# 39

# Putting Pheromones to Work: Paths Forward for Direct Control

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## 1. Introduction

Insect pheromones offer exciting examples of pure science applied to human benefit. Even before the first pheromones had been identified, the potential for practical exploitation was recognized—a potential that has now been realized in many successful schemes using pheromones for direct control of insect pests. Although most uses have been in agriculture and forestry, manipulation of vector insects with behavior-modifying chemicals looks increasingly possible in medical entomology—for example, via the sex pheromones of sandflies (e.g., Hamilton et al. 1994) and oviposition attractants of mosquitoes (e.g., Beehler et al. 1994; Mordue et al. 1992). There still remains the question why the application of pheromones has not been greater.

Each pheromone symposium since the 1960s has emphasized the potential for pest control, but even "potential has a shelf-life" (Atwood 1990). However, we should remember that it is still less than 40 years since the first chemical identification of an insect pheromone and that we have made massive strides since then. Far from being a time for pessimism, I will argue that the basis for optimism is strong and there should be a big push for support. Compared with conventional pesticides, pheromone research has been only modestly funded. The rationale for increasing funding on pheromone research includes the negligible environmental impact of pheromones and increasing evidence of their effectiveness in pest control. Nonetheless, pheromones represent only 2% of the dollar sales of insecticides worldwide (1985 data in Jutsum 1988), despite great efforts on the part of researchers, companies, and extension workers. How far can slow deployment be blamed on unanswered questions in the scientific understanding of pheromone communication as opposed to practical difficulties in implementation? I will return to each of these topics.

Much of the above could have been written any time since 1960, so what makes now a good time? In part this is due to recent significant advances in pheromone research, discussed in this volume, particularly in our understanding of orientation mechanisms (Baker and Vickers this volume, Cardé and Mafra-Neto this volume) and in our ability to measure pheromone concentrations in the field (see below). Developments in neurobiological understanding are also promising. However, equally important are changing attitudes to pest control, by both growers and the public.

## 2. Current Success of Pheromones

We have come a long way since Rothschild (1981) said that "pheromone researchers . . . will have to accept that it may be some years before disruption is accepted as a viable control method for any more than 1 or 2 species." Cardé and Minks (1995) review some of the major successes of direct control of moth pests by pheromones in field crops and orchards: commercially viable formulations as effective as, or better than, the conventional insecticides they replace. Borden (1993) reviews a similar picture of success in the use of pheromones for control or monitoring of forest pests, both beetles and Lepidoptera. Chapters in this part of the volume describe progress within these and other systems.

### 2.1. Using Pheromones: Monitoring and Control

The focus of this section is on using pheromones for direct control of insect pests, but a major use of pheromones continues to be for monitoring pest populations both of crop and orchard pests (Wall 1989), stored products (Burkholder 1990), and forestry pests (Borden 1993). Pheromone-based monitoring provides one of the most effective survey methods for detecting pest species. Trumble (this volume) describes some of the persistent problems with monitoring as a quantitative decision tool—in particular the low correlations between adult male trap catches and caterpillar levels in the crop. However, more sophisticated schemes incorporating decision thresholds have been tried with some success, and significant reductions in pesticide use can result (Wall 1989).

Pheromones have been used for direct control of insect pest populations in three main ways: mass trapping, "lure and kill" (including "push–pull" mechanisms), and mating disruption. Much of what follows emphasizes control of moth pests by mating disruption through use of synthetic sex pheromones released in the field to permeate the crop or provide numerous point sources of synthetic pheromone. In pest moths (among the most important of agricultural pests), because it is the larvae which do the damage, the aim of pheromone intervention is to prevent fertilization of eggs by preventing mates meeting. However, direct control in other systems, especially with bark beetles (Borden 1993; Borden this volume), does not involve interference with sex pheromones but, instead, involves

manipulation of aggregation pheromones and the process of tree colonization, including exploitation of sometimes complex species interactions mediated by semiochemicals. There are many other potential uses of semiochemicals for control (Tumlinson 1988), including marking pheromones such as oviposition marking pheromones in both flies (Prokopy 1981) and moths (e.g., Schoonhoven 1990), oviposition attractants, larval interactions mediated by pheromones, kairomones which modify the behavior of natural enemies (e.g., Pickett et al. 1992; Pickett et al. this volume), and direct control by nonpheromone attractants such as male-lures for tephritid fruit flies for lure and kill (Cunningham et al. 1990). Reviews of pheromone applications to particular crops can be found in Ridgway et al. (1990). Jutsum and Gordon (1989a) and Howse et al. (1996) review applied pheromone use in agriculture more generally.

## 2.2. *How Have Research Agendas Changed?*

This book comes some 20 years after the classic volume edited by Birch (1974). Since then the use of pheromones as control agents has been reviewed regularly (e.g., Shorey and McKelvey 1977; Mitchell 1981; Nordlund et al. 1981; Kydonieus and Beroza 1982; Campion 1984; Wall 1984; Jutsum and Gordon 1989a; Ridgway et al. 1990; Jones 1994). It is sobering to see how little research agendas and concerns have changed since then. Many of the points raised by Birch and successors are still concerns: the mechanism of mating disruption (involving sensory biology and behavior) and the need to understand the population biology (including migration and other characteristics) of the pest species. Other issues have included the difficulty of evaluating the effectiveness of pheromone trials and practical questions of registration. The major question now must be how to move research and applications forward.

Where initially the challenge was chemical—the enormous quantities of material originally needed for analysis are legendary—with the integration of gas chromatography—coupled mass spectrometry (GC–MS) with gas chromatography–electroantennogram/single sensillum recording (GC–EAG/SCR) and the increasing sophistication of chemical analysis, chemical identification is rarely the rate-limiting step. Instead, the persistent problem is the complexity of insect behavior, and in particular our ignorance of behavior in the field. Whereas pheromones can be used for monitoring purposes within a few years of discovery, mating disruption takes much greater understanding.

## 3. Progress in Understanding Mating Disruption: Successes and Problems

Since the effectiveness of direct control with pheromones has been demonstrated in many systems, one could argue that we do not need to understand the mechanisms. It may seem a luxury, but as Sanders (this volume) points out, to improve methods and understand how to change them when they fail, we need to know

how they work. Such an understanding would also help in predicting likely resistance mechanisms (although insects are likely to surprise us). Much of the discussion that follows is devoted to mating disruption in moths, but many of the methodological problems are relevant to all pheromone-mediated control systems.

### 3.1. *Poor Understanding of the Mechanism(s) of Mating Disruption*

In most species, males find the female by flying upwind in response to her pheromone. To prevent successful mating, a number of stages in the mate location and courtship sequence could be interrupted, but long-range orientation may be the link most vulnerable to interference from synthetic pheromone because short-range orientation and courtship may involve other sensory cues (Sanders this volume). Mating disruption describes the result not the mechanism(s) by which this is achieved.

Sanders (this volume) and Cardé (1990) review the supposed mechanisms, much as Bartell (1982) proposed: (1) sensory adaptation (at the peripheral receptor level) or habituation in the CNS (lumped as "sensory fatigue" in Sanders), (2) false-trail-following (competition between natural and synthetic sources), (3) camouflage of natural plumes by ubiquitous high levels of synthetic pheromone, (4) imbalance in sensory input by massive release of a partial pheromone blend, and (5) the effects of antagonists to attraction and pheromone mimics.

As Sanders explains, field results combined with laboratory wind-tunnel tests and electrophysiological recordings can sometimes suggest the main mechanisms which might be involved in particular situations but given the variety of proposed mechanisms, the real breakthrough will be to design critical field and laboratory experiments to distinguish the hypotheses. However, even in one species, many mechanisms may be acting, perhaps synergistically (Cardé 1990).

Below I suggest that collaboration of behavioral and field scientists with neurobiologists might lead to greater understanding.

### 3.1.1. *Orientation Mechanisms and Mating Disruption*

The unifying paradigm is the growing understanding of how males track upwind toward an odor source (Baker 1990; Baker and Vickers this volume; Cardé and Mafra-Neto this volume; Mafra-Neto and Cardé 1994; Vickers and Baker 1994b), building on the work of the last 25 years. The link between male behavior and the filamentous structure of odor plumes (Murlis et al. 1992) has been clarified. The key features seem to be the male's brief surge upwind in response to each antennal contact with filaments of pheromone-laden air and casting on its loss.

The male's response to pheromone "filaments" helps explain why the natural blend is often the most effective for mating disruption (Minks and Cardé 1988). Vickers and Baker's (1992) wind-tunnel experiments show that the individual components of multicomponent blends (the norm) need to be in the same puff

for optimum up-wind flight, in line with other behavioral work showing the importance of the full blend at all distances from the female (Linn and Roelofs 1989). Nonetheless, some mating disruption systems have used off-blends successfully (see Sanders this volume; Arn and Louis this volume).

Sanders (1981) observed that in field trials, "inhibitors" were only effective if released very close to the female (see also Cardé 1990); he suggested that this was due to the structure of plumes, as above: Only if superimposed on the pheromone, in the same filaments, would inhibitory compounds work. Recent laboratory work supports this (Liu and Haynes 1992; Rumbo et al. 1993). Although inhibitors may offer control in some cases (e.g., Bengstsson et al. 1994), the prospect is not generally promising.

### 3.1.2. Primer Effects in Mating Disruption

Most behavioral work on mechanisms has understandably focused on the immediate (releaser) effects of synthetic pheromones during the males' search for the female. Much of the effect could be due to the longer-term (primer) effects of permeation of the field with pheromone during the rest of the day (or even the period of activity immediately preceding flight). Despite pioneering work by Bartell (review 1982) and later work (e.g., Linn and Roelofs 1981; Liu and Haynes 1993b), the effects of pre-exposure of different types and duration are not clear. There is a pressing need to expand the timescale and range of experiments to investigate the more subtle primer effects.

Primer effects also reinforce the need to know where resting animals are. For example, during the day, pink bollworm male adults go down to the base of the plants into the soil and may avoid exposure to the pheromone in the air (Flint et al. 1975).

### 3.1.3. Wider Taxonomic Variations: Generalizing to Other Insect Orders

While our understanding of moth orientation increases, an underlying question remains about how far these inflight mechanisms apply to other insect groups such as beetles, sawflies, and now aphids (Pickett et al. 1992; Pickett et al. this volume) which also use long-distance pheromone communication (Cardé 1990). All moths, through common ancestry, might well share the same mechanisms, but other taxa could have evolved orientation behavior independently. This is important because moth orientation models inform much of the theoretical discussion of disruption. The same question may apply to other pure and applied aspects of mating disruption.

### 3.1.4. Tracking Individual Moths in the Field

Currently a major handicap is that it is not usually possible to track individual moths in the field, except for short distances close to the pheromone source in

experiments (e.g., Willis et al. 1994). An unanswered question is the behavior of males before first contact with the pheromone. Could radiotracking yet come within reach for the larger moths, as miniaturization of electronics continues? This technique would also help answer what the animals do during the day.

### 3.2. Pheromone Concentrations in the Field and the Structure of Plumes

One of the major unknowns in pheromone research is now partly solved: New portable electroantennogram (EAG) and single sensillum recording (SCR) equipment mean that we can now measure instantaneous concentrations of pheromones in the air (Färbert et al this volume; Van de Pers and Minks this volume; Suckling and Karg this volume). As recently as 1990, Arn wrote that the invention of a "sniffer" to monitor concentrations continuously in the field would be "a golden key to pheromone applications" (Arn 1990). Earlier techniques could only average over a longer period by adsorption on a pheromone collector because air concentrations (at pg/liter) are too low for instantaneous measurement by GC–MS. The new systems exploit the sensitivity and specificity of the moth's antenna to its own pheromone and combine this with a mechanism for calibration of the EAG or SCR responses. Whether EAG or SCR is the best technique may depend on the question.

The new techniques will help in two ways—first, by allowing the fine structure of pheromone plumes to be measured directly rather than by proxy of ionized air techniques (Van de Pers and Minks this volume). Already these studies confirm earlier results on plume fine structure (Murlis et al. 1992; Murlis this volume). Second, rather than speculating, we can now investigate the concentrations (and the spatial and temporal patterns) of airborne pheromone which different mating disruption strategies produce (e.g., Färbert et al. this volume). Similarly, the effects of adsorption of pheromones onto leaves and the effects of the canopy on air movements can be investigated (Suckling and Karg this volume). We can now start to measure the "active spaces" of plumes downwind of lures in traps to study trap interference in a new way.

### 3.2.1. Wind-Tunnel Concentrations

The new technologies for pheromone air concentration measurement now mean that laboratory studies can be made more realistic. Until now, pheromone concentrations have usually been given as dose on a source rather than the achieved air concentration.

### 3.3. Complete Blends and Why They Matter

While pheromones for large numbers of insect species have been identified, it is likely that many earlier identifications are incomplete (Tumlinson 1988; Linn and Roelofs 1989). As Borden (1993) points out, mating disruption projects

abandoned in the past might have been using incomplete blends. In some of these trials, real females outcompeted synthetic sources—implying that suboptimal pheromones were being used (e.g., Sanders 1984). It would be worth going back to many of these with a fresh identification of the blend. The role of host plant volatiles as synergists with insect pheromones is also being increasingly recognized for some moths and bark beetles (e.g., Borden this volume; Klein 1981).

Producing effective mating disruption schemes is further complicated by the existence of geographical races using different blends (isomers, enantiomers, ratios) for example bark beetles (Birch 1984; Lanier 1990) and moths such as the European corn borer (*Ostrina nubilalis*) and turnip moth (*Agrotis segetum*) (Löfstedt 1993).

## 3.4. Unsolved Practical Problems for Field Trials

### 3.4.1. Controls and the Large-Scale Needed to Show an Effect

The design of field trials still presents a major practical problem (e.g., Birch 1974; Sanders 1989). Control sites are needed, but flying insects (whether males or fertilized females) and an airborne pheromone do not respect field boundaries. No field is an island. It can be difficult to find matching control plots far enough away to be unaffected by the pheromone treatments on the experimental plots, but close enough to offer similar conditions. As Minks noted (tongue-in-cheek) at the symposium, pheromone trials in a small country like Holland might need experimental controls in Germany! The dilemma of field trials is that small-scale plots might not work, but large-scale experiments, to reduce edge effects, need blends and application rates largely already determined. This reinforces the need to be able to do realistic tests of these factors before field trials. A new review of the design of small plot experiments along the lines of Roelofs and Novak (1981), as well as an up-to-date review of general trial procedures along the lines of Rothschild (1981), would be timely.

### 3.4.2. Problems with Assessing Success of Mating Disruption

In common with IPM trials generally, measuring the effectiveness of mating disruption trials can be difficult and has concerned researchers from the beginning. For example, Minks (1977) argued that monitoring trap catches is not enough. In some cases, it is possible to disrupt trapping but still have mating occur in the plots (e.g., Suckling and Shaw 1992). The difficulty of sampling females is unsolved for most species. Economic endpoints (including percentage damage) are ultimately called for. However, although essential, such measures do not help an understanding of *how* mating disruption succeeds or fails in reducing pest populations (as distinct from the mechanism of interference with male moth behavior). Instead, for this, population studies of the pest are needed (below).

### 3.4.3. Reproducibility of Trials

Field trials are not controlled environments, and variable results between trials and locations can make assessment of efficacy difficult. As Minks (this volume) says of tests of mating disruption of codling moth, most tests were successful but some were not. Borden (this volume) describes similar variability in the success of trials of verbenone to manipulate the mountain pine beetle, *Dendroctonus ponderosae*. The reasons for failure are diverse and we should not dismiss a mating disruption project on basis of one failure [Arn and Louis (this volume) remind us that conventional control can also fail some years]. The failure of otherwise often successful schemes emphasizes our need to better understand what is going on in the field.

### 3.5. Delivery of Pheromones in the Field

McLaughlin et al. (1981), for example, argued that a lack of reliable pheromone delivery systems was a major problem. Since then, many new systems have been developed (Jutsum and Gordon 1989a; Leonhardt 1990), but providing constant release (zero-order) systems remains a problem. Quality control can also be patchy.

Sanders (this volume) discusses the likely effects of different formulations on mating disruption. In some ways, only now does it make sense to make things more sophisticated because now we can measure the concentrations produced (above). A new challenge for dispenser technology comes from our recognition of the need for release blends close to the natural one (Tumlinson 1988).

## 4. The Way Forward: Pure Questions, Applying the Answers

Many of the fundamental questions about the mechanisms of mating disruption and the reasons for success or failure in the field need the combined skills of both pure and applied biologists. Traditionally, many of the leading research scientists working on "pure" pheromone topics have also been very active in applied research. Two links are rare, however: first, neurobiology with mating disruption, and second, population studies of pests with mating disruption field trials.

A consistent theme in reviews over the last 25 years is the need for a deeper understanding of the processes underlying mating disruption instead of continued field trials contributing relatively little to wider questions (e.g., Wall 1984). I fear that reviews 10 years from now will be saying the same thing. What we need now is to bring together the different areas of research. Collaborative research needs encouragement from funding agencies, but pure research would also benefit from the greater understanding that could result. These collaborations do already occur successfully, but the link to population studies is perhaps the

weakest: too applied for university researchers, too fundamental for extension workers.

### 4.1. Clues to Mechanisms of Mating Disruption from Neurobiology and Sensory Physiology

Insect pheromone communication systems have provided remarkably productive models for studying peripheral receptor neurones and their integration into higher neuronal levels, ultimately leading to motor outputs and behavior (Part 2, this volume). Neurobiology has naturally tended to be laboratory-based, and neurobiologists have been perhaps less active in the applied aspects than other pheromone researchers. However, greater collaboration would benefit both sides. Neurobiological research could help in two ways: first, by a direct contribution to the study of mating disruption itself; and second, by providing ways of predicting the likely effects of blends.

A major shortcoming of much mating disruption work is our poor understanding of the physiological mechanisms of the observed effects. For example, what *is* "sensory fatigue" (e.g., see Sanders this volume)? It is a useful shorthand but does not help explain the mechanism (is it adaptation at the peripheral level or habituation in the CNS? and at what level in the CNS?). As Kennedy (1992) argued, this kind of shorthand discourages us from asking the next level of questions. Together with behavioral biologists, these are the questions neurobiologists could help answer by laboratory studies (e.g., Baker et al. 1989). Neurobiologists could also talk with field biologists to help design better field experiments: Applied pheromone researchers are not able to keep up with the latest in neurobiological and behavioral neuroscience.

Second, in the distant future, neurobiology may be able to help interpret EAG and SCR responses which show that an antenna can detect a compound, at the peripheral receptor, but usually give no indication of the behavioral response that would be given by the animal. At the moment we are a very long way from being able to make such predictions of behavior (Part III, this volume). Patterns are starting to emerge in the projections of different receptor neurons into macroglomeruli compartments in the brain (Hansson this volume), but differences between species are not encouraging and the techniques are currently too difficult to use as a tool for other ends.

### 4.2. Clues to Mechanisms of Mating Disruption from Behavioral Ecology, Genetics and an Evolutionary Approach

The significant advances in our understanding of the genetics of pheromone production by female moths and its reception by, and behavior of, males (reviews Löfstedt 1990, 1993; Butlin this volume; Haynes this volume) show the strength of an approach which brings together chemists, biochemists, behavioral biologists, geneticists, and sensory physiologists. The benefits for evolutionary biologists

include unique opportunities for investigating natural selection at the genotype level in nature (Löfstedt 1993; Phelan 1992), and the benefits for the applied biologist include more effective IPM methods and a greater understanding of the potential for resistance.

Many of the questions about the strength of mate selection that interest behavioral ecologists (together with population biologists and geneticists; e.g., see Butlin this volume) are similar to those requiring answers for mating disruption studies. For example, among the questions Löfstedt (1993) asks are: How many female moths (individuals and species) are simultaneously calling in a given habitat? What is the variance in male and female mating success, respectively? How long does it take before a male or female mates? Although the focus of Löfstedt's work is speciation, there is much common ground here for pure and applied biologists. Among the techniques that might be employed to answer these questions, DNA fingerprinting, used more routinely in other ecological specialities, could prove valuable to determine paternity within egg clusters.

Despite the central role of mate finding behavior and courtship underlying mating disruption, our knowledge of these processes, in even the common pest species, is extremely limited (McNeil 1991). In part, this is because most moths fly at night. Nonetheless, this type of more basic behavioral work is desperately needed. Paradoxically we may know more about the more unusual systems such as the saltmarsh moth, *Estigmene acrea* (Arctiidae) where leks of calling males seem to attract females but later in the evening solitary females call (Willis and Birch 1982). We need much more study of what goes on in seemingly conventional moth species. It may seem rather like "me-too"-type studies, but given the variation in behavior that is already apparent these are needed. A greater knowledge of pest behavior might make for fewer surprises later when we start to interfere with mating. Similarly, host selection by beetles needs further study, in addition to interspecific interactions including habitat partition (Borden this volume).

### 4.3. Pest Biology and Population Density Effects

"Research on population dynamics of pest insects hand-in-hand with control methods is one of the most needed areas of applied research" (Birch 1974) but one that happens rarely. The problem is that the life-table assessment, including egg counts, larval counts, and harvest counts needed, are very time-consuming and thus expensive to carry out. The information on population dynamics could also reveal the contribution of beneficials (e.g., predatory mites; see Arn and Louis this volume), increased in numbers by a reduction in spraying, to the overall reduction of the pest population. If significant, this would have implications for spraying for other pests.

High pest population densities are often blamed for failures of mating disruption. Among the ideas suggested are that competition between artificial and real

females will be less effective with increasing population density. Alternatively, male searching strategy at higher densities (or indeed, permeation with phero-mone) may change toward other cues such as visual orientation [although more recent evidence in the species commonly used as the example of this, *Lymantria dispar*, suggests that male behavior does not change (see Willis et al. 1994)]. The reality is that we don't know.

For most species a key unknown population parameter is migration (both short and long) and whether females migrate before or after mating (McNeil et al. this volume). Species in which fertilized females migrate may be poor candidates for mating disruption (Sanders this volume; Trumble this volume).

### 4.4. Resistance to Pheromone Control

Although clear resistance to direct control by pheromones has not yet been reported, pheromones are unlikely to be immune. The existence of geographical races and sibling species differing in pheromone blend should be evidence enough to worry us *a priori*.

An understanding of the potential routes for resistance is one of the major contributions a collaborative approach, involving genetics, biochemistry, sensory, and field biology, could make. Discussing the potential for resistance, McNeil (1992) reviews the evidence for interindividual variation in signal variation and reception (and the genetic basis for these) and records examples of such variation in the age females start pheromone release, pheromone titer, emission rate, proportion of different components present, and variation in the sensory sensitivi-ties and behavior of males. Resistance to a pheromone could entail using other chemical cues, already produced and perceived but not currently part of the pheromone, in place of the original components (Pickett 1992).

Laboratory selection experiments show differing potential for directed change by selection (references in McNeil 1992; Löfstedt 1990). There have been few field studies. Haynes et al. (1984) found no change in emission rates or blend in the pink bollworm *Pectinophora gossypiella* after 3–5 years of mating disruption, although a later increase, perhaps coincidental, in emission rate was noted (Haynes and Baker 1988). That mutations changing pheromone blend can occur was found serendipitously in a laboratory culture of *Trichoplusia ni* and was tracked down to a step in the biosynthesis pathway (Jurenka et al. 1994b; Haynes this volume). Selection of males in the culture led to a broadening of their response spectrum to include the new blend.

It may be that behavioral changes (Haynes et al. 1984; McNeil 1992; Sanders 1989) in features such as mating sites (e.g., "conventional encounter" sites), other mating cues, or selection for dispersal of mated females will prove to be among the most important sources of resistance. Parthenogenetic strains could in theory develop, but there is no evidence of this (see Sanders 1989).

Given the selection pressures we may be generating in successful mating

disruption programs, should we already be considering strategies for minimizing development of resistance, analogous to those proposed for *Bacillus thuringiensis* (see Tabashnik 1994)?

## 5. Putting Pheromones to Work—Progress and Problems with Applications

### 5.1. Barriers to Take Up

While most of this chapter has been about science, it will not surprise the reader that, in common with much of IPM (Dent 1991), the most serious challenges to implementation of pheromones in pest control are probably political and eco-nomic, cogently reviewed by Silverstein (1990). Moving from the science, or even research field trials, to take-up by farmers is the most difficult step (Dent 1991). Each review over the last 25 years has identified the problem which, as the characteristics of pheromones remain the same, have changed little. Here I will focus on some of the principal ones and suggest some ways forward.

### 5.2. Who Pays

The problems of commercial development have been rehearsed many times. It was recognized early that it is unrealistic to expect the large agrochemical companies to develop commercial pheromone technologies for other than a very few major crops, notwithstanding the significant involvement of some large companies (Jutsum and Gordon 1989b). The barriers to commercial interest mostly concern the problem of recouping high development costs. They include small markets (and thus relatively high unit cost of active ingredients), formulation difficulties, marketing and technology transfer difficulties, problems with patentability (Sil-verstein 1990) to which Arn (1990) added the difficulties presented by increasing complexity of pheromones, in both chemistry and biology, and, for pesticide companies, competition with their own conventional products.

There are strong parallels with biological control which shares many of the same barriers to commercial development (Jutsum 1988; Van Lenteren and Woets 1988). The opportunities for recovering development costs commercially may be limited, but government or similar public sector investment can be more than justified by the public benefits: to individual farmers, to consumers, to the environment, and (for Third World countries) in savings of foreign exchange. It is always easy to argue for more funds, but here is a case where public investment would pay dividends: Not all "public goods" come from choices dictated by return on capital narrowly defined by company interest. This comment may seem overpolitical but reflects commercial realities.

Most companies involved in commercialization of pheromones, which tend to be small, do not have the resources for the basic research needed in developing the

technology. Much of the research and extension work will need to be government-supported. However, as Jones (1994) points out, it is ironic that at the same time as politicians are legislating for reductions in conventional pesticide use (below), they seem most keen to reduce the worldwide capacity for scientific research into alternative pest control methods at government and academic institutions. The trends in many western countries toward commercialization and privatization of government research (e.g., HortResearch in New Zealand, CSIRO in Australia, and GHRI and NRI in the United Kingdom) do not bode well. Even today, current investment is small. Van Lenteren and Woets (1988) estimate that the amounts spent on biological control, largely in the public sector, represent about only 1% of investment by chemical companies in pesticide research. Levels of investment in pheromone research are likely to be on the same order.

Campaigning for increased investment will need readily accessible (and up-to-date) information, including successes (e.g., Cardé and Minks 1995), current usage, costs, and benefits [like Klassen et al. (1982) but updated regularly]. Without political lobbying, it is unlikely that we will have progress with phero-mone adoption. A major handicap is the lack of powerful equivalents to chemical industry organizations, although with the formation of the American Semiochemi-cal Association and European Semiochemical Association (Jones 1994) we per-haps have a good beginning.

Changing consumer attitudes toward pesticide use (e.g., Coats 1994; Trumble this volume) are already having effects on the climate for alternatives to conven-tional pest control, and pheromones are likely to benefit. Other incentives for the development of mating disruption and other IPM techniques come from growing insecticide resistance and the rising costs of developing new pesticides.

### 5.3. Extension, Persuasion, and Take-up

Gaining acceptance for pheromone-based pest control, like adoption of other new IPM methods, requires considerable effort. Trumble's (this volume) description of the conservatism of vegetable growers and their reasonable suspicion of new pest control technologies (not all have matched their promise) is typical. Adoption will be more likely if it is clear to farmers that there *must* be change, in response (for example) to pesticide resistance problems (e.g., Suckling and Karg this volume; Staten et al this volume; Trumble this volume). Getting acceptance of ultimately better but less certain pest control methods is difficult. Schemes requir-ing much greater sophistication on the part of farmers will be less successful than those incorporating a more sympathetic appreciation of farmers' perceptions and constraints. Extension workers need to match the pesticide company sales effort at the farm level. The chances of adoption will be improved if mating disruption techniques can be seen to be cost-effective in schemes involving farmers [best of all from the start (Dent 1991)].

Some of the most effective uses of pheromones for mating disruption have

involved region-wide schemes (e.g., Staten et al. this volume; Campion 1984; Jones 1994). Once implemented, involvement of the government can ensure adoption across the whole region, but getting the initial decision can be more difficult than dealing with individual farmers.

Investment in implementation, the key to adoption of pheromone technology, is often skimped, or not properly addressed at all. Unfortunately, this crucial activity is one of the most dependent on public funds.

Pheromones could be very appropriate technology for developing countries, but Silverstein (1990) reports excellent critiques of many current approaches and emphasizes the need for ingenuity and simplicity in the integration of pheromones into pest control systems.

### 5.4. Government Influences Through Legislation

Registration requirements can have a profound effect on pheromone adoption. Weatherston and Minks (1995) suggest that the time and cost required to complete the registration process provide the major hurdle to introduction of semiochemical products into the market place. These authors review the pattern of current regulation in 21 countries. They acknowledge that the special nature of semio-chemicals has been recognized by many national regulatory bodies and the Food and Agricultural Organization of the United Nations but argue that more could be done to harmonize and expedite pheromone registration. Among their propos-als is the suggestion that structure–activity data should be used for environmental and health-risk assessment of pheromones, in the first instance for lepidopteran pheromones, to avoid the need to test each fairly similar pheromone for toxicologi-cal and other properties. Adoption of a 90-day evaluation deadline would also help. They propose developing this approach first with the U.S. Environmental Protection Agency (EPA), but they hope it might be accepted by other national regulatory authorities in time.

Legislation restricting pesticide use will also be important in the future. For example, Trumble (this volume) describes how increasingly restrictive legislation at the state level has dramatically changed use patterns in California (see Weather-ston and Minks 1995 for other initiatives). Carrots can also be used: Arn and Louis (this volume) report that some regional governments in Germany and Switzerland offer subsidies to vineyard growers toward the costs of pheromones.

### 5.5. Selecting Good Target Species for Mating Disruption

Rothschild (1981) feared that there would be few "universal truths" that can be applied to mating disruption, which would mean that each pest species (and crop system?) might have to be studied individually. To make the task manageable, we need to search for patterns, good predictors of success (or likely failure) in pest species and agricultural systems, resting on basic studies on field behavior, pest biology, and mating disruption experience. Testable suggestions for such

characteristics have been made (e.g., Koehler et al. 1977; Rothschild 1981; Sanders 1989 this volume). This challenge should be taken up.

### 5.5.1. Pest Complexes

A major strength of pheromones is their effectiveness as part of IPM schemes, because of their compatibility with biological control agents and other beneficials. Trumble (this volume) describes use of pheromones in IPM of tomato pests in Mexico. Pheromones fit well in the virtuous spiral—for example, in greenhouse IPM (Van Lenteren and Woets 1988), where the use of one biological control agent encourages (or requires) moves from conventional pesticides for other pests.

### 5.6. Chemical Advances

Costs of active ingredients have been a limiting factor in some mating disruption schemes. Developments in synthetic chemistry—in particular, chiral synthesis (driven by the pharmaceutical industry after thalidomide)—may bring down costs. The use of biotechnology for pheromone synthesis could produce biologically correct pheromones cheaply (Lindgren 1990; Pickett 1992).

## 6. Conclusions

Butenandt could have had no idea in 1950, contemplating 500,000 moths to identify the silkworm pheromone, bombykol, that today such a task could be attempted with a single female. Similarly, the idea of measuring pheromone concentrations in the wind would have seemed a fantasy. Problems with mating disruption remain, but in many cases we now have the tools to answer them. Finding the answers needed to make pheromones an even more effective weapon in the direct control of insect pests will be of mutual benefit to both pure and applied biologists.

### Acknowledgments

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