

Application of Pheromones to Pest Control

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Sensory adaptation: a simple sensory event with profound effects on the behaviour of male moths*

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Introduction

I am honored to have been invited to come to CSIRO here in Canberra and deliver this talk. I have always wanted to visit Canberra (and Australia), partly because of all the pioneering pheromone research that has been done here over the years on the oriental fruit moth, a species dear to my heart, by Dr George Rothschild and others. But another reason was because I wanted to visit the laboratory of Dr Roger Bartell and talk with him about his work on the behaviour of moths responding to pheromones. Unfortunately, I am not able to do that, due to his death in 1985. However, I think he possibly might have appreciated some of what I am about to present, and probably would have even found ways to put me on the spot by finding holes in my work that only he could have spotted. Thus, I dedicate this paper to his memory, and hope you will see that in many ways, the work that he contributed so much to continues.

The responses of male moths to sex pheromone obviously fascinated Roger Bartell, just as they immediately did me when I entered the field of sex pheromone research years after he began his work. He, following close behind Harry Shorey, was one of the few initial pioneers in research on pheromone-mediated behaviour. While other early workers were involved in unlocking the mysteries of the structures of the pheromone chemicals themselves, Roger Bartell became enmeshed in trying to explain the sometimes maddeningly fragile nature of the male responses (Bartell and Roelofs, 1973a). He and Shorey invented one of the key bioassay setups that we all relied upon for years until wind tunnels for measuring upwind flight became widely used (Bartell and Shorey, 1969). In trying to find ways to faithfully reproduce the responses day after day – a vexing problem with some species as we all know – he eventually began exploring ways to predictably alter their responses by pre-exposing them to pheromone (Bartell and Roelofs, 1973b; Bartell and Lawrence, 1973; 1976). In the process, he became an expert at understanding the physiological and behavioural bases for the successful disruption of mating by commercial pheromone mating disruptants (Bartell, 1982). He did all this even though he had to (and later chose to) rely on assays that were only correlated with upwind flight.

During the course of exploring various pre-exposure regimes for males, he hit upon the key issue of pulsed versus continuous stimulation (Bartell and Lawrence, 1977a; 1977b). He recognized immediately the ramifications stemming from his results that showed that pulsed pre-exposure was more effective in reducing male response later-on. He reasoned that pulsed pre-exposure prevented adaptation of the antennal neurons, and allowed the more profound, longer-lasting habituation of central olfactory pathways to take place. In his later years, he began correlating his behavioural results with the neurophysiological underpinnings of behaviour, and, teamed with the expertise and knowledge of Eric Rumbo, he thus began to undertake a truly neuroethological approach (Bartell, 1985; Bartell and Rumbo, 1986).

As you will see in this paper, the neuroethological approach is one that I have also taken in my work. Like Roger Bartell, I began first by trying to understand the behaviour, and also used the extinction of the response as the powerful link with which to probe for neurophysiological correlates. The behavioural and neurophysiological events that I have been interested in are much faster – in the order of seconds rather than minutes or hours – than were his. Nevertheless, one of our recent findings is that the cessation of behaviour in some moths is correlated with the adaptation of antennal neurons, a result he might have found pleasing. To get to this point, however, we should first look at what we know about the behaviour of some flying moths.

* Dedicated to the memory of Dr Roger J. Bartell

Manoeuvring mechanisms

In order to control its direction and speed of displacement in the horizontal plane, a moth has only two reactions available at any instant; change its course angle (the direction towards which it is thrusting, relative to the wind line) and change its airspeed (its speed through the air mass next to its body) (Marsh et al., 1978). The two main mechanisms known to be used for pheromone source location by flying moths, *optomotor anemotaxis* (steering with respect to the wind) (Kennedy, 1940; Kennedy and Marsh, 1974) and *self-steered counterturning* (Baker and Kuenen, 1982; Kuenen and Baker, 1983; Baker, 1986; Kennedy, 1983), both rely on these two behavioural reactions. The *direction* of thrust (steering) can be changed by either yawing or rolling the body, the latter having been neglected over the years (Baker and Haynes, 1987; Baker, 1988). The *amount* of thrust can be changed either by a change in total wing force (e.g., wing-beat frequency) or by a change in the vertical angle of the body relative to the ground (pitch angle) (David, 1986). The changes in the strength and direction of the wing force in the horizontal plane are inextricably linked to changes in lift (hence altitude) that are also under visual feedback control (David, 1986). Altitude is also controlled by pheromone-stimulated moths (Preiss and Kramer, 1983), and thus places restrictions on flight in the horizontal plane. Much more needs to be learned about height control in pheromone-stimulated moths (Baker, 1988).

In *optomotor anemotaxis*, feedback for the control of these reactions is derived visually from the apparent movement of images, especially the ground pattern, over the eyes (Kennedy, 1940; Kennedy and Marsh, 1974). The control of course angle is a steering reaction and control of airspeed is a reaction related to the force of thrust created by the moth's wing movements.

In *self-steered counterturning* it is not known what external feedback, if any, is employed (Kennedy, 1983; 1986). The regularity in the tempo of counterturns both in and out of contact with pheromone (Baker and Haynes, 1987; Willis and Baker, 1987) indicate that there is a motor program underlying these reversals. Thus in the performance of self-steered counterturning, the direction and force of the thrust (course angle and airspeed) may need no external feedback whatsoever. The tempo at which the programme runs appears to be set by the concentration at any instant (Baker and Haynes, 1987; Baker, 1986; Kennedy, 1983, 1986).

There is now widespread agreement that pheromone-stimulated flying male moths use *optomotor anemotaxis* to progress upwind toward the source. There has been substantial disagreement, however, as to why the tracks of males flying upwind in a plume have side-to-side deviations back-and-forth across the windline, or zigzags. (Tracks of other species may be said to loop, rather than zigzag. (Baker, 1988), but the question of side-to-side deviations remains). The predominant evidence is that these deviations result from males using self-steered counterturning integrated with *optomotor anemotaxis* (Baker, 1988; Kennedy, 1986; Baker, 1986). There is much support for the existence of counterturning programs in free-flying males of several species (Baker, 1988), among which is the temporal regularity of the lateral deviations (Willis and Baker, 1987; David and Kennedy, 1987), the continuation of the zigzags even in zero wind (Baker and Kuenen, 1982; Kuenen and Baker, 1983; David and Kennedy, 1987) and even the initiation of counterturns in pheromone in zero wind (Baker et al. 1984). *Optomotor anemotaxis* polarizes the otherwise meandering zigzags into an orderly upwind resultant, taking the moth upwind in the plume to the source (Baker et al. 1984).

Not all moths necessarily integrate counterturning with *optomotor anemotaxis* while flying upwind in the plume (Haynes and Baker, 1988), but thus far it appears that all moths do so during casting flight moments after losing the plume (Kennedy, 1983; Baker 1988). Casting flight is not known to occur other than immediately after contact with pheromone, and thus pheromone mediated flight may be considered to be both flight while in contact, or immediately following contact, with pheromone (Baker, 1988), as occurs perhaps hundreds of times during flight within a plume having a fine, filamentous structure (Kennedy, 1983). The zigzag tracks of males not using counterturning while in contact with pheromone may still exhibit some (perhaps less temporally regular) zigzagging due to the moth rapidly losing and contacting the filaments, and thus reiteratively over split-second intervals beginning to go into casting behaviour (involving both counterturning and changes in course angle (Baker and Haynes, 1987) and reverting back into positive *anemotaxis*, attempting to fly straight upwind. This would be similar to the case originally envisioned by Kennedy and Marsh (1974).

A recent model invoking optomotor anemotaxis alone but with an error-plagued visual feedback system, as a cause of zigzags (Preiss and Kramer, 1987) has been recently discredited (David and Kennedy, 1987; Willis and Baker, 1987). Among the problems with this model were the fact that tethered, rather than free-flying males were used, preventing unrestricted movement in all three planes of rotation, which failed to measure lateral flight forces that would have normally occurred during free flight due to rolling (David and Kennedy, 1987; Willis and Baker, 1987; Baker, 1988). Another recent model invoking a form of chemotaxis called transverse klinotaxis as a factor in zigzagging flight (Cardé and Charlton, 1984) has also been refuted (Baker and Haynes, 1987).

A system which uses counterturning during both upwind flight and during casting may have several functions and advantages over straight-line upwind flight. It involves a continuum from narrow to wide zigzagging (Kennedy et al., 1981; Kennedy, 1983), depending on pheromone concentration, which may help facilitate contact with pheromone filaments in the plume, especially during rapid shifts in wind direction (Baker and Haynes, 1987). Secondly, the counterturning may aid the optomotor anemotactic system in more rapidly detecting changes in off-axis image flow due to wind-shifts, that might be below the visual threshold for a longer period during directly upwind flight (Baker, 1985; Cardé, 1984; Kennedy, 1986). *Grapholita molesta* males that wing fan while walking toward the source do not counterturn at all, but rather walk in a straight line directly upwind (Willis and Baker, 1987). Because they have contact with the ground, they get their information about wind direction from pressure differences across their bodies, and they do not need to counterturn to optimize sensing the wind visually.

Behaviour and pheromone concentration fluctuations

The revelation that some male moths need intermittent, not time-averaged, continuous stimulation from pheromone, in order to perform sustained upwind flight first emerged in the form of three papers (Kennedy et al., 1980, 1981; Kennedy, 1982), which showed that male *Adoxophyes orana* would not progress upwind in a uniform cloud of pheromone, but would readily fly upwind in a point-source plume placed in that same cloud. Something about the plume, conjectured to be fluctuating stimulation created by its fine structure, evoked the sustained upwind flight. These results were confirmed with another species, *G. molesta* (Willis and Baker, 1984). Flying males made a brief upwind surge when engulfed by the oncoming front of the pheromone cloud, but within a couple of seconds they became arrested and resumed wide cross-wind casting flight.

Arrestment (cessation of upwind progress while in-flight) had been described many times in the past for *G. molesta* males in excessively concentrated plumes (e.g. Baker and Roelofs, 1981; Kuenen and Baker, 1982). The movements resulting in arrestment are a brief reduction in air-speed, an increase in the course angle, and no change in the counterturning frequency (Willis and Baker, 1988), followed quickly by increased airspeed, still further increases in the course angle, a reduced counterturning frequency as the typical casting flight tracks develop (Baker and Haynes, 1987). The males' requirement for intermittent stimulation was then further experimentally demonstrated (Baker et al., 1985) when *G. molesta* males failed to zigzag upwind in continuous clouds of pheromone but readily did so when these same clouds were pulsed and interspersed with swaths of clean air.

Wright (1958) had earlier pointed out the existence and possible importance of the fine structure of odor plumes to behaviour. Murlis and Jones (1981) used ionized air and an ion detector to investigate further the nature of structured plumes (Murlis, 1986). However, without the accompanying behavioural evidence (Kennedy et al., 1980, 1981; Kennedy, 1982; Willis and Baker, 1988; Baker et al., 1985) that the structure might actually affect the efficacy of the pheromone in evoking upwind flight, Murlis and Jones' work might well have suffered the same fate as Wright's, which was to be cited frequently, but its importance not truly understood.

Male moths, whether they are tiny pyralids or huge *Polyphemus* silk moths, usually respond to the loss of pheromone within 0.4-0.5 sec by means of detectable shift from upwind flight casting flight (Marsh et al., 1981; Baker and Vogt, 1988; Baker and Haynes, 1987). Male *G. molesta* have the fastest response to pheromone loss measured in moths thus far, c. 0.15 sec (Baker and Haynes, 1987). The reaction time (the change to more directly upwind movement) in this species to an

increase in concentration is equally fast (Baker and Haynes, 1987); response latencies of males of other species to an increase in pheromone concentration have not been measured.

The short latencies of response to the onset and loss of pheromone in *G. molesta*, coupled with the knowledge that males flying upwind may contact pheromone filaments only once every second or so (Baker and Haynes, 1988) led to the realization that perhaps the zigzagging flight tracks of this species are shaped not only by the counterturning and anemotactic systems, but also by the split-second adjustments of these systems to the loss and gain of pheromone (Baker and Haynes, 1987). The reiterative change from more directly upwind flight to casting and back again might occur several times each second, and change the width and angles of the track legs, sometimes even resulting in sawtoothed-shaped tracks when the contact and loss occurs regularly according to left and right positions of the moth along its track (Baker and Haynes, 1987). Both the anemotactic and counterturning systems have this rapid reaction to fluctuating concentration, whereas adjustments in airspeed occur much more slowly. The knowledge that behaviour can change after encounters with single filaments of pheromone has suddenly placed a heavy emphasis on understanding the reaction and recovery speeds of neurons and synapses along sensory pathways. The new awareness of the rapidity of behavioural reactions has also resulted in a realization that we must focus more on learning about the speeds of neuronal and biochemical reactions at the receptor and perireceptor levels (Vogt, 1986, 1987).

Behaviour and pheromone blend quality

Another area of behavioural research that has produced substantial recent progress of profound importance to the field of pheromone research has been in the specificity of males' responses to blends of different quantities and qualities. The primary advance has occurred with recent work by Linn et al. (1986, 1987) who demonstrated experimentally that, as first suggested in experiments by Baker and Cardé (1979), males respond to a complete blend of pheromone components at all distances from the source, and not to a hierarchical succession of individual components at different distances (Howse et al., 1986; Rumbo, 1983; Bradshaw et al., 1983; Nakamura, 1979; Nakamura and Kawasaki, 1977).

It has long been known that the optimum blend ratio of pheromone components is that which most closely approximates the natural ratio emitted by females (Roelofs and Cardé, 1977; Cardé and Baker, 1984). The recent evidence from both the field and the laboratory that supports the hypothesis that this optimality is due to greater responses to the blend at all distances centres around the fact that males exhibit the lowest behavioural thresholds (are the most behaviourally sensitive) to the full blend of components compared to partial blends or to individual components. In a laboratory wind tunnel using *Argyrotaenia velutinana*, *G. molesta* and *Trichoplusia ni* both upwind flight and source location were elicited by each species' complete blend of components at 10 to 100-fold lower dosages than were elicited by partial blends (Linn et al., 1986). In the field, the complete blend of *G. molesta* components was effective in evoking wing fanning behaviour in males at twice the distance from the source than the same dosage of incomplete blends (Linn et al. 1987).

What these results mean is that although male behaviour can be evoked by a partial blend of components, it takes an inordinately high dosage to do so, much higher than to the complete blend. This fact precludes the feasibility of two scenarios explaining how flight toward the source might occur without the complete blend being involved. In the first scenario, a male sitting or flying far downwind of a pheromone-emitting female (she emits the complete blend) is thought to perhaps be at a distance at which only his receptors specific for the most abundant component would be firing. Hence this component alone would cause the behaviour. The data, however, show if the concentration at this distance is too low for the complete blend to cause a behavioural response, then it is definitely far too low for this major component alone to do so.

A key point that must be added here is that these behavioural data (Linn et al., 1986; 1987) do not preclude the postulated possibility of significant neuronal firing from only the receptor cells specific to the major component; the data only remove the possibility that such firing from one cell type is sufficient to evoke behaviour. We must be careful to distinguish between the neuronal detection of only one compound in a blend at great distances, and the behavioural response to that single type of neuronal activity at that distance, which is another matter entirely (Baker, 1989).

The former is a virtual certainty, given what we know about emitted blends and the abundance of receptor types on antennae (see below), whereas the latter simply cannot happen, according to our best behavioural data thus far. In a second type of scenario, a flying male might intersect a female-emitted plume at a distance close to the source at which the concentration of a partial blend is above the behavioural threshold for upwind flight. Of course, the data show that the concentration would also be even farther above threshold for the complete blend, and so again the complete blend will be responsible for any upwind flight that occurs.

As for its effect on neurophysiological research, this behavioural framework, centered on the importance of the complete blend, naturally places an emphasis on understanding the *integration* of neuronal activity in response to the individual components, and not merely analyzing the response thresholds and dosage-response curves of isolated, component-specific pathways. This is a profound change in perspective which is already leading to advances in understanding odor-quality encoding at the neuronal level of the CNS.

Neurophysiological correlates of behaviour

Kennedy et al. (1981) hypothesized that adaptation or habituation was the underlying cause of in-flight arrestment of upwind progress in moths entering clouds of uniform pheromone. I then hypothesized that the arrestment that was routinely observed in plumes from sources emitting excessive emission rates or ratios of pheromone might be due to the same factors as arrestment in clouds (Baker 1985). My hypothesis focused on the receptors, and implicated the excessive concentration in the plume filaments as both exceeding the capacity of the receptors to register their true concentration and also to degrade the excessive molecules fast enough to allow sufficient recovery for a cell's accurate response to the next-arriving filament. The results of Rumbo (1983) had earlier demonstrated how the concentration of such rapidly arriving pulses of pheromone can be mis-registered due to insufficient disadaptation of the receptor neurons. My hypothesis thus linked an overt change in behaviour, the cessation of upwind flight, with short-term adaptation of the receptor neurons and the subsequent attenuation of what under lower concentrations should be a rapidly fluctuating receptor neuronal output (Baker, 1985).

A first attempt to experimentally test this hypothesis involved a mobile electroantennogram (EAG) setup that could be used either in the laboratory or out in the field (Baker and Haynes, 1989). We found that the peak-to-trough EAG amplitudes caused by the individual filaments of pheromone in a plume did in fact diminish (attenuate) as an excessively emitting source was approached by *G. molesta* antennae, and that this reduction was correlated with the in-flight arrestment of flying males (Baker and Haynes, 1989), consistent with my hypothesis. However, this study indicated that the attenuation does not need to be total, as I originally envisaged (Baker, 1985). Only a relative smoothing of the signal and reduction in receptor activity appeared to be needed.

Moreover, since the level to which the attenuated signal was now reduced still exceeded levels that had earlier been sufficient to evoke take-off and upwind flight, we concluded that arrestment may occur when reduced receptor output follows higher receptor activity. The decreased neuronal output might then be registered as a decrease in concentration when in fact the actual concentration had increased. We already know that an actual drop in concentration due to flight into clean air causes arrestment and casting flight (Kennedy and Marsh, 1974; Baker and Haynes, 1987), and perhaps the "decrease" due to attenuation would also trigger arrestment and casting.

EAGs are only indirect measures of action potentials, the true signal that is transmitted to the male CNS. Thus, although the EAG results were highly suggestive of adaptation-related effects on behaviour, we recently obtained recordings from single antennal neurons that provides a more direct link between sub-optimal upwind flight in the plume and conditions that interfere with individual antennal neurons' abilities to respond to rapid plume filament-caused fluctuations. Males of the turnip moth, *Agrotis segetum*, change from upwind flight to in-flight arrestment (station-keeping) in response to an excessively concentrated, 300 µg plume of its three components (Löfstedt et al., 1985). No such arrestment is observed when males fly upwind to plumes from 3 or 30 µg sources. Recordings from antennal neurons exposed to these same plumes 70 cm downwind of the source revealed that the firing rates from cells sensitive to (Z)-5-decenyl acetate, the major component, decreased to near zero (adapted) within about 5 seconds after being placed

in the 300 μg plume, whereas such adaptation was not observed when these same neurons were placed in the 3 or 30 μg plumes (Baker et al., 1988). In plumes from the 300 μg source, the cells appeared unable to recover sufficiently from the arrivals of successive high-concentration filaments in order to adequately fire in response to subsequent filaments. The biochemical machinery of the sensilla appeared to be unable to handle these concentrations and clear away pheromone fast enough such that the receptors had sufficient time to disadapt (Rumbo 1983).

Interestingly, 30 out of 32 of the (Z)-5-decenyl acetate-sensitive neurons adapted in the 300 μg plume, but only 5 out of 12 neurons sensitive to a second component, (Z)-7-dodecenyl acetate, adapted when placed in these same 300 μg plumes. Thus a moth flying upwind in the 300 μg plume may not only experience the sensation of an odor decrease when in fact there was none, but also the sensation of blend quality may change due to the decrease in the ratio of firing of cells sensitive to (Z)-5-decenyl acetate compared to those firing in response to (Z)-7-dodecenyl acetate (Baker et al., 1988).

In *G. molesta*, partial adaptation of antennal neurons sensitive to (Z)-8-dodecenyl acetate was observed when the cells were challenged by rapid pulses of the complete pheromone blend, which included the minor components (E)-8-dodecenyl acetate (6%) and (Z)-8-dodecenyl alcohol. Adaptation was facilitated when the cells were chilled by about 6°C, and was characterized by an attenuation and reduction of the cells' fluctuating output in response to 2/s pulses (Baker et al., 1988). Adaptation occurred at the warmer temperature only when the cells were challenged with 3/s or higher pulse frequencies. As in *A. segetum*, the adaptation appears related to an overloading or swamping of the biochemical machinery of the sensilla and receptor cells which would otherwise adequately register and clear away pheromone after bombardment by a rapidly arriving filament in order to get the receptor ready to accurately register the next-arriving filament. Cool temperatures would slow down the biochemical processes involved whereas the airborne filaments would continue to arrive on the antenna just as rapidly as at warmer temperatures. Interestingly, in flight tunnel experiments, Linn et al. (1988) found that males become prematurely arrested in mid-flight more frequently in response to higher concentrations of pheromone at cooler temperatures compared to temperatures 6° higher. Moreover, at higher concentrations and cooler temperatures, the specificity of response to blend ratios shifts now to blends emitting lower proportions of the E isomer. Even the natural 6% E blend becomes deficient in evoking sustained upwind flight, and 2% E becomes optimal under these conditions. Again, the excessive concentration and subsequent differential adaptation of component-specific receptors might thus cause not only the sensation of an overall odor decrease when there was none, but also a change in the pheromone blend ratios, when there was none.

These results with *G. molesta* are again consistent with an adaptation-induced skewing of the neuronal ratio coding for blend quality. The fluctuating output from antennal neurons sensitive to the Z isomer would become reduced relative to cells sensitive to the E isomer with the same plume filaments striking the antenna simultaneously with the same frequency but at lower concentrations (nearly 20 times lower; 6% E isomer). Thus the ratio of action potentials transmitted to higher-order neurons would be too heavily weighted in favor of E-sensitive cells when in fact the actual ratio of molecules of E and Z had never changed. Behaviourally, blends with 2% E now become optimal at sustaining upwind flight.

Interestingly a similar shift in response specificity at higher emission rates in a wind tunnel appears to occur in Roger Bartell's favorite moth, *Epiphyas postvittana* (Muggleston and Foster, 1989 these symposium proceedings). At higher concentrations males exhibit greater levels of sustained upwind flight in response to blends containing lower, unnatural percentages of the diene component than they do at lower concentrations. Again the diene is a minor component (less than 10% in the natural blend relative to the monoene), and thus the swamping-induced adaptation of the cells sensitive to the most abundant component in the airborne blend (the monoene) would explain this shift (Baker et al., 1988). Such a shift does not appear to occur in the pink bollworm, *Pectinophora gossypiella*, although the temperature-related narrowing of the spectrum of blends to which males are most sensitive indicates significant temperature effects were occurring (Linn et al., 1988). The lack of a shift in this species' specificity of response at high concentrations and cold temperatures is consistent with the hypothesis of sensory adaptation, because here there is not much disparity between the abundance of the two components (60:40 ratio of the Z,Z to E,Z isomers) in the airborne blend. Thus the differential adaptation of one class of receptors is not to

be expected, only the concurrent adaptation of *both* classes and the corresponding narrowing of the range of ratios to which males respond compared to at higher temperatures (Linn et al., 1988).

Conclusion

Recent behavioural and neurophysiological evidence points to the adaptation of antennal neurons of moths as being responsible for the alteration of olfactory pathways and contributing to the cessation of upwind flight under some circumstances. Adaptation may not become apparent until the neurons are challenged with rapid pulses similar to the frequency of contact that they would experience in a filamentous plume, and at the high concentrations or low temperatures that promote arrestment of upwind flight. There appears to be a link between the adaptation of these neurons due to high concentrations and a shift in the blend ratio to which males optimally respond. There is thus evidence for a link between blend quality and quantity due to differential adaptation, as predicted by Kaissling (1987). There are no doubt other, longer-term effects of CNS habituation as well longer-term adaptation that may also alter in more profound ways the expression of behaviour (Rumbo, 1983; Bartell, 1985; Bartell and Rumbo, 1986). These, especially habituation, will be the ones which are most likely to yield effective suppression of mate location and mating following field application of disruptants (Bartell, 1982). Our experiments dealt with far more rapid exposures of moths and neurons to pulsed pheromone stimulation than Roger Bartell's. Appropriately, however, our work, coupled with other recent behavioural findings (Löfstedt et al., 1985; Linn et al., 1988; Muggleston and Foster, 1989) similarly brings together many of the very same elements of blend quality, quantity, habituation and adaptation that so fascinated this fine scientist.

Literature cited

- Baker, T.C., and Cardé, R.T. 1979. Analysis of pheromone-mediated behaviours in male *Grapholitha molesta*, the oriental fruit moth (Lepidoptera: Tortricidae) *Environmental Entomology* 8, 956-968.
- Baker, T.C., and Kuenen, L.P.S. 1982. Pheromone source location by flying moths; a supplementary non-anemotactic mechanism. *Science (Washington D.C.)* 216, 424-427.
- Baker, T.C., Willis, M.A., and Phelan, P.L. 1984. Optomotor anemotaxis polarizes self-steered zigzagging in flying moths. *Physiological Entomology* 9, 365-376.
- Baker, T.C. 1985. Chemical control of behaviour, *in*: Comprehensive insect physiology, biochemistry and pharmacology. Volume 9, Eds G.A. Kerkut and L.S. Gilbert. Pergamon Press, Ltd., New York, pp. 621-672.
- Baker, T.C., Willis, M.A., Haynes, K.F., and Phelan, P.L. 1985. A pulsed cloud of pheromone elicits upwind flight in male moths. *Physiological Entomology* 10, 257-265.
- Baker, T.C. 1986. Pheromone-modulated movements of flying moths, *in*: Mechanisms in insect olfaction. Eds T.L. Payne, C.E. Kennedy and M.C. Birch. Clarendon Press, Oxford, pp. 39-48.
- Baker T.C., and Haynes, K.F. 1987. Manoeuvres used by flying male oriental fruit moths to relocate a sex pheromone plume in an experimentally shifted wind-field. *Physiological Entomology* 12, 263-279.
- Baker T.C., and Vogt, R.G. 1988. Measured behavioural latency in response to sex-pheromone loss in the large silk moth *Antheraea polyphemus*. *Journal of Experimental Biology* 137, 29-38.
- Baker T.C., and Haynes, K.F. 1989. Field and laboratory electroantennographic measurements of pheromone plume structure correlated with oriental fruit moth behaviour. *Physiological Entomology* 13, in press.
- Baker T.C., Hansson, B.S., Löfstedt, C., and Löfstedt, J. 1988. Adaptation of antennal neurons in moths is associated with cessation of pheromone-mediated upwind flight. *Proceedings of the National Academy of Sciences of the United States of America* 85, 9826-9830.

- Baker, T.C. 1989. Pheromones and flight behaviour, *in*: Insect Flight, Eds G.G. Goldsworthy and C. Wheeler, CRC Press, Boca Raton, Florida. pp. 231-255.
- Bartell, R.J. 1982. Mechanism of communication disruption by pheromone in the control of Lepidoptera: a review. *Physiological Entomology* 7, 353-364.
- Bartell, R.J. 1985. Pheromone-mediated behaviour of male lightbrown apple moth, *Epiphyas postvittana*, correlated with adaptation of pheromone receptors. *Physiological Entomology* 10, 121-126.
- Bartell, R.J., and Lawrence, L.A. 1973. Reduction in responsiveness of males of *Epiphyas postvittana* (Lepidoptera) to sex pheromone following previous brief pheromonal exposure. *Journal of Insect Physiology* 19, 845-855.
- Bartell, R.J., and Lawrence, L.A. 1976. Reduction in responsiveness of male light-brown apple moth following previous brief pheromonal exposure is concentration dependent. *Journal of the Australian Entomological Society* 15, 236.
- Bartell, R.J., and Lawrence, L.A. 1977a. Reduction in responsiveness of male apple moths, *Epiphyas postvittana*, to sex pheromone following pulsed pheromonal exposure. *Physiological Entomology* 2, 1-6.
- Bartell, R.J., and Lawrence, L.A. 1977b. Reduction in responsiveness of male light-brown apple moths, *Epiphyas postvittana*, to sex pheromone following pulsed pre-exposure to pheromone components. *Physiological Entomology* 2, 89-95.
- Bartell, R.J., and Roelofs, W.L. 1973a. Evidence for natural secondary compounds which modify the response of males of the redbanded leaf-roller to female sex pheromone. *Annals of the Entomological Society of America* 66, 481-483.
- Bartell, R.J., and Roelofs, W.L. 1973b. Inhibition of sexual response in males of the moth, *Argyrotaenia velutinana* by brief exposures to synthetic pheromone or its geometrical isomer. *Journal of Insect Physiology* 19, 655-661.
- Bartell, R.J., and Rumbo, E.R. 1986. Correlations between electrophysiological and behavioural responses elicited by pheromone, *in*: Mechanisms in insect olfaction. Eds T.L. Payne, C.E. Kennedy and M.C. Birch. Clarendon Press, Oxford, pp. 169-174
- Bartell, R.J., and Shorey, H.H. 1969. A quantitative bioassay for the sex pheromone of *Epiphyas postvittana* (Lepidoptera) and factors limiting male responsiveness. *Journal of Insect Physiology* 15, 33-40.
- Bradshaw, J.W.S., Baker, R., and Lisk, J.C. 1983. Separate orientation and releaser components in a sex pheromone. *Nature* 304, 265-267.
- Cardé, R.T. 1984. Chemo-orientation in flying insects, *in*: Chemical ecology of insects. Eds W.J. Bell and R.T. Cardé, Chapman and Hall, London and New York, pp. 111-124.
- Cardé, R.T., and Baker, T.C. 1984. Sexual communication with pheromones, *in*: Chemical ecology of insects. Eds W. Bell and R.T. Cardé, Chapman and Hall, London and New York, pp. 355-383.
- Cardé, R.T., and Charlton, R.E. 1984. Olfactory sexual communication in Lepidoptera; strategy, sensitivity and selectivity, Symposium of the Royal Entomological Society of London, 12, 241-265.
- David, C.T. 1986. Mechanisms of directional flight in wind, *in*: Mechanisms in insect olfaction. Eds T.L. Payne, M.C. Birch and C. Kennedy, Clarendon Press, Oxford. pp. 49-57.
- David, C.T., and Kennedy, J.S. 1987. The steering of zigzagging flight by male gypsy moths. *Naturwissenschaften* 74, 194-195.
- Haynes, K.F., and Baker, T.C. 1989. An analysis of anemotactic flight in female moths stimulated by host odour and comparison to the males' response to sex pheromone. *Physiological Entomology* 14, in press.

- Howse, P.E., Lisk, J.C., and Bradshaw, J.W.S. 1986. The role of pheromones in the control of behavioural sequences in insects, *in: Mechanisms in insect olfaction*. Eds. T.L. Payne, M.C. Birch and C.E.J. Kennedy. Clarendon Press, Oxford. pp. 157-162.
- Kaissling, K.E. 1987. R.H. Wright Lectures on Insect Olfaction. Ed. K. Colbow. Simon Fraser University, Burnaby, B.C., Canada.
- Kennedy, J.S. 1940. The visual responses of flying mosquitoes. *Proceedings of the Zoological Society of London, A* 109, 221-242.
- Kennedy, J.S., and Marsh, D. 1974. Pheromone-regulated anemotaxis in flying moths. *Science (Washington D.C.)* 184, 999-1001.
- Kennedy, J.S. 1978. The concepts of olfactory 'arrestment' and 'attraction'. *Physiological Entomology* 3, 91-98.
- Kennedy, J.S., Ludlow, A.R., and Sanders, C.J. 1980. Guidance system used in moth sex attraction. *Nature (London)* 295, 475-477.
- Kennedy, J.S., Ludlow, A.R., and Sanders, C.J. 1981. Guidance of flying male moths by wind-borne sex pheromone. *Physiological Entomology* 6, 395-412.
- Kennedy, J.S. 1982. Mechanism of moth sex attraction: a modified view based on wind-tunnel experiments with flying male *Adoxophyes*. *Les colloques de l'INRA* 7, 189-192.
- Kennedy J.S. 1983. Zigzagging and casting as a response to windborne odour: a review. *Physiological Entomology* 8, 109-120.
- Kennedy, J.S. 1986. Some current issues in orientation to odour sources, *in: Mechanisms in insect olfaction*. Eds T.L. Payne, M.C. Birch and C. Kennedy. Clarendon Press, Oxford. pp. 11-25.
- Kuenen, L.P.S., and Baker, T.C. 1982. The effects of pheromone concentration on the flight behaviour of the oriental fruit moth, *Grapholitha molesta*. *Physiological Entomology* 7, 423-434.
- Kuenen, L.P.S., and Baker, T.C. 1983. A non-anemotactic mechanism used in pheromone source location by flying moths. *Physiological Entomology* 8, 277-289.
- Linn, C.E., Jr, Campbell, M.G., and Roelofs, W.L. 1986. Male moth sensitivity to multicomponent pheromone: critical role of female-released blend in determining the functional role of components and active space of the pheromone. *Journal of Chemical Ecology* 12, 659-668.
- Linn, C.E., Jr, Campbell, M.G., and Roelofs, W.L. 1987. Pheromone components and active spaces: what do moths smell where do they smell it? *Science (Washington D.C.)* 237, 650-652.
- Linn, C.E., Campbell, M.G., and Roelofs, W.L. 1988. Temperature modulation of behavioural thresholds controlling male moth sex pheromone response specificity. *Physiological Entomology* 13, 59-67.
- Löfstedt, C., Linn, C.E., Jr, and Löfqvist, J. 1985. Behavioral responses of male turnip moths, *Agrotis segetum*, to sex pheromone in a flight tunnel and in the field. *Journal of Chemical Ecology* 11, 1209-1221.
- Marsh, D., Kennedy, J.S., and Ludlow, A.R. 1978. An analysis of anemotactic zigzagging flight in male moths stimulated by pheromone. *Physiological Entomology* 3, 221-240.
- Marsh, D., Kennedy, J.S., and Ludlow, A.R. 1981. Analysis of zigzagging flight in moths: a correction. *Physiological Entomology* 6, 225.
- 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. *Physiological Entomology* 6, 71-86.
- Murlis, J. 1986. The structure of odour plumes, *in: Mechanisms in insect olfaction*. Eds T.L. Payne, M.C. Birch and C.E.J. Kennedy. Clarendon Press, Oxford. pp. 27-38.

- Nakamura, K., and Kawasaki, F. 1977. The active space of *Spodoptera litura* (F) sex pheromone and the pheromone component determining this space. *Applied Entomology and Zoology* 12, 162-177.
- Nakamura, K. 1979. Effect of the minor component of the sex pheromone on the male orientation to pheromone source in *Spodoptera litura* (F). *Chem. Rev. Insect (Russia)* 4, 153-156.
- Preiss, R., and Kramer, E. 1986. Mechanism of pheromone orientation in flying moths. *Naturwissenschaften* 73, 555-557.
- Roelofs, W.L., and Cardé, R.T. 1977. Responses of Lepidoptera to synthetic sex pheromone chemicals and their analogues. *Annual Review of Entomology* 22, 377-405.
- Rumbo, E.R. 1983. Differences between single cell responses to different components of the sex pheromone in males of the light-brown apple moth (*Epiphyas postvittana*). *Physiological Entomology* 8, 195-201.
- Vogt, R.G., and Riddiford, L.M. 1986. Pheromone reception, a kinetic equilibrium, in: Mechanisms in insect olfaction. Eds T.L. Payne, M.C. Birch and C.E.J. Kennedy, Clarendon Press, Oxford. pp. 201-208.
- Vogt, R.G. 1987. The molecular basis of pheromone reception: its influence on behavior, in: Pheromone biochemistry. Eds G.D. Prestwich and G.L. Blomquist, Academic Press, New York. pp. 385-431.
- Willis, M.A., and Baker, T.C. 1984. Effects of intermittent and continuous pheromone stimulation on the flight behaviour of the oriental fruit moth, *Grapholita molesta*. *Physiological Entomology* 9, 341-358.
- Willis, M.A., and Baker, T.C. 1987. Comparison of manoeuvres used by walking versus flying *Grapholita molesta* males during pheromone-mediated upwind movement. *Journal of Insect Physiology* 33, 875-883.
- Willis, M.A., and Baker, T.C. 1988. Effects of varying sex pheromone component ratios on the zigzagging flight movements of the oriental fruit moth, *Grapholita molesta*. *Journal of Insect Behavior* 1, 357-371.