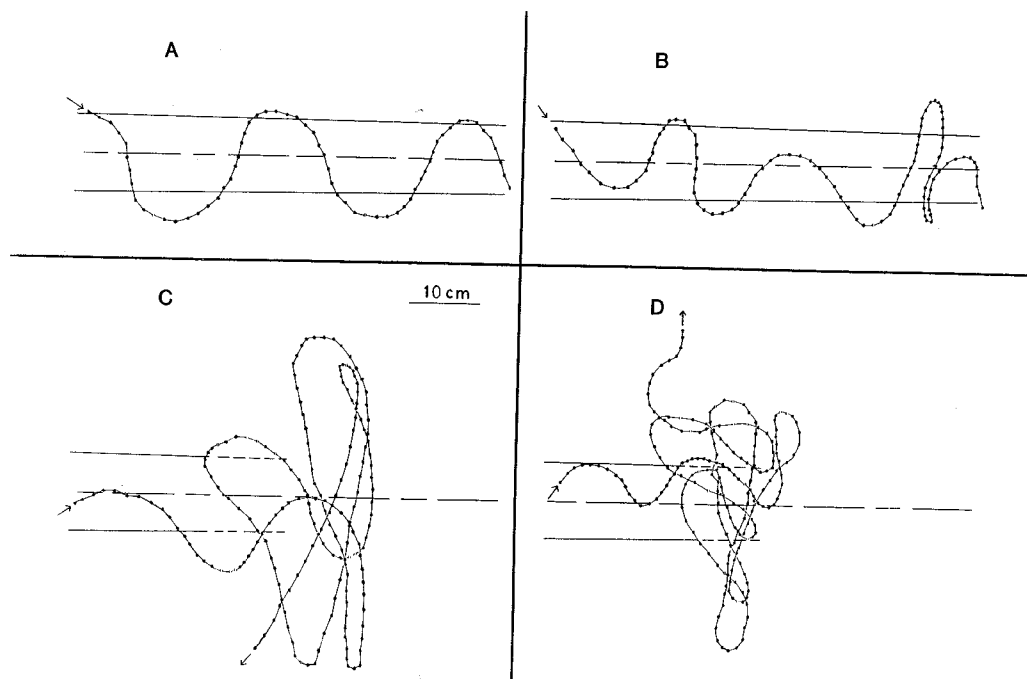


FIG. 13. Top view of video-recorded tracks of *Grapholita molesta* males flying up a wind tunnel along a stationary pheromone plume after wind had been stopped. **A and B:** controls; moths were flying up-tunnel in zero wind with the stationary plume allowed to remain intact all the way to the source. These males made it to within 15 and 5 cm of the source, which was 105 cm to the right of each figure. **C and D:** The pheromone source had been removed and the wind stopped before these males had entered the field of view. These males did not make it near the source, but rather their tracks changed significantly upon flying out of the up-tunnel end of the truncated stationary plume into clean air. This was evidence that the pheromone itself modulates the program of zig-zagging movements, apart from any anemotactic orientation. Dots are the moths' position each 1/60 s. The position of the stationary plume in still air is indicated by the solid straight lines in each figure, the central dashed lines the plumes' axes, and double dashed lines the truncated up-tunnel ends of the plumes. (From Kuenen, L. and Baker, T., 1983.)

by Kennedy, J. (1978, 1983) such a direct response to the gradient in the plume is highly unlikely because of the instantaneous plume's broken, filamentous structure. The plume's structure may, however, serve to provide intermittent stimulation that avoids adaptation of the nervous system (Wright, R., 1958; Kennedy, J. *et al.*, 1980, 1981; Baker, T. *et al.*, 1984) (see following sections).

Other evidence for a self-steered program of zig-zags comes from recent experiments in which oriental fruit-moths were provided various regimes of pre-exposure to wind, some involving no pre-exposure whatsoever (Baker, T. *et al.*, 1984). With no pre-exposure to wind, males introduced into a stationary pheromone plume exhibited the characteristic side-to-side zig-zagging usually seen with wind on (Fig. 14A,B). When introduced into stationary clean air, males seldom took flight, but

when they did, the tracks were relatively straight and directed toward the ceiling's lights (Fig. 14C). One aspect of the zig-zagging tracks in still air was clearly different than in wind. The zig-zags had no consistent direction, often meandering slowly about in the plume, sometimes carrying the moth out of the plume area, sometimes displacing it down-tunnel away from the source. Males also zig-zagged up-tunnel toward the source, which was located successfully a surprisingly high 21% of the time. A key difference to the zig-zagging in zero wind is, of course, that the male's course and track are identical. Again the pheromone seemed to switch on the program of counterturns rather than guide each counterturn directly (Kennedy, J., 1983). Such programs may be different for different insect groups (Bell, W. and Tobin, T., 1982).

In the oriental fruit-moth there is evidence that

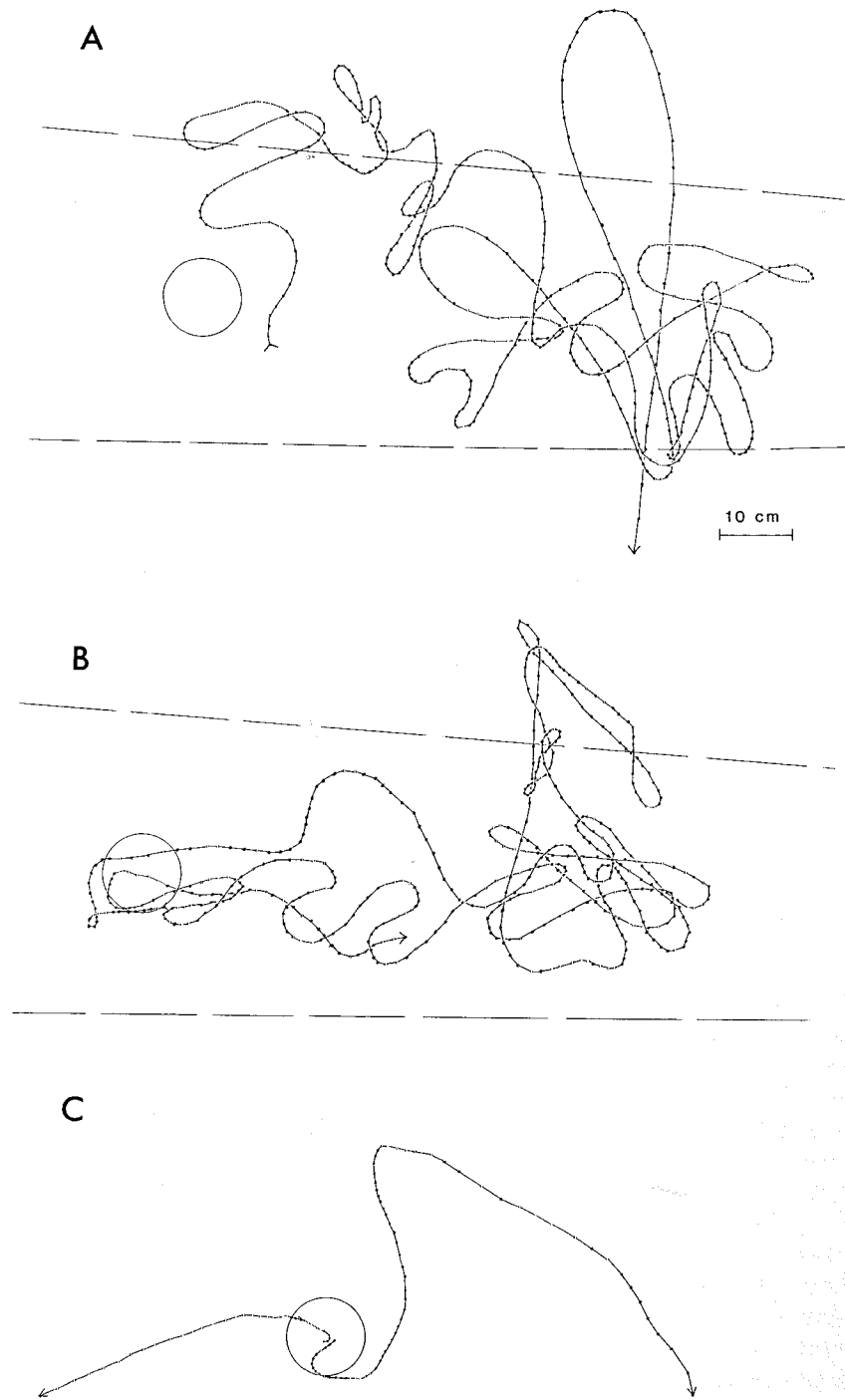


FIG. 14. Top view of video-recorded tracks of *Grapholita molesta* males after they were introduced, in windless conditions, into a stationary pheromone plume (A,B, dashed lines designate plume boundaries) and into clean air (C, tracks of two males). The circle at left represents the top of the screen cone from which males took flight and the black dots are the males' positions each 1/60 s. The presence of pheromone triggers a more sinuous, zig-zagging track than that produced in clean air. (From Baker, T *et al.*, 1984.)

the zig-zagging is not only initiated by the pheromone but its frequency is modulated by the ambient concentration (Kuenen, L. and Baker, T., 1982a). At higher concentrations, angular velocity is higher, making the angular-to-linear velocity ratio greater, and the result is that the tracks are narrower with the more frequent zig-zags confined closer to the plume's axis than at low concentrations (Fig. 12). That the reversals occur as part of an internal program superimposed upon anemotaxis and not steered according to each loss of pheromone at the plume's boundaries was indicated by the fact that, although the theoretical width of the "active space" of the plume increases with higher concentration point sources, the tracks are narrower, not wider. This is the converse of what would be expected if each turn were steered by an excursion outside the active space.

Interestingly when *Grapholita molesta* males are walking, higher concentrations cause angular velocity to increase, just as in flight, but on the ground the males make more severe turns involving long loops instead of the side-to-side oscillations in flight. On the ground males can do this because tarsal contact permits the male to face in any direction while maintaining control over its displacement. While flying in wind the animal must continue to face upwind and turn back and forth across it, or else lose its ability to control its progress.

Recent results with the oriental fruit-moth provide even more evidence for a concentration-modulated zig-zag program independent of plume boundaries. Males were allowed to fly up a plume and they initiated wider, less frequent zig-zags after its removal in wind. But when a relatively uniform cloud of pheromone was then introduced and it reached the moths, the zig-zagging narrowed significantly and this was accompanied by a brief upwind surge (Willis, M. and Baker, T., 1983). Kennedy, J. *et al.* (1980, 1981) had already observed this same effect with *Adoxophyes orana* in a cloud of its pheromone. In both species the males appeared to adapt quickly to the uniform pheromone cloud, and the reversal frequency reverted within several seconds back to a level not different from clean air. Also the upwind displacement reverted to arrestment concurrently with wider casting movements. The conclusion that some form of adaptation had

caused the arrestment is supported by the fact that when a point source plume was introduced into the cloud the males readily flew up it in the typical zig-zag flight (Willis, M. and Baker, T., 1984; Kennedy, J. *et al.*, 1980, 1981) (see next section).

Another indirect reaction to concentration is an orthokinetic one and is integrated with the program of counterturning. Higher concentrations, either in a plume or a cloud, cause the velocity to decrease (Cardé, R. and Hagaman, T., 1979; Kuenen, L. and Baker, T., 1982b). The increase in the angular-to-linear velocity ratio that occurs is accentuated by this reduction in linear velocity that accompanies the greater angular velocity.

Anemotaxis (section 3.3) is integrated with these two mechanisms, essentially by giving polarity to the signal in the form of drift. If a male that has begun flying upwind in a pheromone plume suddenly has the wind reduced to zero, it very often can continue on to the source by continuing to zig-zag up the plume. But examination of the tracks of males that do not reach the source reveals that they often continue to zig-zag while straying off-line (Baker, T. *et al.*, 1984). Merely experiencing wind while sitting or walking in the release cage before take-off, either in or out of the pheromone plume, is not enough to orient the zig-zags in the direction of the pheromone source. The males must experience in-flight drift before the wind is stopped in order for there to be a probability of locating the source higher than 21%, the percentage of success with no pre-exposure to wind at all. These tracks meander around in the general area of the plume in zig-zag fashion, but with few males showing rapid displacement. Once drift has been experienced, the polarity is established, and displacement toward the source is pronounced. Therefore, the pre-wind-lull wind information appears to be gained by flying males only, presumably through optomotor drift compensation, and this accounts for the heightened success at locating the source in zero wind when males are allowed to take off into wind before it is stopped (Baker, T. *et al.*, 1984).

3.5 The function of zig-zagging programs

The integration of the mechanisms discussed above are likely to be used by other flying insects responding to various odors although their programs of

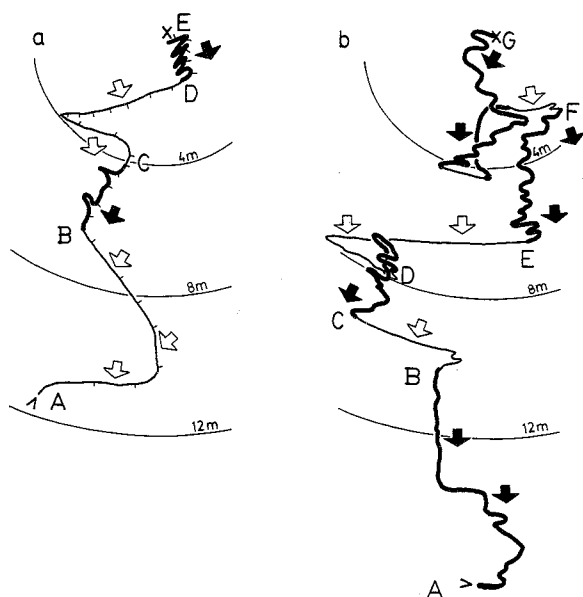


FIG. 15. Tracks, video-recorded from above, of *L. dispar* males flying toward a pheromone source (x) in the field. Thick black line is the male's track when in contact with the pheromone plume, and each solid black arrow is the wind's direction during each period of pheromone contact. Thin black line is the track when the male had lost the pheromone plume, and each hollow arrow denotes the wind's direction during these periods of flight in clean air. Tick marks denote one-second intervals. Note how progress is nearly directly upwind with narrow high-frequency zig-zags when in pheromone contact and nearly always 90° cross-wind with low-frequency zig-zags when pheromone is lost. During these periods in pheromone-free air, if the wind swings sharply (as in A-B and C-D of a and B-C and D-E of b), the 90° cross-wind movement often brings the male back into contact with pheromone at a point much closer to the source than where the pheromone was lost. (From David, C. *et al.*, 1983)

movement may be different (Bell, W. and Tobin, T., 1982). For instance, *Drosophila* flying to banana host odor fly upwind with nearly perfectly straight tracks (David, C., 1982b). Walking insects are known to zig-zag (Kramer, E., 1975) or loop (Baker, T. *et al.*, 1981) in response to increased concentrations of odor. But why do so many flying moths use zig-zagging flight? What is its function?

First, it appears that the reversals allow the animal to scan repeatedly for changes in concentration. The narrow reversals when in high concentration make it more likely that they will be able to "lock on" to a more concentrated plume. The wide reversals when the concentration drops make quick re-location of the plume more likely. All this, of course, is integrated with anemotaxis, and when

concentration is higher the male steers more upwind, allowing less drift and when the concentration drops, nearly 90° cross-wind, allowing greater drift.

The usual benefit of wider reversals is re-location of a lost plume, but a surprising discovery by David, C. *et al.* (1983) has demonstrated another important function of such wide cross-wind zig-zagging or "casting". It was not discovered before this because most moth tracks had been recorded in wind tunnels with non-shifting wind fields. David, C. *et al.* (1983) tracked gypsy moths in the field as they flew in response to pheromone. The location of the plume was marked by soap bubbles. From a previous study (David, C. *et al.*, 1982), it was already known that surprisingly often, regardless of the wind direction near the source, the direction of movement of any parcels of air carrying pheromone nearly always will be on a line pointing away from the source. This is because, regardless of wind shifts, the parcels tend to continue to move in their previously established direction. In this study the male's tracks were decidedly narrow and zig-zagging when apparently in contact with pheromone, and the concurrent displacement was decidedly upwind. When a male flew out of the plume, however, due to a shift in wind direction, a new function for the wide cross-wind casting became apparent. As the clean parcel of wind shifted direction, the ever-widening casts shifted to remain perpendicular to it and the plume was finally re-located, the moth often being much closer to the source upon regaining the plume than when it had lost it (Fig. 15) (David, C. *et al.*, 1983). Thus the higher velocity, lower zig-zag frequency casts at right angles to the wind can themselves contribute to towards-source displacement. This is a previously overlooked advantage of zig-zagging, especially the wide casting type.

Experiments in zero wind also suggest that zig-zagging may function as a more sensitive indicator of wind direction than straight-line flight since, in the latter, lack of transverse image movement across the eyes can have ambiguous meaning: the moth may be in zero wind, or it may be flying directly up or downwind. By continually oscillating left and right, the first onset of wind, or the first shift in its direction, may be detected sooner than in straight-line flight.

FIG. 16
a unif
clean
bottom
comple
provid

3.6 To

Two se
indicat
of odo
cessful
an idea
(1958),
frequer
moths s
lation t
anemot
stimula
progres
J. *et al*
confirm
a differ

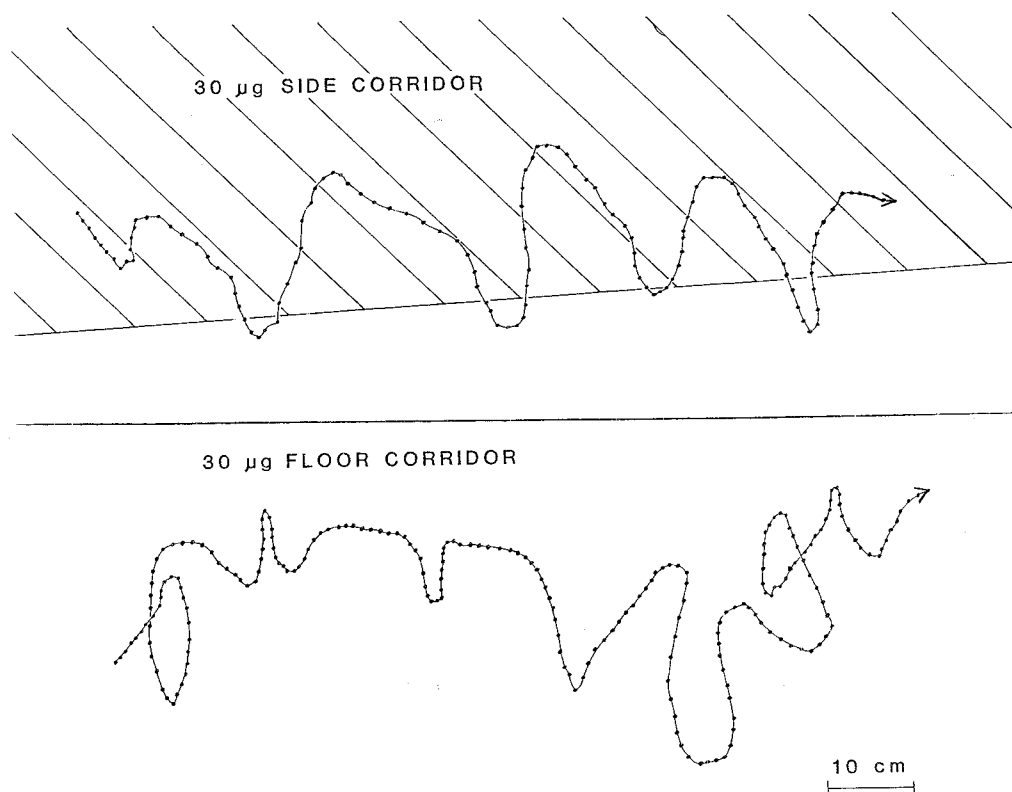


FIG. 16. Tracks, video-recorded from above, of *Grapholita molesta* males flying upwind in a wind tunnel along an edge formed by a uniform cloud of pheromone and clean air. Wind is from the right. *Top*: Male zig-zagging along the vertical edge formed by a clean air-pheromone side corridor. *Bottom*: With the tunnel rotated 90° to make the uniform pheromone corridor occupy the bottom half of the tunnel, a male successfully zig-zags upwind along the horizontal edge to the front of the tunnel. In a tunnel completely permeated with pheromone (not shown) males do not fly upwind, and therefore the phasic pheromone stimulation provided by the mixing of pheromone and clean air along the vertical and horizontal edge of these half-permeated tunnels appears necessary for zig-zagging upwind flight. (From Willis, M. and Baker, T., 1983).

3.6 Tonic vs. phasic pheromone stimulation

Two separate experiments by different groups now indicate that a broken, filamentous airborne plume of odor may be essential for some insects for successful source location. The filaments, contrary to an idea first proposed (later rejected) by Wright, R. (1958), do not seem to guide insects by the frequency of their encounters with them. Rather the moths seem to require a phasic, up-and-down stimulation to maintain the program of zig-zagging plus anemotaxis. They appear to adapt quickly to tonic stimulation by a uniform cloud. The lack of upwind progress in a cloud was first observed by Kennedy, J. *et al.* (1980, 1981) with *Adoxophyes orana* and confirmed by Willis, M. and Baker, T. (1984) with a different species, *G. molesta*. Both Kennedy, J. *et*

al. (1980, 1981) and Willis, M. and Baker, T. (1984) found that males seemed to very often "lock on" to the "edge" formed by clean air next to a side corridor of uniform pheromone. The *G. molesta* very often zig-zagged right up the edge to the upwind end of the tunnel (Fig. 16).

The appearance at first was that the moth was turning back each time it strayed into clear air, but of course from previous studies it was known that the moth was going to reverse its track, clean air or not, as part of its endogenous counterturning program (see section 3). The border likely was not a sharp pheromone-air boundary, but rather a "ragged" edge of pheromone-air filaments produced by small amounts of turbulence. The male would "lock on" and zig-zag upwind along an edge in part because the edge itself was a phasic stimulus,

somewhat like a filamentous plume. This latter explanation received support when the tunnel was turned on its side, producing a corridor of pheromone in the bottom one-third of the tunnel. Males released at the downwind end zig-zagged up the tunnel at the horizontal pheromone air-boundary in a manner similar to when the boundary was vertical (Fig 16). Thus the edge itself seemed likely to be a phasic stimulus, and maintained the counterturning program, although this is not to say that a moth does not augment this stimulation by flying into and out of pheromone contact as it zig-zags upwind along a vertical edge, or a point source plume for that matter. Tonic stimulation, either clean air or constant pheromone, usually results in arrestment

and this happens very quickly. If a phasic stimulus (a point-source-produced plume), is superimposed on this tonic one, attraction up the plume results (Kennedy, J. *et al.*, 1980, 1981; Willis, M. and Baker, T., 1984).

3.7 A new hypothesis

The results of experiments with uniform clouds which produce tonic pheromone stimulation and in-flight arrestment may be informative in explaining why high concentrations of pheromone from a point source sometimes result in in-flight arrestment within or close to the plume. One reason may be that at a certain concentration, as the male flies up

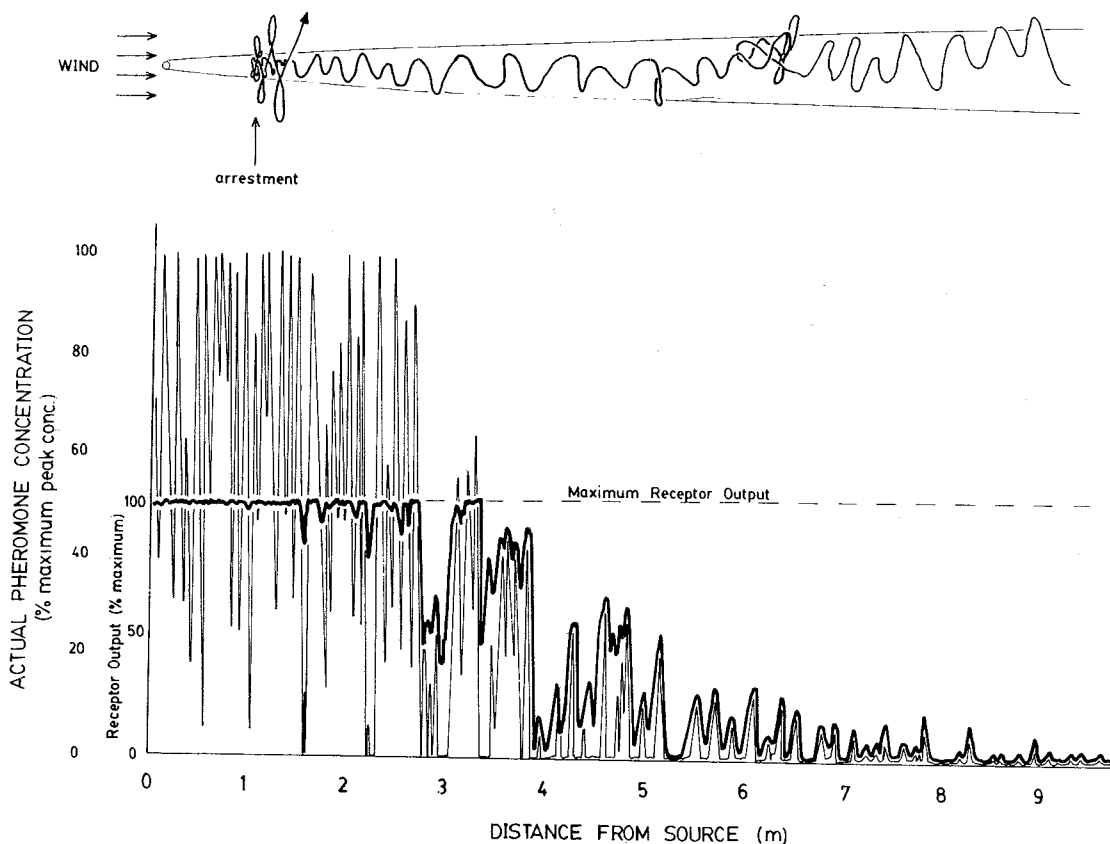


FIG. 17 Hypothetical relationship between instantaneous concentrations along a pheromone plume in the field and receptor output, explaining arrestment of upwind flight in a male approaching a high-concentration pheromone source (*top*). *Bottom*: Thin line represents instantaneous pheromone concentration as a percentage of its maximum peak value along the axis of the plume (modeled after data from Murlis, J. and Jones, C., 1981), thick line represents hypothetical receptor output along same axis. As the male approaches the source its receptor output reaches its maximum even though peak concentrations continue to rise. The male will continue its upwind progress as long as the low concentrations are low enough to cause phasic, up-and-down receptor output at intervals between peak receptor output. Eventually, though, the low concentration "troughs" become too high, receptor output effectively becomes tonic, and arrestment occurs.

the plume toward the source, the stimulation effectively becomes tonic. The sensory system may have reached its capacity and cannot increase its firing rate even if higher concentrations are encountered. Of course higher concentrations *will* be encountered as the male continues to approach the source. The plume's filaments will become more concentrated, but since the maximal neuronal output has been exceeded, the higher concentration cannot be registered on the sensory level. Thus the "highs" of the high-low phasic stimulation eventually cannot neurophysiologically get any higher, but at that distance from the source the "lows" still are low enough that they provide enough of a contrast to the sensory system that the signal is still registered as phasic. With further progress up the plume, however, the lows will continue to increase in concentration, and the difference in the lows and the highs will narrow to such an extent (Fig. 17) at some point near the source that the stimulus will become neurophysiologically tonic. Arrestment then will occur within the plume. The program of zig-zagging that makes the turns very frequent and narrow at high concentrations actually would contribute to the effect because it would prevent the male from making very many wide excursions into clean air to get a lower "low". At some point near the source even the few brief excursions out of the plume would not be enough, and progress is halted.

The idea that a moth flying up a plume is continually combatting habituation goes back a long way (Shorey, H., 1973; Bartell, R., 1977; Bartell, R. and Lawrence, L., 1977). However, this new hypothesis does not invoke habituation as a cause of arrestment, but rather it links receptor saturation and arrestment to temporal aspects of plume stimulation, and implies that some CNS elements need fluctuating stimulation from the receptors in order to continue the proper output that results in upwind zig-zagging flight. It also explains why *G. molesta* males do not habituate as well to pre-exposures to ultra-high concentrations of the natural blend of components as they do to lower concentrations (Linn, C. and Roelofs, W., personal communication). The plumes from an excessively high loading, even 1 m or so away from the source, would likely present a tonic stimulus with a plateau level of highs and lows that are virtually continually high. Thus receptor saturation will have occurred and less

habituation of the CNS will be possible, assuming the CNS neurons, require fluctuating input, for optimal activity. Pulsed pheromone signals much lower (1 min) than produced by a filamentous plume (*ca.* 1 s^{-1}) are known to be more effective than a continuous signal in producing habituation (Bartell, R. and Lawrence, L., 1977; Kuenen, L. and Baker, T., 1981) and reducing the subsequent upwind flight responses of males. It would not be surprising if the moderate concentrations that optimally habituate males during pre-exposure are the ones that produce the optimal levels of phasic ups and downs that increase the habituation of the CNS.

4 CHEMICAL CONTROL OF BEHAVIORS BY MAN

The ever-increasingly intensive study of chemical communication in insects over the past 10 years has resulted in novel and effective methods for the monitoring and suppression of insect populations.

Many behavior-modifying chemicals show promise of being useful for helping in this suppression. Not surprisingly compounds used in mate-finding have so far proven to be the most useful (section 4.3) but those from other behavioral categories have recently been shown to have possibilities in pest management. Two of these categories are host-finding and compounds used in defense of relatives (alarm and oviposition deterrents).

4.1 Host-finding

Work by Nordlund, Lewis, and Jones over the years (see Nordlund, D. *et al.*, 1981) has demonstrated in the laboratory and field how applications of kairomone can help increase parasitization of *Heliothis* eggs by *Trichogramma evanescens* parasites. Lewis, W. *et al.* (1972) found that *Heliothis zea* moth scales stimulated searching by the parasites. Tricosane was identified as the most active hydrocarbon in the scales (Jones, R. *et al.*, 1973).

Initially their work showed that broadcast applications of moth scale extract were better than spot applications at increasing percentage parasitization of the eggs in the lab and field (Lewis, W. *et al.*,

stimulus
posed
results
1. and

clouds
and in-
laining
rom a
stment
may be
lies up

ceptor
r: Thin
plume
vis. As
e. The
ceptor
ceptor

1975). The parasites apparently spent more time in the area of application and "searched" more thoroughly than in untreated areas. Further experiments, however, revealed that spot applications around the eggs, not broadcasts, helped increase percentage parasitization from 18% to greater than 33%. Although this was a significant increase it is hard to say whether use of this compound would be cost-effective in an agricultural system. Another use of tricosane applications has perhaps more promise using the kairomone in conjunction with mass releases of the parasites. If lab-reared *Trichogramma* are exposed to the compound in their laboratory containers just prior to release in the field, percentage parasitization is significantly increased, presumably because the parasite is more likely to be arrested and search in the immediate area of the release rather than immediately fly out of the target area (Gross, H. *et al.*, 1975).

4.2 Defense of relatives

The behavioral effects of the aphid alarm pheromone (*E*)- β -farnesene were discussed earlier (section 2.6). Recently, Wohlers, P. (1981a,b, 1982) demonstrated that the alarm pheromone, (*E*)- β -farnesene, broadcast onto host plants caused alates of *Acyrtosiphon pisum* to probe for a shorter period and to take flight faster than on untreated leaves. They seemed to habituate fairly quickly to the pheromone, however. Nevertheless these results were encouraging for using this compound in the field to reduce feeding. The appealing aspect of this approach to controlling aphid-borne viral infections of plants is that the pheromone conceivably might reduce alightment and "test" probing, which can spread certain viruses quickly among crop plants. Dawson, G. *et al.* (1982) demonstrated a reduction in beet yellow virus transmission by *Myzus persicae*, when (*E*)- β -farnesene derivatives were applied to plants in the laboratory. Although some laboratory behavioral observations dictate caution in using the alarm pheromone (it may increase movement and test probes on plants for some species) (Phelan, P. and Miller, J., 1982), these field trials are encouraging. Another potentially useful way to use alarm pheromone is to apply it just prior to insecticide sprays. It significantly reduces aphid populations compared to insecticide alone, presum-

ably by increasing the movements of aphids and hence their exposure to toxicant (Griffiths, D. and Pickett, J., 1980).

Another class of pheromones that falls into the category of "defense of relatives" is that called "oviposition-detering" pheromone (Prokopy, R., 1981a). Among the many species of *Rhagoletis* flies it is not clear whether the same blend of chemicals is used, but their effectiveness within a species of causing gravid females to move off a fruit without ovipositing has been demonstrated convincingly (Prokopy, R., 1972, 1981b). The blends of compounds have yet to be identified and synthesized for even one species, and for the time being the efficacy of such a synthetic blend at reducing oviposition in fruits must be viewed from the remarkable results of Katsoyannos, B. and Boller, E. (1976, 1980) using naturally deposited pheromone. After laboriously extracting pheromone from the surface of thousands of fruit in which female *Rhagoletis cerasi* had oviposited, the pheromone solution was broadcast-sprayed onto selected cherry trees in an orchard in Switzerland. *R. cerasi* larval damage to fruit on the sprayed trees was reduced by up to 90% over the unsprayed trees. The pattern of application envisaged for commercial control of these flies is one in which the majority of trees in an orchard would be sprayed and selected trees would be left untreated as "trap trees". This is because the internal "drive" to oviposit would otherwise conceivably become great enough to override the deterring effect of ubiquitously applied pheromone (Prokopy, R., 1981b), and the fruits of the unsprayed trees might provide outlets for oviposition that could be easily disposed of by the grower.

4.3 Mate-finding

Pheromones used in mate-finding have proven to be the most effective for pest-management so far, for a variety of reasons. First, because response thresholds are so low and the active spaces so large (see section 2.1), small quantities are extremely potent in eliciting behavioral effects over tens of meters or more. Secondly, these are the most species-specific of the behavior-modifying chemicals. One species can be targeted for control or monitoring with no effect on the rest of the agroecosystem. Also, for monitoring, relatively little

exper
Thir
comp
lowe
insect
are h
phero
popul
(2) ma
disrup
slow-r
The
specie
will no
tive p
thesize
compl
in the
beetle
that t
optimi
to the
the nu
50% (T
peak a
conjun
models
suscept
vae (Ri
1976).
prophecy
of prec
of usin
events -
for a le
relative
ing trap
flights tl
these va
damage
ledge at
levels, es
to chan
Further
damage
research
is entere
needed.
accurate

expertise is required for insect identification. Thirdly, for direct suppression of a population, these compounds work best when population density is lowest, and this nicely complements conventional insecticides which are best used when populations are high. The three main usages of mate-finding pheromones are: (1) monitoring and detection of populations coupled with timed insecticide sprays; (2) mass trapping to reduce populations directly; (3) disruption of mating by broadcast applications of slow-release formulations.

The population fluctuations of so many insect species are monitored by pheromone traps that I will not attempt to review them all. So many effective pheromones have been identified and synthesized that it is now possible to monitor the entire complement of species in a system, as for instance, in the whole array of stored-products moths and beetle pests (Burkholder, W., 1981). Suffice it to say that the timing of insecticide sprays has been optimized by pheromone trapping on many crops to the extent that growers have been able to reduce the numbers of insecticide applications by up to 50% (Madsen, H., 1981). The traps monitor the peak adult flights, and these peaks are used in conjunction with heat-accumulation and computer models to predict the peak occurrence of future susceptible stages, such as emerging first-instar larvae (Riedl, H. and Croft, B., 1974; Riedl, H. *et al.*, 1976). The grower can then abandon the traditional prophylactic, spray-on-schedule approach in favor of precision applications. Undoubtedly this mode of using monitoring traps — for phenological events — will remain as the most widely used one for a long time to come. One reason is that it is relatively easy to obtain reliable data from monitoring traps as to the *relative* peaks and valleys of adult flights throughout a season without having to relate these values to the *absolute* population levels of damage. These would require much more knowledge about the factors affecting absolute capture levels, especially fluctuations in the active space due to changes in the response threshold each day. Furthermore, accurate correlation of physical damage levels with capture levels requires a large research effort. When the economic threshold level is entered in, still more knowledge and research is needed. Of course, even without monitoring traps, accurate characterization of economic thresholds

for most crop systems remains as a major challenge to entomologists.

These problems notwithstanding, some relationships of absolute population levels (or damage) with captures of insects in sex pheromone traps *are* known, and are being utilized at present for control programs. One example is the simple but effective system of Madsen, H. (1981) for the codling moth in apple orchards in British Columbia, Canada. Under conditions in that region, when the capture of males exceeds two per trap in two consecutive weeks, insecticide spraying is called for. Of course, in arriving at these numbers, much research went into determining standard spacing and placement of traps within the trees. Earlier studies (Vakenti, J. and Madsen, H., 1976) had established that one trap per hectare adequately monitored the populations, and problems with accounting for the possible immigration from neighboring orchards had to be addressed. Of course, if the release rate from the lure (in this case rubber vial caps) is reduced due to aging over the course of the season the two per trap threshold may no longer be accurate, as the active space will on average have grown smaller. Therefore, Madsen recommends replacing the lures every 6 weeks. In order for such a treatment threshold to remain accurate, the trap surfaces themselves must remain uniformly sticky throughout the season. Riedl, H. (1980) showed that when more than 20–30 males have been captured in small traps and 50–70 in large traps, the sticky surface must be rejuvenated or replaced in order to keep the capture readings accurate.

The immigration problem addressed by Madsen, H. (1981) for codling moths points out the importance of knowing the drawing range of monitoring traps. Knowledge of the active spaces for different loading and emission rates of lures can provide a way to “tailor” a trap for a particular-sized field or portion of a crop to optimize the sampling area without drawing in males from outside the crop and possibly overestimating the potential damage. This problem was implicated in monitoring the Angoumois grain moth on corn in France (Stockel, J. and Sureau, F., 1981) and addressed by Baker, T. and Roelofs, W. (1981) for the oriental fruit-moth. After measuring the active distances for several lure loading rates, Baker and Roelofs suggested that low loading rates would allow smaller areas to be

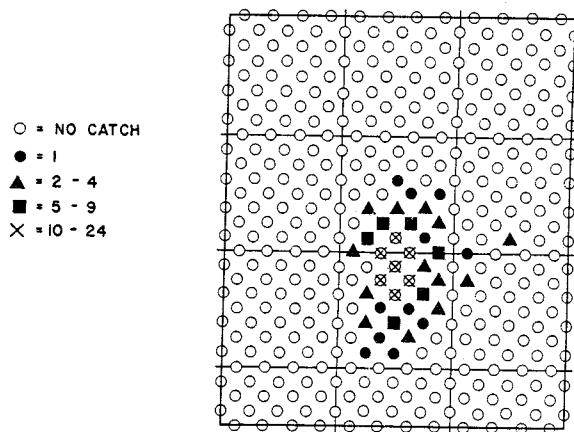


FIG. 18. Spatial distribution of capture of wild gypsy moth males in an isolated infestation in Oakland County, Michigan, 1979. Traps were deployed at 12 per km². Data supplied by the Michigan Department of Agriculture and USDA-PPQ. (From Elkinton, J. and Cardé, R., 1981.)

sampled without fear of drawing in males from outside that area, and larger dosages could be used in the center of larger areas needing monitoring.

A mark-release-recapture technique was used by Elkinton, J. and Cardé, R. (1981) to estimate the absolute population levels that correspond to capture rates of gypsy moth males in sex pheromone monitoring traps. In contrast to many other species, pheromone traps cannot be used to time insecticide sprays at the vulnerable (larval) stages because there is only one generation per year and the adults are on the wing and being monitored after the last larvae have pupated (Elkinton, J. and Cardé, R., 1981). For this species in many states in the USA there is a great need to detect the presence of the moth when population densities are lowest, because in many cases prompt insecticide spraying around the foci of new infestation can eliminate new infestations. Because the females often attach their egg masses to vehicles, new outbreaks often appear spuriously, far from heavily infested areas. In Michigan such local infestations, often traceable to a single egg mass on a vehicle, have been detected by a trapping grid set up by the Michigan Department of Agriculture. Traps were placed 12 per km², and often the pattern of capture pointed clearly to the focus of the infestation (Fig. 18) (Elkinton, J. and Cardé, R., 1981). The mark-release-recapture results showed that about 4% of all males released in a uniform disper-

sion were recaptured. Hence a capture of one male in the Michigan grid should mean on average that there are at least 24 other males in the area.

Mass trapping of populations is a second way of using mate-finding pheromones. Probably the largest mass trapping effort ever was that performed in Norway and Sweden for the suppression of spruce bark beetle, *Ips typographus*, populations in 1979 (Lie, R. and Bakke, A., 1981). Over 600,000 traps baited with the beetle's aggregation pheromone were placed in spruce forests throughout the country. In Sweden over 300,000 traps were deployed. The total beetles captured in both countries was estimated at 4.5 billion, and Lie, R. and Bakke, A. (1981) believe that better trap placement and improvement in trap design would have substantially increased capture rates and the overall efficacy of the program. Nevertheless the program was rated as a success because tree mortality levels were kept the same as the previous year and without the program, large increases in damage had been expected. A very low level of predators (0.2% of the *Ips* capture) were captured and so the program should have minimally affected biological control of the *Ips* beetles.

Lanier, G. (1981) demonstrated that mass trapping *Scolytus multistriatus* beetles with their aggregation pheromone could help reduce the incidence of Dutch elm disease. One area near Syracuse, New York having ca. 20% of the trees infected with Dutch elm disease was treated by placing nearly one pheromone-baited trap per tree. After 5 years the incidence of disease was reduced to 2%. In addition, Lanier, G. (1981) demonstrated that in elm groves not already infested with beetles, a very few pheromone-baited traps can help protect the trees from being infected with the disease. The combination of pheromone traps plus "trap trees" killed by injections of cacodylic acid was shown to be a commercially feasible means of suppressing elm bark beetle populations and reducing the incidence of Dutch elm disease. The trap tree method works because the injection not only kills the brood already present in the tree, but the tree remains attractive to beetles. Incoming beetles bore into the trees and lay eggs, but brood production is reduced by ca. 97% over the levels expected to emerge from living, untreated trees. Thus future infestations are reduced.

Payl
used a
demon
tion o
frontal
dispen
center
adults
infestec
no long
the pop
new, he
because
back or
The t
is as a
locatio
pherom
elsewhe
Roelofs
1977) ar
concept
pletely
in the pe
the field
Mitchell
volves a
release c
devices r
end to al
(Albany
(sandwic
the mole
ally evap
con Cc
pheromo
insectid
and mati
bination
currently
species (C
C., 1982).
pheromoi
sponse th
of the fen
may be a
pheromoi
their wing
wise could

Payne, T. (1981) and Richerson, J. *et al.* (1980) used a modification of the trap tree strategy and demonstrated its potential as a way to halt infestation of the southern pine beetle, *Dendroctonus frontalis*. The species' aggregation pheromone was dispensed in vials on already-attacked trees in the center of a "spot" infestation. Newly emerged adults then tended to be attracted to the already-infested trees to mate and lay eggs. These trees were no longer optimal for rapid population growth, and the population increase was not only reduced but new, healthy trees were kept from being attacked because the beetles that did emerge were re-directed back onto the old, weakened trees.

The third major use of mate-finding pheromones is as a broadcast application to disrupt mate-location and mating. This possible use of pheromones has been examined thoroughly elsewhere (Gaston, L. *et al.*, 1967; Cardé, R., 1976; Roelofs, W. and Cardé, R., 1977; Shorey, H., 1974, 1977) and so I will not go into a lengthy review. The concept has been shown to work repeatedly in completely preventing location of females, reduction in the percentage of mated females recovered from the field, and reduction in damage to crops (see Mitchell, E., 1981). The general methodology involves applying the pheromone formulated in slow-release dispensers to the crop. The slow-release devices may be: (1) tiny hollow fibers sealed at one end to allow slow volatilization out of the open end (Albany International); (2) plastic laminated flakes (sandwiches) having a central pheromone reservoir, the molecules migrating through the plastic to finally evaporate slowly from the flake's surface (Hercon Corp.); (3) micro-capsules containing pheromone that can be sprayed from conventional insecticide sprayers. The disruption of mate-finding and mating is apparently accomplished by a combination of at least two mechanisms that work concurrently to one degree or another depending on the species (Cardé, R., 1981; Bartell, R., 1982; Sanders, C., 1982). The overall atmospheric concentration of pheromone may habituate males, raising their response threshold, thereby reducing the active space of the female-emitted pheromone. Secondly, males may be attracted to the point sources of synthetic pheromone and spend time walking and fanning their wings around them, wasting time that otherwise could be spent locating a female. These males

may also habituate as a result of the high concentrations experienced at these sources. Bartell, R. (1982) has described three other possible mechanisms that may contribute to disruption of mate location in other situations.

There have been a large number of demonstrations of reduced damage in crops treated with disruptant formulations. For instance, aerial applications of slow-release formulation of the sex pheromone of the western pine shoot borer *Eucosma sonomana* resulted in 67–88% reduction in damage from this pest (Sower, L. *et al.*, 1981).

The mating disruption technique has been used successfully commercially on cotton over the last 5 years to control a major pest, the pink bollworm, *Pectinophora gossypiella*. In 1980 and 1981 over 100,000 acres of cotton were treated with the disruptant in the southwestern United States. Beginning when the cotton is in a pre-bloom state called "pin-square" up until the first bloom, growers aerially apply the pheromone every 10–14 days. Most often the slow-release formulation has been Nomate[®], the hollow fibers (Albany International), but in 1982 20% of the applications were with the laminated flakes Disrupt[®] (Hercon Corp.). Years of data have demonstrated that mate-location and mating are reduced 90–100% in average population densities (Shorey, H. *et al.*, 1976; Brooks, T. *et al.*, 1979; Doane, C. and Brooks, T., 1981) and that damage can be maintained at commercially acceptable levels while costing about the same as conventional insecticides (Gaston, L. *et al.*, 1977; Brooks, T. *et al.*, 1979; Doane, C. and Brooks, T., 1981).

Growers' acceptance of the technique has been good and the US acreage applied with disruptant has grown from 20,000 in 1978 to 40,000 in 1979, to over 120,000 in 1982. Many growers in the Imperial Valley of California were so satisfied with their pheromone programs that they organized a mandatory treatment program in 1982 that required that all growers in the valley apply at least four treatments of pheromone to their cotton acreage early in the season. The program was successful at increasing yields compared to the year before and to nearby valleys not on the program, and avoiding a crippling whitefly problem that had occurred the previous year apparently due to overspraying of pyrethroids. Further refinements to the technique should help overcome some failures that are

experienced each year by at least a few growers. Usually these can be traced to: (1) the grower waiting too long to put on the first application, hence much mating has already occurred; (2) the grower attempts to reduce the amount applied or to increase the length of time between applications; (3) the grower attempts to continue the application under population pressures that are too high. This last point is important because under commercial conditions later in the season population pressures can begin to increase to levels where the disruptant does not work as well, and at this point the early season pheromone program should be dropped and replaced with insecticide sprays. But the early treatment with disruptants will have served its purpose. Predators and parasites are preserved that keep *Heliothis* sp. and other pests under control because insecticide spraying is delayed while the disruptant does its job. Monitoring with pink bollworm pheromone traps is an important part of a disruptant program, because even in early season if nightly captures of males in pheromone-treated fields exceeds three or four per trap (usually it is zero) the population density is considered too high for effective disruption.

Clearly pheromone disruption is a tool that fits in well with cotton pest management. It works best when *P. gossypiella* populations are lowest, in the early season, and this is precisely the time when beneficial insects should be preserved and allowed to increase in number. The value of the behavior-modifying chemical is, in this case, much greater when measured in the context of the *entire* pest management scheme than might have been anticipated from its isolated effects of reducing mating and pink bollworm damage.

Recently growers have added small amounts (1/50 of normal rate) of pyrethroid to the formulation. The pyrethroid is contained in the polybutene sticker that makes the aerially applied hollow fibers or flakes adhere to the cotton leaves. Many growers maintain that this "attracticide" technique allows them to reduce the absolute amount of pheromone applied while maintaining the same level of pink bollworm control. The males attracted to the pheromone point sources presumably pick up a lethal dose of insecticide that takes them out of the mating population for good. Whether there may also be sub-lethal behavioral

effects that help in reducing mate location remains to be seen, and the efficacy of the attracticide technique needs further examination. It looks promising, and populations of beneficial insects are not reduced (George Butler, personal communication; Las, A. *et al.*, 1982). Obviously if more pheromones are to be used in the attracticide mode it is even more imperative that the optimal natural blend of components be formulated because males must be attracted all the way to a point source to contact the toxin. Here the other mode of action of disruption, area-wide habituation, would be counterproductive, and for many species dosages and application rates of an optimal blend might need to be altered to favor attraction to such point sources at the expense of atmospheric permeation and habituation. Or, perhaps those species that are especially susceptible to area-wide habituation — possibly because they have ultra-low emission rates and male thresholds — may not need to have insecticides added to the formulation because disruption may be easier for these species.

The commercial use of pink bollworm pheromone over several successive years in Arizona and California brings up the question of whether intensive use could lead to "resistance" to the pheromone in pink bollworm populations. The resistance might be manifested as increased emission rates by females or changes in the ratios of the two sex pheromone components away from the ratio of applied synthetic components (Cardé, R., 1976). In the pink bollworm there is evidence that if there were females in the population that could emit higher amounts of pheromone, they could overcome the effect of the disruptant, because higher release rates of synthetic pheromone in sticky traps resulted in significantly more captures of males in a disruptant-treated field (Doane, C. and Brooks, T., 1981). Additionally behavioral "resistance" might take the form of increased tendency for dispersal by calling females that are unsuccessful in attracting a male in disruptant-treated fields. Such females may be more likely to reach untreated fields or borders where males can locate them and mate. Then the females could return to the pheromone-treated fields to lay eggs. An initial study examining populations of pink bollworms from pheromone-treated and conventionally treated fields found no evidence so far that resistance has developed in the

pheromone
et al.
Th
beha
supp
not
ogist
mark
cally
contr
that
biolo
doing
not b
pany
profit
the co
"faile
beha
the p
may s
for it
lation
rator
nique
even
modif
econo

ALCOCK
Sun
ALCOCK
bee
ALEXANI
muf
AMOORE
odo
ANESHAN
Bioc
(Bra
BAKER,
patt
BAKER, T
al fr
side
pher
BAKER, T
beha
(Lep
BAKER, T
flyin
216,
BAKER, T
male
comj

pheromone emission rates and ratios (Haynes, K. *et al.*, 1984).

The first successful commercial experience with a behavior-modifying chemical used for population suppression points out some economic problems not usually considered by entomologists and biologists. The final test of the technology is in the market-place, and here a technique that is biologically powerful and proven to be efficacious in controlling populations is now buffeted by forces that have nothing to do with whether or not it works biologically. The technique may be successful in doing what it is supposed to but may be dropped, not because it does not make a profit for the company, but because it does not make *enough* of a profit. It may fit into pest management but not into the company's financial projections and it will have "failed". Conversely another product containing behavior-modifying compounds (such as many of the pheromone traps being sold to homeowners) may sell extremely well but be essentially worthless for its advertised purpose of suppressing populations of a given species. And so as more "bio-rational" behavior-modifying chemicals and techniques reach the commercial level, it will become even more clear the most powerful behavioral modifier is money, and it is transported by shifting economic winds.

REFERENCES

- ALCOCK, J (1979) *Animal Behavior* 2nd edition Sinauer Associates Sunderland, Massachusetts
- ALCOCK, J (1982) Natural selection and communication among bark beetles. *Fla. Ent.* 65, 17-32
- ALEXANDER, R. D (1962) Evolutionary change in cricket acoustical communication. *Evolution* 16, 443-467
- AMOORE, J. E., PALMIERI, G and WANKE, E (1967) Molecular shape and odour: pattern analysis by PAPA. *Nature* 216, 1084-1087
- ANESHANSLEY, D., EISNER, T., WIDOM, J. M and WIDOM, B (1969) Biochemistry at 100°C: the explosive discharge of bombardier beetles (*Brachinus*). *Science* 165, 61-63
- BAKER, T. C (1983) Variations in male oriental fruit moth courtship patterns due to male competition. *Experientia* 39, 112-114
- BAKER, T. C and CARDÉ, R. T (1979a) Courtship behavior of the Oriental fruit moth (*Grapholitha molesta*): experimental analysis and consideration of the role of sexual selection in the evolution of courtship pheromones in the Lepidoptera. *Ann. Ent. Soc. Amer.* 72, 173-188
- BAKER, T. C and CARDÉ, R. T (1979b) Analysis of pheromone-mediated behaviors in male *Grapholitha molesta*, the Oriental fruit moth (Lepidoptera: Tortricidae). *Environ. Ent.* 8: 956-968
- BAKER, T. C and KUENEN, L. P. S (1982) Pheromone source location by flying moths: A supplementary non-anemotactic mechanism. *Science* 216, 424-427
- BAKER, T. C and ROELOFS, W (1976) Electroantennogram responses of the male moth, *Argyrotaenia velutinana*, to mixtures of sex pheromone components of the female. *J. Insect Physiol.* 22, 1357-1364
- BAKER, T. C and ROELOFS, W. L (1981) Initiation and termination of Oriental fruit moth male response to pheromone concentrations in the field. *Environ. Ent.* 10, 211-218
- BAKER, T. C., CARDÉ, R. T and MILLER, J. R (1980) Oriental fruit moth pheromone component emission rates measured after collection by glass-surface adsorption. *J. Chem. Ecol.* 6, 749-758
- BAKER, T. C., CARDÉ, R. T and ROELOFS, W. L (1976) Electroantennogram responses of the male moth, *Argyrotaenia velutinana*, to mixtures of sex pheromone components of the female. *J. Chem. Ecol.* 2, 333-352
- BAKER, T. C., MEYER, W. and ROELOFS, W. L (1981) Sex pheromone dosage and blend specificity of response by Oriental fruit moth males. *Ent. Exp. et Appl.* 30, 269-279
- BAKER, T. C., NISHIDA, R. and ROELOFS, W. L (1982) Close-range attraction of female oriental fruit moths to herbal scent of male hairpencils. *Science* 214, 1359-1361
- BAKER, T. C., WILLIS, M. A. and PHELAN, P. L (1984) Pre-wind-lull optomotor anemotaxis contributes to successful pheromone source location by flying moths. *Physiol. Ent.* (In preparation.)
- BAKKE, A. and KVAMME, T. (1981) Kairomone response in *Thanasimus* predators to pheromone components of *Ips typographus*. *J. Chem. Ecol.* 7, 305-312
- BARTELL, R. J. (1977) Behavioral responses of Lepidoptera to pheromones. In *Chemical Control of Insect Behavior, Theory and Application* Edited by H. H. Shorey and J. J. McKelvey. Pages 201-213. Wiley-Interscience, New York
- BARTELL, R. J. (1982) Mechanisms of communication disruption by pheromone in the control of Lepidoptera: a review. *Physiol. Ent.* 7, 353-364
- BARTELL, R. J. and LAWRENCE, L. A. (1977) Reduction of responsiveness of male apple moths, *Epiphyas postvittana*, to sex pheromone following pulsed pheromonal exposure. *Physiol. Ent.* 2, 1-6
- BEDARD, W. D., WOOD, W. L., TILDEN, P. E., LINDAHL, K. Q., JI, SILVERSTEIN, R. M. and RODIN, J. O. (1980) Field responses of the western pine beetle and one of its predators to host- and beetle-produced compounds. *J. Chem. Ecol.* 6, 625-641
- BELL, W. J. and KRAMER, E. (1979) Search and anemotactic orientation in cockroaches. *J. Insect Physiol.* 25, 631-640
- BELL, W. J. and KRAMER, E. (1980) Sex pheromone stimulated orientation responses by the American cockroach on a servosphere apparatus. *J. Chem. Ecol.* 6, 287-295
- BELL, W. J. and SCHAL, C. (1980) Patterns of turning in courtship orientation of the male German cockroach. *Anim. Behav.* 28, 86-94
- BELL, W. J. and TOBIN, T. (1981) Orientation to sex pheromone in the American cockroach: analysis of chemo-orientation mechanisms. *J. Ins. Physiol.* 27, 501-508
- BELL, W. J. and TOBIN, T. (1982) Chemo-orientation. *Biol. Rev.* 57, 219-260
- BENNET-CLARK, H. C. (1970) The mechanism and efficiency of sound production in mole crickets. *J. Exp. Biol.* 52, 619-652
- BENNET-CLARK, H. C., LEROY, Y. and TSACAS, L. (1980) Species and sex-specific songs and courtship behaviour in the genus *Zaprionus* (Diptera: Drosophilidae). *Anim. Behav.* 28, 230-255
- BIRCH, M. C. (1970) Pre-courtship uses of abdominal brushes by the nocturnal moth, *Phlogophora meticulosa* (L.) (Lepidoptera: Noctuidae). *Anim. Behav.* 18, 310-316
- BIRCH, M. C. (1974) Aphrodisiac pheromones in insects. In *Pheromones*. Edited by M. C. Birch. Pages 115-134. North Holland, Amsterdam.
- BIOSTAD, L. B., and ROELOFS, W. L. (1983) Sex pheromone biosynthesis in *Trichoplusia ni*: key steps involve delta-11 desaturation and chain shortening. *Science* 220, 1387-1389
- BIOSTAD, L. B., WOLF, W. A. and ROELOFS, W. L. (1981) Total lipid analysis of the sex pheromone gland of the redbanded leafroller moth *Argyrotaenia velutinana*, with reference to pheromone biosynthesis. *Insect Biochem.* 11, 73-80
- BLUM, M. S. (1974) Pheromonal sociality in the Hymenoptera. In *Pheromones*. Edited by M. C. Birch. Pages 222-249. Elsevier, New York
- BLUM, M. S. (1979) Hymenopterous pheromones: optimizing the specificity and acuity of the signal. In *Chemical Ecology. Odor Communication in Animals*. Edited by F. J. Ritter. Pages 201-211. Elsevier/North-Holland, Amsterdam

- BLUM, M. S., PADAVONI, F. and AMANIE, E. (1968) Alkanones and terpenes in the mandibular glands of *Atta* species (Hymenoptera: Formicidae). *Comp Biochem Physiol* 26, 291-299
- BOECKH, J. and BOECKH, V. (1979) Threshold and odor specificity of pheromone-sensitive neurons in the deutocerebrum of *Antheraea pernyi* and *A. polyphemus* (Saturniidae). *J Comp Physiol* 132, 235-242
- BOGGS, C. L. and GILBERT, L. E. (1979) Male contribution to egg production in butterflies: first evidence for transfer of nutrients at mating. *Science* 206, 83-84
- BOPPRÉ, M. (1978) Chemical communication, plant relationships, and mimicry in the evolution of danaid butterflies. *Ent Exp App* 24, 264-277
- BOPPRÉ, M. (1981) Adult Lepidoptera "feeding" at withered *Heliotropium* plants (Boraginaceae) in East Africa. *Ecol Ent* 6, 449-452
- BOSSERT, W. H. and WILSON, E. O. (1963) The analysis of olfactory communication among animals. *J Theor Biol* 5, 443-469
- BROOKS, T. W., DOANE, C. C. and STATEN, R. T. (1979) Experience with the first commercial pheromone communication disruption for suppression of an agricultural pest. In *Chemical Ecology Odour Communication in Animals*. Pages 375-388. Edited by F. J. Ritter. Elsevier/North-Holland, Amsterdam
- BROWN, J. L. (1975) *The Evolution of Behavior*, 1st edition. W. W. Norton, New York
- BROWER, L., VAN ZANDT BROWER, J. and CRANSTON, F. P. (1965) Courtship behavior of the queen butterfly, *Danaus gilippus berenice* (Cramer). *Zoologica* 50, 1-39
- BURKHOLDER, W. E. (1981) Biomonitoring for stored-product insects. In *Management of Insect Pests with Semiochemicals*. Edited by E. R. Mitchell. Pages 29-40. Plenum, New York
- CADE, W. (1981) Alternative male strategies: genetic differences in crickets. *Science* 212, 563-564
- CALLAHAN, P. S. (1975) Insect antennae with special reference to the mechanism of scent detection and the evolution of the sensilla. *Int J Insect Morph Embryol* 4, 381-430
- CAMMAERTS, M.-C. (1980) Systemes d'approvisionnement chez *Myrmica scabrinodis* (Formicidae). *Insect Soc* 27, 328-342
- CARDÉ, R. T. (1976) Utilization of pheromones in the population management of moth pests. *Environ Health Persp* 133-144
- CARDÉ, R. T. (1981) Disruption of long-distance pheromone communication in the oriental fruit moth: camouflaging the natural aerial trails from females? In *Management of Insect Pests with Semiochemicals*. Edited by E. R. Mitchell. Pages 385-398. Plenum, New York
- CARDÉ, R. T. and HAGAMAN, T. E. (1979) Behavioral responses of the gypsy moth in a wind tunnel to air-borne enantiomers of disparlure. *Environ Ent* 8, 475-484
- CARDÉ, R. T. and ROELOFS, W. L. (1973) Temperature modification of male sex pheromone response and factors affecting female calling in *Holomelina immaculata* (Lepidoptera: Arctiidae). *Canad Ent* 105, 1505-1512
- CARDÉ, R. T. and ROELOFS, W. L. (1977) Attraction of redbanded leafroller moths, *Agyrotaenta velutinana*, to blends of (Z) and (E)-11-tridecenyl acetates. *J Chem Ecol* 3, 143-149
- CARDÉ, R. T., BAKER, T. C. and ROELOFS, W. L. (1976) Sex attractant responses of male Oriental fruit moths to a range of component ratios: pheromone polymorphism? *Experientia* 32, 1406-1407
- CARDÉ, R. T., CARDÉ, A. M., HILL, A. S. and ROELOFS, W. L. (1977) Sex pheromone specificity as a reproductive isolating mechanism among the sibling species *Archips argyrosplis* and *A. mortuanus* and other sympatric tortricine moths (Lepidoptera: Tortricidae). *J Chem Ecol* 3, 71-84
- CARDÉ, R. T., DOANE, C. C., GRANETT, J., HILL, A. S., KOCHANSKY, J. and ROELOFS, W. L. (1977) Attractancy of racemic disparlure and certain analogues to male gypsy moths and the effects of trap placement. *Environ Ent* 6, 765-767
- CHAPMAN, O. L., KLUN, J. A., MATTES, K. C., SHERIDAN, R. S. and MANI, S. (1978) Chemoreceptors in Lepidoptera: stereochemical differentiation of dual receptors for an achiral pheromone. *Science* 201, 926-928
- CLEARWATER, J. R. (1972) Chemistry and function of a pheromone produced by the male of the southern armyworm *Pseudaletia separata*. *J Insect Physiol* 18, 781-789
- CONNER, W. E., EISNER, T., VANDER MEER, R. K., GUERRERO, A., GHIRINGELLI, D. and MEINWALD, J. (1980) Sex attractant of an arctiid moth (*Utethesia ornatrix*): a pulsed chemical signal. *Behav Ecol Sociobiol* 7, 55-63
- CONNER, W. E., EISNER, T., VANDER MEER, R. K., GUERRERO, A. and MEINWALD, J. (1981) Precopulatory sexual interaction in an arctiid moth (*Utethesia ornatrix*): role of a pheromone derived from dietary alkaloids. *Behav Ecol Sociobiol* 9, 227-235
- DAVID, C. T. (1982a) Competition between fixed and moving stripes in the control of orientation by flying *Drosophila*. *Physiol Ent* 7, 151-156
- DAVID, C. T. (1982b) Compensation for height in the control of ground-speed by *Drosophila* in a new, "barber's pole" wind tunnel. *J Comp Physiol* 147, 485-493
- DAVID, C. T., KENNEDY, J. S. and LUDLOW, A. R. (1983) Finding of a sex pheromone source by gypsy moths released in the field. *Nature* 303, 804-806
- DAVID, C. T., KENNEDY, J. S., LUDLOW, A. R., PERRY, J. N. and WALL, C. (1982) A re-appraisal of insect flight towards a point source of wind-borne odor. *J Chem Ecol* 8, 1207-1215
- DAWKINS, R. (1976) *The Selfish Gene*. Oxford University Press, New York
- DAWSON, G. W., GIBSON, R. W., GRIFFITHS, D. C., PICKETT, J. A., RICE, A. D. and WOODCOCK, C. M. (1982) Aphid alarm pheromone derivatives affecting settling and transmission of plant viruses. *J Chem Ecol* 8, 1377-1388
- DAYKIN, P. N. and KELLOGG, F. E. (1965) A two-air-stream observation chamber for studying responses of flying insects. *Canad Ent* 97, 264-268
- DAYKIN, P. N., KELLOGG, F. E. and WRIGHT, R. H. (1965) Host-finding and repulsion of *Aedes aegypti*. *Canad Ent* 97, 239-263
- DETHIER, V. G., BARTON-BROWN, L. and SMITH, C. N. (1960) The designation of chemicals in terms of the responses they elicit from insects. *J Econ Ent* 53, 134-136
- DINDONIS, L. L. and MILLER, J. R. (1980a) Host-finding responses of onion and seedcorn flies to healthy and decomposing onions and several synthetic constituents of onion. *Environ Ent* 9, 467-472
- DINDONIS, L. L. and MILLER, J. R. (1980b) Host-finding behavior of onion flies *Hylemya antiqua*. *Environ Ent* 9, 769-772
- DINDONIS, L. L. and MILLER, J. R. (1981) Onion fly and little house fly host finding selectively mediated by decomposing onion and microbial volatiles. *J Chem Ecol* 7, 419-426
- DOANE, C. C. and BROOKS, T. W. (1981) Research and development of pheromones for insect control with emphasis on the pink bollworm. In *Management of Insect Pests with Semiochemicals*. Edited by E. R. Mitchell. Pages 285-303. Plenum, New York
- DODSON, C. H., DRESSLER, R. L., HILLS, H. G., ADAMS, R. M. and WILLIAMS, N. H. (1969) Biologically active compounds in orchid fragrances. *Science* 164, 1243-1249
- DRESSLER, R. L. (1968) Pollination by euglossine bees. *Evolution* 22, 202-210
- DU, J. W. and ROELOFS, W. L. (1982) Artificial selection for new pheromone strains of redbanded leafroller moths. National Meeting, Ent Soc. Am., Toronto
- EBERHARD, W. G. (1977) Aggressive chemical mimicry by a bolas spider. *Science* 198, 1173-1175
- EDGAR, J. A. (1975) Danainae (Lep.) and 1,2-dehydropyrrrolizidine alkaloid-containing plants—with reference to observations made in the New Hebrides. *Phil Trans Roy Soc Lond B*, 272, 467-476
- EDGAR, J. A., CULVENOR, C. C. J. and ROBINSON, G. S. (1973) Hairpencil dihydropyrrrolizidine derivatives of Danainae from the New Hebrides. *J Aust Ent Soc* 12, 144-150
- EDGAR, J. A., CULVENOR, C. C. J. and SMITH, L. W. (1971) Dihydropyrrrolizidine derivatives in the "hairpencil" secretions of danaid butterflies. *Experientia* 27, 761-762
- EDGAR, J. A., CULVENOR, C. C. J. and PLISKE, T. E. (1976) Isolation of a lactone, structurally related to the esterifying acids of pyrrolizidine alkaloids, from the coastal fringes of male ithomiinae. *J Chem Ecol* 2, 263-270
- EHRlich, P. R. and RAVEN, P. H. (1964) Butterflies and plants: a study in co-evolution. *Evolution* 18, 586-608
- EISNER, T. (1958) The protective role of the spray mechanism of the bombardier beetle, *Brachinus ballistarius* Lec. *J Insect Physiol* 2, 215-220

- SHIRIN, D. (1970) Defensive spray of a phasmid insect. *Science* 148, 966-968.
- EISNER, T. (1970) Chemical defense against predation in arthropods. In *Chemical Ecology* Edited by E. Sondheimer and J. B. Simeone Pages 157-217 Academic Press New York.
- EISNER, T. (1972) Chemical ecology: on arthropods and how they live as chemists. *Verhandl. Deuts. Zool. Gesell.* 65, 123-137.
- EISNER, T. and MEINWALD, J. (1966) Defensive secretions of arthropods. *Science* 153, 1341-1350.
- EISNER, T., KRISTON, I. and ANESHANSLEY, D. J. (1976) Defensive behavior of a termite. *Behav. Ecol. Sociobiol.* 1, 83-125.
- EISNER, T., HICKS, K., EISNER, M. and ROBSON, D. S. (1978) "Wolf-in-sheep's clothing" strategy of a predaceous insect larva. *Science* 199, 790-794.
- EISNER, T., MEINWALD, J., MONRO, A. and GHENT, R. (1961) Defense mechanisms of arthropods. I. The composition and function of the spray of the whipscorpion, *Mastigoproctus giganteus* (Lucas) (Arachnida, Pedipalpida). *J. Insect Physiol.* 6, 272-298.
- EISNER, T. E., JOHNESSEE, J. S., CARREL, J., HENDRY, L. B. and MEINWALD, J. (1974) Defensive use by an insect of a plant resin. *Science* 184, 996-999.
- ELKINTON, J. S. and CARDÉ, R. T. (1981) The use of pheromone traps to monitor distribution and population trends of the gypsy moth. In *Management of Insect Pests with Semiochemicals* Edited by E. R. Mitchell Pages 41-55 Plenum New York.
- ELKINTON, J. S. and CARDÉ, R. T. (1983) Evaluation of time-average dispersion models for estimating pheromone concentration in a deciduous forest. *J. Chem. Ecol.* (In press).
- EVANS, H. E. (1977) Extrinsic vs. intrinsic factors in the evolution of insect sociality. *Bioscience* 27, 613-617.
- EWING, A. W. (1979) Complex courtship songs in the *Drosophila funebris* species group: escape from an evolutionary bottleneck. *Anim. Behav.* 27, 343-349.
- FARKAS, S. R. and SHOREY, H. H. (1972) Chemical trail-following by flying insects: a mechanism for orientation to a distant odor source. *Science* 178, 67-68.
- FEENEY, P. (1976) Plant apparency and chemical defense. *Recent Adv. Phytochem.* 10, 1-40.
- FEIN, B. I., REISSIG, W. H. and ROELOFS, W. L. (1982) Identification of apple volatiles attractive to the apple maggot *Rhagoletis pomonella*. *J. Chem. Ecol.* 8, 1473-1487.
- FISHER, R. A. (1958) *The Genetical Theory of Natural Selection*, 2nd revised edition. Dover, New York.
- FITZGERALD, T. D. and EDGERLY, J. S. (1979) Specificity of trail markers of forest and Eastern tent caterpillars. *J. Chem. Ecol.* 5, 565-574.
- FITZGERALD, T. D. and GALLAGHER, E. M. (1976) A chemical trail factor from the silk of the Eastern tent caterpillar *Malacosoma americanum* (Lepidoptera: Lasiocampidae). *J. Chem. Ecol.* 2, 187-193.
- FORREST, T. G. (1982) Acoustic communication and baffling behaviors of crickets. *Fla. Ent.* 65, 33-44.
- FRAENKEL, G. S. and GUNN, D. L. (1940) *The Orientation of Animals*, revised edition, 1961. Dover, New York.
- GASTON, L., SHOREY, H. H. and SAARIO, C. (1967) Insect population control by the use of sex pheromones to inhibit orientation between sexes. *Nature* 213, 1155.
- GASTON, L. K., KAAE, R. S., SHOREY, H. H. and SELLERS, D. (1977) Controlling the pink bollworm by disrupting sex pheromone communication between adult moths. *Science* 196, 904-905.
- GEORGE, J. A. and MULLINS, J. (1980) Hairpencils on males of the oriental fruit moth, *Grapholitha molesta* (Busck) (Lepidoptera: Tortricidae). *Proc. Ent. Soc. Ont.* 111, 21-31.
- GOFF, A. M. and NAULI, L. R. (1974) Aphid cornicle secretions ineffective against attack by parasitoid wasps. *Environ. Ent.* 3, 565-566.
- GOULD, J. L. (1975) Honey bee recruitment: The dance-language controversy. *Science* 189, 685-693.
- GOULD, J. L. (1982) *Ethology: The Mechanisms and Evolution of Behavior* 1st edition. W. W. Norton, New York.
- GRANT, G. G. (1970) Evidence for a male sex pheromone in the noctuid *Trichoplusia ni*. *Nature* 227, 1345-1346.
- GRANT, G. G. (1971) Electroantennogram responses to the scent brush secretions of several male moths. *Ann. Ent. Soc. Amer.* 64, 1428-1431.
- GRANT, G. G. (1976) Courtship behavior of a phycitid moth, *Vitula edmondsae*. *Ann. Ent. Soc. Amer.* 69, 445-449.
- GRANT, G. G. (1978) Morphology of the presumed male pheromone glands on the forewings of tortricid and phycitid moths. *Ann. Ent. Soc. Amer.* 71, 423-431.
- GRANT, G. G. and BRADY, U. E. (1975) Courtship behavior of phycitid moths. I. Comparison of *Plodia interpunctella* and *Cadra cautella* and role of male scent glands. *Canad. J. Zool.* 53, 813-826.
- GRANT, G. G., SMITHWICK, E. B. and BRADY, U. E. (1975) Courtship behavior of phycitid moths. II. Behavioral and pheromonal isolation of *Plodia interpunctella* and *Cadra cautella* in the laboratory.
- GREENFIELD, M. D. (1981) Moth sex pheromones: an evolutionary perspective. *Florida Ent.* 64, 4-17.
- GRIFFITHS, D. C. and PICKETT, J. A. (1980) A potential application of aphid alarm pheromones. *Ent. Exp. Appl.* 27, 199-201.
- GROSS, H. R. JR., LEWIS, W. J. and JONES, R. L. (1975) Kairomones and their use for management of entomophagous insects. III. Stimulation of *Trichogramma achaeae*, *T. pretiosum*, and *Microplitis croceipes* with host-seeking stimuli at time of release to improve their efficiency. *J. Chem. Ecol.* 1, 431-438.
- GRULA, J. W., MCCHESENEY, J. D. and TAYLOR, O. R., JR. (1980) Aphrodisiac pheromones of the sulfur butterflies *Colias eurytheme* and *C. philodice* (Lepidoptera: Pieridae). *J. Chem. Ecol.* 6, 241-256.
- HAGSTRUM, D. W. and DAVIS, L. R., JR. (1982) Mate-seeking behaviour and reduced mating by *Ephesia cautella* (Walker) in a sex pheromone-permeated atmosphere. *J. Chem. Ecol.* 8, 507-515.
- HAMILTON, W. D. (1964) The genetical theory of social behaviour (I and II). *J. Theor. Biol.* 7, 1-16, 17-32.
- HANGARTNER, W. (1967) Spezifität und Inaktivierung des Spurpheromons von *Lasius fuliginosus* Latr. und Orientierung der Arbeiterinnen im Duftfeld. *Zeits. Vergh. Phys.* 57, 103-136.
- HANGARTNER, W. (1969) Structure and variability of the individual odor trail in *Solenopsis geminata* Fabr. (Hymenoptera, Formicidae). *Z. Vergh. Physiol.* 62, 111-120.
- HAVUKKALA, I. (1980) Klinokinetic and klinotactic humidity reactions of the beetles *Hylobius abietis* and *Tenebrio molitor*. *Physiol. Ent.* 5, 133-140.
- HAWKINS, W. A. (1978) Effects of sex pheromone concentration on locomotion in the male American cockroach. *J. Chem. Ecol.* 4, 149-169.
- HAYNES, K. F., GASTON, L. K., POPE, M., MISTROI and BAKER, I. C. (1984) The potential for evolution of resistance to pheromones: interindividual and interpopulational variation in the chemical communication system of the pink bollworm moth (In preparation).
- HILL, A. S. and ROELOFS, W. L. (1981) Sex pheromone of the saltmarsh caterpillar moth, *Estigmene acrea*. *J. Chem. Ecol.* 7, 655-668.
- HIRAI, K., SHOREY, H. H. and GASTON, L. K. (1978) Competition among courting male moths: male-to-male inhibitory pheromone. *Science* 202, 644-645.
- HÖLDOBLER, B., MÖGLICH, M. and MASCHWITZ, U. (1974) Communication by tandem running in the ant *Camponotus sericeus*. *J. Comp. Physiol.* 90, 105-127.
- HÖLDOBLER, B. and TRANIELLO, J. (1980) Tandem running pheromone in ponerine ants. *Naturwissenschaften* 67, 360.
- HÖLDOBLER, B. and WILSON, E. O. (1978) The multiple recruitment systems of the African weaver ant, *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* 3, 19-60.
- HÖLDOBLER, B., STANTON, R. C. and MARKL, H. (1978) Recruitment and food-retrieving behavior in *Novomessor* (Formicidae, Hymenoptera). *Behav. Ecol. Sociobiol.* 4, 163-181.
- HOWARD, R. W., MCDANIEL, C. A. and BLOMQUIST, G. J. (1980) Chemical mimicry as an integrating mechanism: cuticular hydrocarbons of a termitophile and its host. *Science* 210, 431-433.
- HOY, R., HAHN, J. and PAUL, R. C. (1977) Hybrid cricket auditory behavior: evidence for genetic coupling in animal communication. *Science* 195, 81-84.
- JONES, R. L., LEWIS, W. J., BOWMAN, M. C., BEROZA, M., BIERL, B. A. and SPARKS, A. N. (1973) Host-seeking stimulants (kairomones) for the egg parasite *Trichogramma evanescens*. *Environ. Ent.* 2, 593-596.
- KATSOYANNOS, B. I. and BOLLER, E. F. (1976) First field application of oviposition-detering marking pheromone of European cherry fruit fly. *Environ. Ent.* 5, 151-152.
- KATSOYANNOS, B. I. and BOLLER, E. F. (1980) Second field application of oviposition-detering pheromone of the European cherry fruit fly, *Rhagoletis cerasi* L. (Diptera: Tephritidae). *Z. Ang. Ent.* 89, 278-281.

- KENNEDY, J. S. (1940) The visual responses of flying mosquitoes. *Proc Zool Soc. Lond. A* 109, 221-242.
- KENNEDY, J. S. (1977) Olfactory responses to distant plants and other odour sources. In *Chemical Control of Insect Behavior. Theory and Application* Edited by H. H. Shorey and J. J. McKelvey. Pages 67-91. John Wiley, New York.
- KENNEDY, J. S. (1978) The concepts of olfactory arrestment and attraction. *Physiol. Ent.* 3, 91-98.
- KENNEDY, J. S. (1983) Zigzagging and casting as a programmed response to wind-borne odour — a review. *Physiol. Ent.* 8, 109-120.
- KENNEDY, J. S. and MARSH, D. (1974) Pheromone-regulated anemotaxis in flying moths. *Science* 184, 999-1001.
- KLUN, J. A. and MAINI, S. (1979) Genetic basis of an insect chemical communication system: the European corn borer. *Environ. Ent.* 8, 423-426.
- KOCHANSKY, J., TETTE, J., TASCHENBERG, E. F., CARDÉ, R. T., KAISLING, K. E. and ROELOFS, W. L. (1975) Sex pheromone of the moth, *Antheraea polyphemus*. *J. Insect Physiol.* 21, 1977-1983.
- KRAMER, E. (1975) Orientation of the male silk moth to the sex attractant bombykol. In *Olfaction and Taste*. Vol. 5. Edited by D. Denton and J. P. Coghlan. Pages 329-335. Academic Press, New York.
- KRASNOV, S. B. (1981) The mating behavior of *Ephesia ehetella* (Hübner) and *E. figulilella* Gregson. M.S. thesis, University of Florida.
- KUENEN, L. P. S. and BAKER, T. C. (1981) Habituation versus sensory adaptation as the cause of reduced attraction following pulsed and constant sex pheromone pre-exposure in *Trichoplusia ni*. *J. Insect Physiol.* 27, 721-726.
- KUENEN, L. P. S. and BAKER, T. C. (1982a) Optomotor regulation of ground velocity in moths during flight to sex pheromone at different heights. *Physiol. Ent.* 7, 193-202.
- KUENEN, L. P. S. and BAKER, T. C. (1982b) The effects of pheromone concentration on the flight behavior of the Oriental fruit moth, *Grapholitha molesta*. *Physiol. Ent.* 7, 423-434.
- KUENEN, L. P. S. and BAKER, T. C. (1983) A non-anemotactic mechanism used in pheromone source location by flying moths. *Physiol. Ent.* 8, 277-289.
- KULLENBERG, B. and BERGSTRÖM, G. (1973) The pollination of *Ophrys* orchids. *Nobel Symposium* (Stockholm) 25, 253-258.
- KULLENBERG, B. and BERGSTRÖM, G. (1976) Hymenoptera Aculeata males as pollinators of *Ophrys* orchids. *Zoo Scripta* 5, 13-23.
- LALLI, A. B., SELIGER, H. H., BIGGLEY, W. H. and LLOYD, J. E. (1980) Ecology of colors of firefly bioluminescence. *Science* 210, 560-562.
- LANE, A. P. (1977) Tandem running in *Leptothorax unifasciatus* (Formicidae: Myrmecinae): new data concerning recruitment and orientation in this species. In *Proc. Eighth Int. Cong. IUSSI* Wageningen, Neth. pp 65-66.
- LANIER, G. N. (1981) Deployment of traps in a barrier strategy to reduce populations of the European elm bark beetle, and the incidence of Dutch elm disease. In *Management of Insect Pests with Semiochemicals*. Edited by E. R. Mitchell. Pages 115-131. Plenum, New York.
- LAS, A. S., BULLER, G. D., JR., WELLMAN, R. A. and DOANE, C. C. (1982) Effect of gossypol-permethrin mixture upon abundance of predaceous insects in flowering cotton. Joint Meeting *Ent. Soc. Am. and Ent. Soc. Canad.* 1982 Toronto.
- LEWIS, W. J., JONES, R. L. and SPARKS, A. N. (1972) A host-seeking stimulant for the egg parasite *Trichogramma evanescens*: its source and a demonstration of its laboratory and field activity. *Ann. Ent. Soc. Amer.* 65, 1087-1089.
- LEWIS, W. J., JONES, R. L., NORDLUND, D. A. and GROSS, H. R., JR. (1975) Kairomones and their use for management of entomophagous insects II. Mechanisms causing increase in rate of parasitization by *Trichogramma* sp. *J. Chem. Ecol.* 1, 349-360.
- LIE, R. and BAKKE, A. (1981) Practical results from the mass trapping of *Ips typographus* in Scandinavia. In *Management of Insect Pests with Semiochemicals*. Edited by E. R. Mitchell. Pages 175-181. Plenum, New York.
- LINDAUER, M. (1961) *Communication Among Social Bees*. Harvard University Press, Cambridge, Massachusetts.
- LINN, C. E. JR. and ROELOFS, W. L. (1981) Modification of sex pheromone blend discrimination in male oriental fruit moths by pre-exposure to (E)-8-dodecenyl acetate. *Physiol. Ent.* 6, 421-429.
- LLOYD, J. E. (1966) Studies on the flash communication system in *Photinus* fireflies. *Mis. Publ. Mus. Zool. Univ. Mich.* No. 130.
- MADSEN, H. F. (1981) Monitoring codling moth populations in British Columbia apple orchards. In *Management of Insect Pests with Semiochemicals*. Edited by E. R. Mitchell. Pages 57-62. Plenum, New York.
- MARSH, D., KENNEDY, J. S. and LUDLOW, A. R. (1978) An analysis of anemotactic zigzagging flight in male moths stimulated by pheromone. *Physiol. Ent.* 3, 221-240.
- MARTIN, H. (1965) Osmotropotaxis in the honey bee. *Nature* 208, 59-63.
- MCGURK, D. J., FROST, J., EISENBRAUN, E. J., VICK, K., DREW, W. and YOUNG, J. (1966) Volatile compounds in ants: identification of 4-methyl-3-heptanone from *Pogonomyrmex* ants. *J. Insect Physiol.* 12, 1435-1441.
- MEINWALD, J. and MEINWALD, Y. C. (1966) Structure and synthesis of the major components in the hairpencil secretion of a male butterfly, *Lycorea ceres ceres* (Cramer). *J. Amer. Chem. Soc.* 88, 1305-1310.
- MEINWALD, J., MEINWALD, Y. C. and MAZZOCCHI, P. H. (1969) Sex pheromone of the queen butterfly: chemistry. *Science* 164, 1174-1175.
- MEINWALD, J., BORIACK, C. J., SCHNEIDER, D., BOPPRE, M., WOOD, W. F. and EISNER, T. (1974) Volatile ketones in the hairpencil secretion of danaid butterflies (Amauris and Danaus). *Experientia* 30, 722-723.
- MEINWALD, J., THOMPSON, W. R., EISNER, T. and OWEN, D. F. (1971) Pheromones VII. African monarch: major components of the hairpencil secretion. *Tet. Lett.* 38, 3485-3488.
- MILLER, J. R. and ROELOFS, W. L. (1978) Sustained-flight tunnel for measuring insect responses to wind-borne sex pheromones. *J. Chem. Ecol.* 4, 187-198.
- MITCHELL, E. R. (1981) *Management of Insect Pests with Semiochemicals, Concepts and Practice*. Plenum Press, New York.
- MÖGLICH, M. and HÖLDOBLER, B. (1975) Communication and orientation during foraging and emigration in the ant *Formica fusca*. *J. Comp. Physiol.* 101, 275-288.
- MÖGLICH, M. and MASCHWITZ, U. (1974) Tandem calling, a new kind of signal in ant communication. *Science* 186, 1046-1047.
- MONTGOMERY, M. E. and NAULT, L. R. (1977) Comparative responses of aphids to the alarm pheromone (E)- β -farnesene. *Ent. Exp. Appl.* 22, 236-242.
- MURLIS, J. and JONES, C. D. (1981) Fine-scale structure of odour plumes in relation to insect orientation to distant pheromone and other attractant sources. *Physiol. Ent.* 6, 71-86.
- NAULT, L. R. and MONTGOMERY, M. E. (1977) Aphid pheromones. In *Aphids as Virus Vectors*. Edited by K. Harris and K. Maramorosch. Pages 527-545. Academic Press, New York.
- NAULT, L. R. and MONTGOMERY, M. E. (1979) Aphid alarm pheromones. *Misc. Pub. Entomol. Soc. Amer.* 11, 23-31.
- NAULT, L. R. and PHELAN, P. L. (1983) Alarm pheromones and sociality in pre-social insects. In *Chemical Ecology of Insects*. Edited by W. J. Bell and R. T. Cardé. Chapman & Hall, London. (In press.)
- NAULT, L. R., MONTGOMERY, M. E. and BOWERS, W. L. (1976) Antaphid association: role of aphid alarm pheromone. *Science* 192, 1349-1351.
- NISHIDA, R., BAKER, T. C. and ROELOFS, W. L. (1982) "Hairpencil" pheromone components of male Oriental fruit moths, *Grapholitha molesta*. *J. Chem. Ecol.* 8, 947-959.
- NISHIDA, R., KUWAHARA, Y., FUKAMI, H. and ISHII, S. (1979) Female sex pheromone of the German cockroach, *Blattella germanica* (L.) (Orthoptera: Blattellidae), responsible for male wing-raising: IV. The absolute configuration of the pheromone, 3, 11-dimethyl-2-nonacosanone. *J. Chem. Ecol.* 5, 289-298.
- NORDLUND, D. A., JONES, R. L. and LEWIS, W. J. (1981) *Semiochemicals: Their Role in Pest Control*. John Wiley, New York.
- O'CONNELL, R. J. (1975) Olfactory receptor responses to sex pheromone components in the redbanded leafroller moth. *J. Gen. Physiol.* 65, 179-205.
- O'DONALD, P. (1967) A general model of sexual and natural selection. *Heredity* 22, 499-518.
- PARRY, K. and MORGAN, E. D. (1979) Pheromones of ants: a review. *Physiol. Ent.* 4, 161-189.
- PAYNE, T. L. (1981) Disruption of southern pine beetle infestations with attractants and inhibitors. In *Management of Insect Pests with Semiochemicals*. Edited by E. R. Mitchell. Pages 365-383. Plenum, New York.

- PETTY, R. L., BOPPRÉ, M., SCHNEIDER, D. and MEINWALD, J. (1977) Identification and localization of volatile hairpencil components in male *Amauris ochlea* butterflies (Danaiidae) *Experientia* 33, 1324-1326.
- PHELAN, P. L. and MILLER, J. R. (1982) Post-landing behavior of alate *Myzus persicae* as altered by (*E*)- β -farnesene and three carboxylic acids. *Ent. Exp. Appl.* 32, 46-53.
- PHELAN, P. L., MONTGOMERY, M. E. and NAULT, L. R. (1976) Orientation and locomotion of apterous aphids dislodged from their hosts by alarm pheromone. *Ann. Ent. Soc. Amer.* 69, 1153-1156.
- PLISKE, T. E. (1975a) Attraction of Lepidoptera to plants containing pyrrolizidine alkaloids. *Environ. Ent.* 4, 455-473.
- PLISKE, T. E. (1975b) Courtship behavior and use of chemical communication by males of certain species of ithomiine butterflies (Nymphalidae:Lepidoptera). *Ann. Ent. Soc. Amer.* 68, 935-942.
- PLISKE, T. E. and EISNER, T. (1969) Sex pheromone of the queen butterfly: biology. *Science* 164, 1170-1172.
- POPE, M., MISTRO, T., GASTON, L. K. and BAKER, T. C. (1982) Composition, quantification, and periodicity of sex pheromone gland volatiles from individual *Heliothis virescens* females. *J. Chem. Ecol.* 8, 1043-1055.
- PRESTWICH, G. D. (1979) Chemical defense by termite soldiers. *J. Chem. Ecol.* 5, 459-480.
- PRESTWICH, G. D. and COLLINS, M. S. (1981) Macrocyclic lactones as the defensive substances of the termite genus *Armitermes*. *Tet. Lett.* 22, 4587-4590.
- PRESTWICH, G. D. and COLLINS, M. S. (1982) Chemical defense secretions of the termite soldiers of *Acorhinotermes* and *Rhinotermes* (Isoptera, Rhinotermitinae): Ketones, vinyl ketones, and β -ketoaldehydes derived from fatty acids. *J. Chem. Ecol.* 8, 147-161.
- PRICE, P. W. (1975) *Insect Ecology*. John Wiley, New York.
- PROKOPY, R. J. (1972) Evidence for a marking pheromone deterring repeated oviposition in apple maggot flies. *Environ. Ent.* 1, 326-332.
- PROKOPY, R. J. (1980) Mating behavior of frugivorous Tephritidae in nature. *Proc. Symp. Nat. Inst. Agr. Sci. Jap.* 1980, 37-46.
- PROKOPY, R. J. (1981a) Eideictic pheromones that influence spacing patterns of phytophagous insects. In *Semiochemicals: Their Role in Pest Control*. Edited by D. A. Nordlund, R. L. Jones, and W. J. Lewis. Pages 181-213. John Wiley, New York.
- PROKOPY, R. J. (1981b) Oviposition deterring pheromone system of apple maggot flies. In *Management of Insect Pests with Semiochemicals*. Edited by E. R. Mitchell. Pages 471-494. Plenum, New York.
- PROKOPY, R. J. and BUSH, G. L. (1972) Mating behavior in *Rhagoletis pomonella* III. Male aggregation in response to an arrestant. *Can. Entomol.* 104, 275-283.
- RICHERSON, J. V., MCCARTY, F. A. and PAYNE, T. L. (1980) Disruption of southern pine beetle infestations with frontalure. *Environ. Ent.* 9, 90-93.
- RIEDEL, H. (1980) The importance of pheromone trap density and trap maintenance for the development of standardized monitoring procedures for the codling moth (Lepidoptera: Tortricidae). *Canad. Ent.* 112, 655-663.
- RIEDEL, H. and CROFT, B. A. (1974) A study of pheromone trap catches in relation to codling moth (Lepidoptera: Olethreutidae) damage. *Canad. Ent.* 106, 525-537.
- RIEDEL, H., CROFT, B. A. and HOWITT, A. G. (1976) Forecasting codling moth phenology based on pheromone trap catches and physiological-time models. *Canad. Ent.* 108, 449-460.
- RILEY, R. G., SILVERSTEIN, R. M. and MOSER, J. C. (1974) Isolation, identification, synthesis and biological activity of volatile compounds from the heads of *Atta* ants. *J. Insect Physiol.* 20, 1629-1637.
- ROBERTSON, P. L., DUDZINSKI, M. L. and ORTON, C. J. (1980) Exocrine gland involvement in trailing behavior in the Argentine ant (Formicidae:Dolichoderinae). *Anim. Behav.* 28, 1255-1273.
- ROELOFS, W. L. (1977) The scope and limitation of the electroantennogram technique in identifying pheromone components. In *Crop Protection Agents, Their Biological Evaluation*, Edited by N. R. McFarlane. Pages 147-165. Academic Press, New York.
- ROELOFS, W. L. and BROWN, R. L. (1982) Pheromones and evolutionary relationships of Tortricidae. *Ann. Rev. Ecol. Syst.* 13, 395-422.
- ROELOFS, W. L. and CARDÉ, R. T. (1977) Responses of Lepidoptera to synthetic sex pheromone chemicals and their analogues. *Ann. Rev. Ent.* 22, 377-405.
- ROELOFS, W. L., DU, J.-W., LINN, C. and BIÖSTAD, L. (1983) Directional selection of the redbanded leafroller moth sex pheromone blend. In *Evolutionary Genetics of Invertebrate Behavior*. Edited by M. D. Huettel. Plenum, New York. (In press).
- ROHLF, F. J. and DAVENPORT, D. (1969) Simulation of simple models of animal behavior with a digital computer. *J. Theor. Biol.* 23, 400-424.
- ROITBERG, B. D., VAN LENTEREN, J. C., VAN ALPHEN, J. J. M., GALIS, F. and PROKOPY, R. J. (1982) Foraging behaviour of *Rhagoletis pomonella*, a parasite of hawthorn (*Crataegis viridis*) in nature. *J. Anim. Ecol.* 51, 307-325.
- ROITBERG, B. D. and PROKOPY, R. J. (1981) Experience required for pheromone recognition in the apple maggot fly. *Nature* 292, 540-541.
- RUDINSKY, J. A. and RYKER, L. C. (1976) Sound production in Scolytidae: Rivalry and premating stridulation of male Douglas-fir beetle. *J. Insect Physiol.* 22, 997-1003.
- RUDINSKY, J. A. and RYKER, L. C. (1977) Olfactory and auditory signals mediating behavioral patterns of bark beetles. In *Comportement des insectes et milieu trophique*. Pages 195-209. C.N.R.S. Paris, France.
- RUST, M. K., BURK, I. and BELL, W. G. (1976) Pheromone-stimulated locomotory and orientation responses in the American cockroach. *Anim. Behav.* 24, 52-67.
- RUTOWSKI, R. L. (1977) Chemical communication in the courtship of the small sulphur butterfly, *Eurema lisa* (Lepidoptera:Pieridae). *J. Comp. Physiol.* 115, 75-85.
- RUTOWSKI, R. L. (1980) Male scent-producing structures in *Colias* butterflies. *J. Chem. Ecol.* 6, 13-26.
- SANDERS, C. J. (1982) Disruption of male spruce budworm orientation to calling females in a wind tunnel by synthetic pheromone. *J. Chem. Ecol.* 8, 493-506.
- SCHAL, C., TOBIN, T. R., SURBER, J. L., VOGEL, G., TOURELLOT, M. K., LEBAN, R., SIZEMORE, R. and BELL, W. J. (1983) Search strategy of sex pheromone stimulated male German cockroaches. *J. Ins. Physiol.* 29, 575-579.
- SCHILDKNECHT, H. and HOLOUBEK, K. (1961) Die bombardier-käfer und ihre explosionschemie V. Mitteilungen über inskten-abwehrstoffe. *Angew. Chem.* 73, 1-7.
- SCHILDKNECHT, H., MASCHWITZ, E. and MASCHWITZ, U. (1968) Die explosionschemie der bombardierkäfer (Coleoptera:Carabidae) III. Mitt: Isolierung und charakterisierung der explosionskatalysatoren. *Z. Naturf.* 23b, 1213-1218.
- SCHNEIDER, D., BOPPRÉ, M., ZWEIF, J., SCHNEIDER, H., THOMPSON, W. R., BORIACK, C. J., PETTY, R. L. and MEINWALD, J. (1975) A pheromone precursor and its uptake in male *Danaus* butterflies. *J. Comp. Physiol.* 97, 245-256.
- SCHNEIDER, D., BOPPRÉ, M., ZWEIF, J., HORSLEY, A. B., BELL, T. W., MEINWALD, J., HANSEN, K. and DIEHL, E. W. (1982) Scent organ development in *Cretonotos* moths: regulation by pyrrolizidine alkaloids. *Science* 215, 1264-1265.
- SHANNON, C. E. and WEAVER, W. (1949) *The Mathematical Theory of Communication*. University of Illinois Press, Urbana.
- SHOREY, H. H. (1973) Behavioral responses to insect pheromones. *Ann. Rev. Ent.* 18, 349-380.
- SHOREY, H. H. (1974) Environmental and physiological control of insect sex pheromone behavior. In *Pheromones*. Edited by M. C. Birch. Pages 62-80. Elsevier, New York.
- SHOREY, H. H. (1977) Manipulation of insect pests of agricultural crops. In *Chemical Control of Insect Behavior: Theory and Application*. Edited by H. H. Shorey and J. J. McKelvey, Jr. Pages 353-367. Wiley-Interscience, New York.
- SHOREY, H. H., GASTON, I. K. and KAAE, R. S. (1976) Air-permeation with gossypine for control of the pink bollworm. In *Pest Management with Insect Sex Attractants*. Edited by M. Beroza. ACS Symposium Series 23. Washington, DC.
- SILBERGLIED, R. E. and TAYLOR, O. R., Jr. (1978) Ultraviolet reflection and its behavioral role in the courtship of the sulfur butterflies *Colias eurytheme* and *C. philodice* (Lepidoptera:Pieridae). *Behav. Ecol. Sociobiol.* 3, 203-243.
- SOWER, I. L., DATERMAN, G. E. and SARTWELL, C. (1981) Control of moth pests by mating disruption in forests of the western United States. In *Management of Insect Pests with Semiochemicals*. Edited by E. R. Mitchell. Pages 351-364. Plenum, New York.

- SPIETH, H. T. (1968). Evolutionary implications of sexual behavior in *Drosophila*. *Evol Biol* 2, 157-193.
- STOCKEL, J. and SUREAU, F. (1981). Monitoring for the angoumois grain moth in corn. In *Management of Insect Pests with Semiochemicals*. Edited by E. R. Mitchell. Pages 63-73. Plenum New York.
- SUTTON, O. G. (1953). *Micrometeorology*. McGraw-Hill New York.
- SZLEP, R. and JACOBI, T. (1967). The mechanism of recruitment to mass foraging in colonies of *Monomorium venustum* Smith. *M. subopacum* ssp. *pholnicium* Em., *Tapinoma israelis* For. and *T. simothi* v. *pholnicium* Em. *Insecta Sociata* 14, 25-40.
- THORNHILL, R. (1979a). Male and female sexual selection and the evolution of mating strategies in insects. In *Sexual Selection and Reproductive Competition in Insects*. Edited by M. S. Blum and N. A. Blum. Pages 81-121. Academic Press New York.
- THORNHILL, R. (1979b). Adaptive female-mimicking behavior in a scorpionfly. *Science* 205, 412-414.
- TOBIN, T. R. (1981). Pheromone orientation: role of internal control mechanisms. *Science* 214, 1147-1149.
- TOBIN, T. R., SEELINGER, G. and BELL, W. J. (1981). Behavioral responses of male *Periplaneta americana* to periplanone β , a synthetic component of the female sex pheromone. *J. Chem. Ecol.* 7, 969-979.
- TRIVERS, R. L. (1972). Parental investment and sexual selection. In *Sexual Selection and the Descent of Man 1871-1971*. Edited by B. Campbell. Pages 135-179. Aldine, Chicago.
- VAKENTI, J. M. and MADSEN, H. F. (1976). Codling moth (Lepidoptera: Olethreutidae): monitoring populations in apple orchards with sex pheromone traps. *Canad. Ent.* 108, 433-438.
- VANDER MEER, R. K. and WOJCIK, D. P. (1982). Chemical mimicry in the myrmecophilous beetle *Myrmecaphodius excavaticollis*. *Science* 218, 806-808.
- VETTER, R. S. (1980). Defensive behavior of the black widow spider *Lauodectus hesperus* (Araneae: Theridiidae). *Behav. Ecol. Sociobiol.* 7, 187-193.
- VISSER, J. H. and AVÉ, D. A. (1978). General green leaf volatiles in the olfactory orientation of the Colorado potato beetle, *Leptinotarsa decemlineata*. *Ent. Exp. Appl.* 24, 738-749.
- VISSER, J. H. and NIELSEN, J. K. (1977). Specificity in the olfactory orientation of the Colorado potato beetle, *Leptinotarsa decemlineata*. *Ent. Exp. Appl.* 21, 14-22.
- VISSER, J. H., VAN STRATEN, S. and MAARSE, H. (1979). Isolation and identification of volatiles in the foliage of potato, *Solanum tuberosum*, a host plant of the Colorado beetle, *Leptinotarsa decemlineata*. *J. Chem. Ecol.* 5, 13-25.
- VON FRISCH, K. (1967). *The Dance Language and Orientation of Bees*. Belknap Press Cambridge, Massachusetts.
- WAAGE, J. K. (1978). Arrestment responses of the parasitoid, *Nemeritis canescens*, to a contact chemical produced by its host, *Plodia interpunctella*. *Physiol. Ent.* 3, 135-146.
- WENNER, A. M., WELLS, P. H. and JOHNSON, D. L. (1969). Honey bee recruitment to food source: olfaction or language? *Science* 164, 84-86.
- WILLIS, M. A. and BIRCH, M. C. (1982). Male lek formation and female calling in a population of the arctiid moth *Estigmene acrea*. *Science* 218, 168-170.
- WILLIS, M. A. and BAKER, I. C. (1984). Effects of phasic and tonic pheromone stimulation on the flight behaviour of the Oriental fruit moth, *Grapholitha molesta* (Busck). *Physiol. Ent.* (Submitted).
- WILSON, E. O. (1958). A chemical releaser of alarm and digging behavior in the ant *Pogonomyrmex badius* (Latreille). *Psyche* 65, 41-51.
- WILSON, E. O. (1962a). Chemical communication among workers of the fire ant, *Solenopsis saevissima* (Fr. Smith) 1. The organization of mass-foraging. *Anim. Behav.* 10, 134-147.
- WILSON, E. O. (1962b). Chemical communication among workers of the fire ant, *Solenopsis saevissima* (Fr. Smith) 3. The experimental induction of social responses. *Anim. Behav.* 10, 159-164.
- WILSON, E. O. (1974). *The Insect Societies*, 3rd edition. Belknap Press, Cambridge, Massachusetts.
- WOHLERS, P. (1981a). Effects of the alarm pheromone (*E*)- β -farnesene on dispersal behaviour of the pea aphid *Acyrthosiphon pisum*. *Ent. Exp. Appl.* 29, 117-124.
- WOHLERS, P. (1981b). Aphid avoidance of plants contaminated with alarm pheromone (*E*)- β -farnesene. *Z. Ang. Ent.* 92, 329-336.
- WOHLERS, P. (1982). Effect of alarm pheromone (*E*)- β -farnesene on aphid behaviour during flight and after landing on plants. *Z. Ang. Ent.* 93, 102-108.
- WOOD, D. L., BROWNE, L. E., BEDARD, W. D., IILDEN, P. L., SILVERSTEIN, R. M. and RODIN, J. O. (1968). Response of *Ips confusus* to synthetic sex pheromones in nature. *Science* 159, 1373-1374.
- WRIGHT, R. H. (1958). The olfactory guidance of flying insects. *Canad. Ent.* 90, 81-89.
- WRIGHT, R. H. (1973). Understanding olfaction. *Soap Perf. Cosmet.* 46, 571-576.
- ZAGATTI, P. (1981). Comportement sexual de la pyrale de la canne à sucre *Eldana saccharina* (Wlk.) lié à deux phéromones émises par le mâle. *Behaviour* 78, 81-98.

1 Int
2 Di
3 Su
4 Co
5 Th
5.1
5.2
5.3
6 Et
6.1
6.2
6.3
6.4
6.5
6.6
7 Co
Ro

The
evol
of "
may
cessi
this
livin
sider
reco
integ
whic
tinct
evol
sing
root
ally

COMPREHENSIVE
INSECT PHYSIOLOGY
BIOCHEMISTRY AND
PHARMACOLOGY

Volume 9

BEHAVIOUR

Executive Editors

G. A. KERKUT

*Department of Neurophysiology,
University of Southampton, UK*

L. I. GILBERT

*Department of Biology,
University of North Carolina, USA*



PERGAMON PRESS

OXFORD · NEW YORK · TORONTO · SYDNEY · PARIS · FRANKFURT

UK	Pergamon Press Ltd., Headington Hill Hall, Oxford OX3 0BW, England
USA	Pergamon Press Inc., Maxwell House, Fairview Park, Elmsford, New York 10523, USA
CANADA	Pergamon Press Canada Ltd., Suite 104, 150 Consumers Road, Willowdale, Ontario M2J 1P9, Canada
AUSTRALIA	Pergamon Press (Aust.) Pty. Ltd., P.O. Box 544, Potts Point, N.S.W. 2011, Australia
FRANCE	Pergamon Press SARL, 24 rue des Ecoles, 75240 Paris, Cedex 05, France
FEDERAL REPUBLIC OF GERMANY	Pergamon Press GmbH, Hammerweg 6, D-6242 Kronberg-Taunus, Federal Republic of Germany

Copyright © 1985 Pergamon Press Ltd.

All Rights Reserved. No part of this publication may be reproduced, stored in a retrieval system or transmitted in any form or by any means, electronic, electrostatic, magnetic tape, mechanical, photocopying, recording or otherwise, without permission in writing from the publishers.

First edition 1985

Library of Congress Cataloging in Publication Data

Main entry under title:

Comprehensive insect physiology, biochemistry, and pharmacology

Contents: v. 1. Embryogenesis and reproduction.

I. Insects—Physiology—Collected works. I. Kerkut, G. A.

II. Gilbert, Lawrence I. (Lawrence Irwin), 1929—

QL495.C64 1984 595.7'01 83-25743

British Library Cataloguing in Publication Data

Comprehensive insect physiology, biochemistry and pharmacology

I. Insects

I. Kerkut, G. A. II. Gilbert, Lawrence I.

595.7 QL463

ISBN 0-08-030810-4 (volume 9)

ISBN 0-08-026850-1 (set)

Filmset by Filmtypes Services Ltd., Scarborough
Printed in Great Britain by A. Wheaton & Co. Ltd., Exeter