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## Pheromones of the housefly

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# Chapter 8

## GENERAL DISCUSSION

The housefly is a highly successful insect species and creates considerable problems especially in the agricultural sector. The substantial production losses, occurrence of stress by their irritating presence (Axtell and Arends, 1990), and the fact that flies can act as transmitters of many bacterial and viral pathogens (Pospischil, 1994), has strongly stimulated the demand for an adequate control of the flies. The customary approach is to apply insecticides. However, the rapidly spreading resistance of *Musca domestica* to the environmentally unfriendly insecticides (Chapman and Morgan 1992, Pospischil et al. 1996), has led to more frequent application of increasingly higher doses of insecticides. This has caused severe chemical contamination of the environment.

The main questions we were dealing with in the present study were:

1. Does the production of cuticular hydrocarbons that affect the behaviour of the flies, differ in different fly populations (laboratory versus wild-type strains) and, if so, do the behavioural responses of these strains to these hydrocarbons differ?
2. Does an oviposition-stimulating pheromone exist in *M. domestica*?
3. Can we use these semiochemicals for environmentally friendly control of houseflies?

We found that the behavioural role of one of the cuticular substances, (Z)-9-tricosene ('muscalure'), as a female sex pheromone is overestimated. (Z)-9-tricosene is commonly considered to be the most important component of the female sex pheromone of the housefly since behavioural studies have shown that it is attractive to male *M. domestica* and induces sexual behaviour in males. However, our results showed that wild-type strains produce muscalure hardly or not at all (Chapter 2). As a consequence, we concluded that this chemical is not indispensable for reproduction of

*M. domestica*. This implies that, in contrast to what has been advanced by Uebel et al. (1978) and Adams and Holt (1987), the oxidation products of muscalure, (Z)-9,10-epoxytricosane and (Z)-14-tricosen-10-one, also may not be essential to induce sexual activity in male flies. We propose that, if present, (Z)-9-tricosene, being the most volatile of the cuticular hydrocarbons of the females, is perceived easier by the males than other less volatile hydrocarbons of females and therefore may be the most 'suitable' hydrocarbon for short-range attraction. Other hydrocarbons may also play a role in inducing sexual behaviour in males. In contrast to experiments in the laboratory where a single hydrocarbon can be tested for its behavioural effects on males, this situation will not be met in nature. In natural conditions, a male fly approaching a female, will never be exposed to a single hydrocarbon. It will always occur in combination with other components of a complex blend. We therefore considered the idea that the males only respond to one chemical out of a complex mixture of chemicals present on the cuticle of females rather questionable. Single-cell responses to muscalure do not markedly differ from the responses to other cuticular hydrocarbons. In fact, Kelling (2001) showed that single cells in the antennae of both male and female *M. domestica* respond to many different chemicals and therefore all cells are probably generalists. This situation is totally different from that in, for example, several species of moths where specialist cells in the antennae detect sex pheromones. This specificity for pheromone molecules is not present in houseflies. We showed that EAG responses to (Z)-9-tricosene were somewhat lower than to (Z)-9-heneicosene, which is 2 C atoms shorter, and higher than the responses to (Z)-9-heptacosene, which is 4 C atoms longer. This again suggests that the perception of substances, and thereby the behaviour of the males, may be determined to a considerable extent by their volatility. These findings suggested that a mixture of cuticular lipids may form the most suitable attractant to be used in control methods. For practical purposes a mixture of a small number of chemicals should be composed that approximates the natural blend as close as possible and that can be produced easily. A good starting point for field experiments should be a mixture of (Z)-9-tricosene and (Z)-9-heptacosene, because these chemicals have proven to induce sexual behaviour and are relatively easily to synthesize (Chapters 3 and 5). The addition of (Z)-9-heneicosene, which lowers the melting point and makes the mixture more volatile, should be considered.

We found that selection processes in isolated housefly populations may lead to the production of higher amounts of muscalure by the females (Chapters 2 and 3) and that relative humidity and temperature may affect the production of cuticular hydrocarbons by both males and females (Chapter 4). Lower relative humidity and higher temperatures may lead to higher amounts of these substances on the flies and to a relative increase of long-chain saturated hydrocarbons. These changes may account for concomitant changes in cuticular permeability to water, as has been found in several species of arthropods (Toolson and Hadley, 1979; Hadley and Schultz, 1987). In the tiger beetles, *Cicindela obsoleta* and *C. oregano*, for example, Hadley and Schultz (1987) showed a significant negative correlation between water loss rate and the quantity of saturated hydrocarbons. Gibbs *et al.* (1995) suggested that a potential consequence of pheromone production by female houseflies may be that cuticular transpiration is increased because the pheromone components are unsaturated or methyl-branched, which tends to lower melting temperatures. We propose that in an environment where rapid changes in temperature and humidity may occur, the presence of muscalure may negatively interfere with the water barrier function of the cuticular layer. In our opinion, this is the main reason why muscalure was not or hardly produced by the wild-type flies we collected in stables in The Netherlands. In laboratory cultures that are usually kept at a constant temperature of about 25 °C this negative effect will not be met, even at a rather high production level of muscalure. Females living in the laboratory in successive generations will, therefore, produce this substance with its relatively high volatility and attractiveness to males, in higher amounts. This leads to the conclusion that results obtained from laboratory housefly populations cannot simply be considered valid for wild-type populations. In addition, differences in hydrocarbon composition may be expected between housefly populations living at different climatic circumstances and feeding from substrates of different composition. As to the latter, it has been observed that the amounts of (Z)-9-heptacosene are significantly higher on females fed with sugar than on those fed with protein (Adams and Nelson, 1990).

It may be assumed that males may be more sensitive to blends of hydrocarbons that are in close harmony with the cuticular hydrocarbon composition of the females of their own strain. This implies that, if these semiochemicals are used for control purposes, the composition of the hydrocarbon blend has to be adjusted to the local situation.

Houseflies prefer to deposit their eggs in clusters at one and the same site in crevices in rough substrates, especially when these have a smell of decaying animal products. We found strong indications that an oviposition pheromone is deposited together with the eggs (Chapter 7). Identification and synthesis of this oviposition-stimulating pheromone should be one of the main goals in future research. Attracting pregnant females using pheromones to places where they can be killed may be a very effective way of controlling the flies.

The new 'self-loading' technique for semiochemicals described in Chapter 5 can also be used in behavioural studies on other insects. The use of aggressive solvents, which may affect the condition and behaviour of the animals is avoided. Moreover, using this technique, the distribution of the semiochemicals over the various body parts mimics the natural distribution better than when these substances are applied in a solvent to the thorax of the insect.

Up till now hardly any attention has been paid to the behaviour of females during copulatory attempts of males. Without protrusion of the ovipositor by a female copulation cannot be established. It is still unknown why some males are immediately 'accepted' by females and other males not or only after they have made several strikes. The described technique allows, for example, males to be loaded in a non-aggressive way with different amounts of various semiochemicals for studying the sexual behaviour of the females to these males.

The radar-Doppler technique (Chapter 6) provides a relatively easy way to find out which semiochemicals induce behavioural responses in flies. In this way biologically active and non-active substances can be separated relatively easily before the above experiments are carried out. The technique is also suitable for studies on other insect species.