3 Methods in Studying Insect Behaviour

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3.1. Introduction

At its simplest, behaviour is what animals do – in particular their actions and reactions. Behaviour is central to the ecology of insects and thus underlies most questions in entomology. It may be an explicit part of a project but even with the most applied question, ultimately, the behaviour of insects determines if and how they become pests, whether it is how they get to the crop or what they feed on.

Where the focus of projects can differ is in the type of question being asked or addressed. The same behaviour can be looked at in complementary ways – the 'tuer why' (Tinbergen, 1963): its immediate cause (or control); its development during the life of the individual (ontogeny); its function, and how it evolved. While your current question might be the mechanism or immediate stimulus for the behaviour, it may be that looking at another 'why' might provide new insight. For example, the proximate question of host plant selection by an insect might be partly explained by its evolutionary history as shown by patterns among related species. Much of the most successful behavioural work combines these approaches.

This chapter is designed for two types of researcher – those interested in behaviour for its own sake; and those whose initial question is not behavioural but who find they need to understand more about how their insects behave in a particular system. Behavioural approaches have proved useful for a wide variety of applied problems in entomology, including assessing potential biocontrol agents (see this volume, Chapter 11), studies of resistant plant varieties (see this volume, Chapter 6) and of pesticide resistance (see this volume, Chapter 10). As an example, consider the mode of action for the increased pest resistance of glossy leaved cabbage, Brassica oleracea, varieties over normal-leafed varieties (see Uilenbroek et al., 1995; this volume, Chapter 6). The resistance is not based on toxicity – indeed there was no
resistance to diamondback moth, Plutella xylostella, in greenhouse experiments, whereas in field experiments, the populations showed a higher level of resistance. The key to resistance in the field might then be the number of other factors, such as the availability of food, the presence of predators, and the effectiveness of disease control, that can influence the overall level of resistance.

The same is true for other organisms, such as the cabbage white butterfly, Pieris brassicae, which has been shown to be more resistant to the parasitoid wasp, Asobara tumidula, in greenhouse experiments, whereas in field experiments, the population showed a higher level of resistance. The key to resistance in the field might then be the number of other factors, such as the availability of food, the presence of predators, and the effectiveness of disease control, that can influence the overall level of resistance.

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3.2.2 Recording and Observing Behaviour

For many experiments, there may be a relatively simple and direct way to record and observe the behaviour of an organism. For example, if you are observing the behaviour of a bird, you may be able to simply watch the bird and record its actions. However, in other experiments, it may be necessary to use more sophisticated techniques, such as video recording or computer-aided observation.

One of the most interesting and fruitful lines of research in this area has been the development of techniques for recording and observing the behaviour of individual organisms. This has been particularly useful in the study of social insects, such as ants and bees, which are known to have a high degree of communication and cooperation. By recording and observing the behaviour of individual ants and bees, researchers have been able to gain a better understanding of the ways in which these insects communicate and cooperate.

Another important area of research has been the development of techniques for recording and observing the behaviour of animals in their natural environments. This has been particularly useful in the study of animals, such as birds and mammals, which are known to have a high degree of communication and cooperation. By recording and observing the behaviour of individual birds and mammals, researchers have been able to gain a better understanding of the ways in which these animals communicate and cooperate.
3.3.1 Recording the data

Having made your preliminary observations, it will be time to begin collecting data on your subject. In this chapter, we will discuss the basic procedures for collecting data on animal behaviour. We will cover the following topics:

- Recording data
- Analyzing data
- Presenting data

Recording data

When you have established the behaviour of the subject of interest, you can begin to record the data. This can be done using a number of different methods, such as:

- Video recording
- Audio recording
- Digital photography

Video recording

Video recording is a popular method for recording animal behaviour. It allows you to capture the behaviour of the subject in detail, and can be used to study a variety of behaviours, such as:

- Social interactions
- Foraging
- Mating

When recording video, it is important to:

- Ensure that the camera is steady
- Keep the camera close to the subject
- Avoid interference

Audio recording

Audio recording is a useful method for studying the sounds produced by animals. It can be used to study:

- Vocalizations
- Communication

When recording audio, it is important to:

- Use a good quality microphone
- Avoid background noise
- Record in a quiet environment

Digital photography

Digital photography is a useful method for recording static images of animal behaviour. It can be used to study:

- Habitat
- Feeding
- Reproduction

When recording images, it is important to:

- Use a good quality camera
- Avoid movement
- Record in a well-lit environment

Analyzing data

Once you have collected the data, you can begin to analyze it. This can be done using a number of different methods, such as:

- Quantitative analysis
- Qualitative analysis
- Statistical analysis

Quantitative analysis

Quantitative analysis is a method for analyzing data that involves the use of numerical data. It can be used to study:

- Frequency
- Duration
- Intensity

When performing quantitative analysis, it is important to:

- Use appropriate statistical tests
- Check for outliers
- Ensure that the data is normally distributed

Qualitative analysis

Qualitative analysis is a method for analyzing data that involves the use of non-numerical data. It can be used to study:

- Patterns
- Trends
- Relationships

When performing qualitative analysis, it is important to:

- Use appropriate methods
- Check for bias
- Ensure that the data is complete

Statistical analysis

Statistical analysis is a method for analyzing data that involves the use of statistical tests. It can be used to study:

- Correlation
- Regression
- ANOVA

When performing statistical analysis, it is important to:

- Use appropriate tests
- Check for assumptions
- Ensure that the data is accurate

Presenting data

Once you have analyzed the data, you can begin to present it. This can be done using a number of different methods, such as:

- Graphs
- Tables
- Figures

Graphs

Graphs are a useful method for presenting data. They can be used to:

- Display patterns
- Show trends
- Compare data

When creating graphs, it is important to:

- Use appropriate scales
- Label axes
- Use colors

Tables

Tables are a useful method for presenting data. They can be used to:

- Show data
- Compare data
- Present results

When creating tables, it is important to:

- Use appropriate headings
- Sort data
- Use colors

Figures

Figures are a useful method for presenting data. They can be used to:

- Display patterns
- Show trends
- Compare data

When creating figures, it is important to:

- Use appropriate scales
- Label axes
- Use colors

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AMAZING IMAGES TO TRACK MOVEMENT

Videos are often used to record the paths of animals. However, it is worth asking, the

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ACTOGRAPHS AND OTHER AUTOMATIC RECORDING METHODS
For some kinds of questions, such as those on activity rhythms, automatic data collection offers major advantages, not least that it makes the investigation of circadian rhythms possible without sleep deprivation for the experimenter. The behaviour usually needs to be fairly simple one, such as an increase or decrease in movement in a cage, which can be detected easily. By careful design of the sensors it may be possible to allow the system to distinguish different behaviours. One disadvantage of using an actograph is that one cannot see what is happening and this may limit one’s scope for thinking of the next experiment.

An important feature of whatever method is used is that it should not be detectable by, or change the behaviour of, the insects themselves. The technique needs to be validated by observation to confirm the effectiveness of the recording mechanism and that it accurately reflects the insects’ behaviour.

There are many different mechanisms but basically all actographs detect movement by breaking a light beam or a change of some sort detected electronically (e.g. actographs used levers to exaggerate the scale of movement and traced a track on a smoked drum) and are limited only by your ingenuity. New techniques are likely to be developed as new transducers are invented and electronic devices get cheaper. Amongst the methods used to detect movement so far are roller-cages, infrared, ultrasound, wing beat sound, vibration, changes in capacitance, temperature, Doppler shift radar (e.g. Kurosaki and Brady, 1994; Snowball and Holmquist, 1994). As the output is often an electrical signal, most systems can now be linked to a data logger or a computer via an analog/digital converter card which allows for easier analysis (e.g. Berriswine et al., 1965, for a flight mill, but the same principles apply) RECORDER ENVIRONMENTAL VARIABLES

The small size of insects means that they are usually more affected by the environment than larger animals. Temperature is a major factor influencing their behaviour. It can thus be very important to be able to measure this, together with relative humidity. Meteorological station data may be inappropriate since it is not what the insects are experiencing. Rather, one needs micrometeorological data taken on a scale relevant to the insect. Unwin and Cobet (1991) and Unwin (1980) consider a range of methods. Data loggers may be useful for recording the data over a period of time.

Some insects are able to maintain internal temperatures well above ambient and thermanregulatory behaviour has become a new field of study (Henrich, 1993). The standard way of recording internal temperatures, stabbing the thorax with a thermocouple for example, has been criticized by Stone and Willmer (1989). Jones (1982) used a blue pigment, which faded in sunlight, mixed in yellow paint and painted on to snail shells. Suitably calibrated, the fading from green allowed estimation of how much time the animal had spent in the sun (it works equally well with beetles).

3.2.4. Statistics and experimental design

Determining preferences, for example for one plant species over another, is a common aim of experiments in insect behaviour. In a thoughtful essay, Singer (1986) discusses the definition of preference (which is not straightforward) and the merits of a range of experimental designs: no choice, sequential choice, and simultaneous choice (where all the alternatives are offered at the same time). Different results can be obtained depending on the preference testing technique. Although Singer discusses oviposition behaviour, his conclusions have wide relevance to anyone using preference tests.

In no choice tests, celling effects (in which all stimul get high responses) or, conversely, floor effects (where almost none respond) may be resolved by trying another behavioural measure, for example latency (Martin and Bateson, 1993).
3.3. Factors Influencing Behaviour

Any investigation of insect behaviour needs to be informed by an understanding of the fundamental processes that influence the expression of behavio

The response of an insect is determined not only by the stimulus but also by the physiological state of the insect and the context in which it is acting. For example, when a female moth is searching for a mate, it may respond to pheromones produced by males in the vicinity, but if it has recently been feeding on a host plant, it may be less responsive to pheromones from males not in the vicinity.

In many cases, the response of an insect to a stimulus is modulated by the insect's internal state. For example, a female moth may be more responsive to pheromones from males when it is ovipositing than when it is not ovipositing. Similarly, a male moth may be more responsive to pheromones from females when it has recently fed on a host plant than when it has not fed.

In addition to internal state, the response of an insect to a stimulus is also influenced by the social context in which it is acting. For example, a female moth may be more responsive to pheromones from males when it is in the presence of other females than when it is alone.

3.3.1. Internal State

The internal state of an insect is determined by a variety of factors, including its physiological state, its biological state, and its psychological state.

Physiological state

The physiological state of an insect is determined by a variety of factors, including its age, its sex, and its reproductive status. For example, a female moth may be more responsive to pheromones from males when it is ovipositing than when it is not ovipositing. Similarly, a male moth may be more responsive to pheromones from females when it has recently fed on a host plant than when it has not fed.

Biological state

The biological state of an insect is determined by a variety of factors, including its age, its sex, and its reproductive status. For example, a female moth may be more responsive to pheromones from males when it is ovipositing than when it is not ovipositing. Similarly, a male moth may be more responsive to pheromones from females when it has recently fed on a host plant than when it has not fed.

Psychological state

The psychological state of an insect is determined by a variety of factors, including its experience, its motivation, and its learning. For example, a female moth may be more responsive to pheromones from males when it has been exposed to pheromones from males than when it has not been exposed to pheromones from males. Similarly, a male moth may be more responsive to pheromones from females when it has been exposed to pheromones from females than when it has not been exposed to pheromones from females.

3.3.2. Social Context

The social context of an insect is determined by a variety of factors, including the presence or absence of other insects, the density of other insects, and the interactions between other insects.

Presence or absence of other insects

The presence or absence of other insects can have a significant impact on the response of an insect to a stimulus. For example, a female moth may be more responsive to pheromones from males when it is in the presence of other females than when it is alone. Similarly, a male moth may be more responsive to pheromones from females when it is in the presence of other males than when it is alone.

Density of other insects

The density of other insects can also have a significant impact on the response of an insect to a stimulus. For example, a female moth may be more responsive to pheromones from males when the density of other females is high than when the density of other females is low. Similarly, a male moth may be more responsive to pheromones from females when the density of other males is high than when the density of other males is low.

Interactions between other insects

The interactions between other insects can also have a significant impact on the response of an insect to a stimulus. For example, a female moth may be more responsive to pheromones from males when it is in the presence of other females that are ovipositing than when it is in the presence of other females that are not ovipositing. Similarly, a male moth may be more responsive to pheromones from females when it is in the presence of other males that have recently fed on a host plant than when it is in the presence of other males that have not fed on a host plant.

3.3.3. Environmental Factors

The environmental factors that influence the response of an insect to a stimulus include temperature, humidity, light, and wind.

Temperature

Temperature can have a significant impact on the response of an insect to a stimulus. For example, a female moth may be more responsive to pheromones from males when the temperature is high than when the temperature is low. Similarly, a male moth may be more responsive to pheromones from females when the temperature is high than when the temperature is low.

Humidity

Humidity can also have a significant impact on the response of an insect to a stimulus. For example, a female moth may be more responsive to pheromones from males when the humidity is high than when the humidity is low. Similarly, a male moth may be more responsive to pheromones from females when the humidity is high than when the humidity is low.

Light

Light can also have a significant impact on the response of an insect to a stimulus. For example, a female moth may be more responsive to pheromones from males when it is in the presence of light than when it is in the absence of light. Similarly, a male moth may be more responsive to pheromones from females when it is in the presence of light than when it is in the absence of light.

Wind

Wind can also have a significant impact on the response of an insect to a stimulus. For example, a female moth may be more responsive to pheromones from males when it is in the presence of wind than when it is in the absence of wind. Similarly, a male moth may be more responsive to pheromones from females when it is in the presence of wind than when it is in the absence of wind.
3.3.4. Post-experience and learning

While very few studies have explicitly addressed associative learning in the same way that they have in simpler organisms, there are indications that at least some animals may be capable of learning and forming associations with olfactory stimuli in the same way that they do with visual or auditory stimuli. One such example is the honeybee, which has been shown to be capable of learning associations between specific odours and landmarks or other environmental cues (Williams and Hansell, 1992). Other studies have suggested that birds and certain other species may also be capable of learning from olfactory stimuli, although the evidence for this is less robust. Overall, the evidence suggests that associative learning and olfactory memory may be more widespread than previously thought, but further research is needed to fully understand the mechanisms involved.

3.3.5. Communication and signal competition

The ability of animals to communicate with each other through the use of odours is a key factor in the evolution of sociality. In many species, the release of pheromones is a critical component of social interaction, and the ability of individuals to detect and interpret these signals is essential for the maintenance of social structure. However, the exploitation of pheromone signals by different individuals or groups can also lead to signal competition, which can have important consequences for the functioning of social systems. For example, in some species, the release of pheromones by dominant individuals can suppress the response of subordinates, leading to reduced aggression and increased cooperation. Overall, the study of pheromone communication and signal competition is a rapidly growing field, with important implications for our understanding of animal sociality and behaviour.

3.4. Conclusions

In conclusion, the study of pheromones and animal communication has provided important insights into the evolution of sociality and the mechanisms underlying cooperation and competition in animal societies. While there is still much to be learned about the role of pheromones in different species and contexts, the evidence suggests that these signals are a critical component of social behaviour in a wide range of taxa. Further research is needed to fully understand the complex interactions between pheromones and other forms of communication, as well as the role of social learning and experience in the evolution of pheromone-based communication systems.
insects should not be used more than once in an experiment if possible as later behaviour may be influenced by a first treatment. The implications of insect learning to pest management are examined by Prokopy and Lewis (1993) who make the point that both beneficial insects and pests show learning of various kinds. A well established phenomenon is the effect of artificial rearing conditions on the behaviour of parasitoids for release, which may reduce their effectiveness in the field. Learning could also affect other phenomena such as pest population estimates based on mark-release-recapture, if handled insects behave differently. Pest habituation, or conversely sensitization, could affect the effectiveness of pest resistance.

1.3.5. External stimuli

External stimuli such as visual, auditory or olfactory stimuli are some of the most obvious influences on behaviour and are the ones that can most easily be manipulated by the experimenter. Most behavioural experiments involve changing these external stimuli (see below). While external stimuli presented to the animal might be kept constant, they will not always produce the same inputs as peripheral receptor responses are influenced by physiological variables—e.g. locust taste chemoreceptors are influenced by haemolymph levels of nutrients such as amino acids, being less responsive when levels of that nutrient are high (see Simpson et al., 1985).

Taking account of the way animal perceptual worlds differ from ours is always important in behaviour but perhaps especially for work on insects. Olfaction and taste are much more important in insects and even apparently familiar senses such as vision are different from our own both in spectral sensitivity and acuity.

1.3.6. Integration

The theme developed by Harris and Foster (1995), in an excellent review, is the integration of internal and external sensory inputs in behaviour. Internal factors include, for example, those that change with age, prior experience, and mating status. Moreover, despite the desire of the experimenter to concentrate on one external stimulus, for example host odours, the majority of insect behaviours may be driven by combined inputs from many senses—from vision as well as chemosensory (see also Prokopy, 1986).

While single sensory inputs, such as a chemical stimulus, can be investigated by themselves, multicausal and possibly multi-level tests can tease out the stimuli involved in behaviours, and may sometimes show interactive effects of stimuli that would be missed had they each been tested alone (Harris and Foster, 1995). A good example is that of the aggregation behaviour of Hessian flies, Mayetiola destructor, a pest of wheat which lays its eggs on the leaves. In a three-way factorial experiment testing colour, chemical, and tactile stimuli, Harris and Rose (1996) found all three stimuli had a significant effect on numbers of eggs laid (and all possible first and second order interactions were also significant; see Fig. 3.1). From this one might conclude that the three stimuli were all integrated in the response. However, as Harris and Foster (1995) point out, a second experiment (Harris et al., 1993), which investigated the behaviours leading to egg-laying, as well as number of eggs laid, showed that although colour influenced approach and landing behaviour it did not affect the number of eggs laid once the female had landed, whereas chemical stimuli were important at each stage. There are some disadvantages of more complex factorial experiments: logistic problems of carrying out enough replicates and interpretation of interactions are among these.

Fig. 3.1. Integration of stimulus: the role of colour, chemical, and tactile cues in oviposition by Hessian flies, Mayetiola destructor, on plant models. A 2 x 2 factorial gave eight combinations of stimuli. Wax coated paper-leaf leaves were coloured green (comparing with uncoloured white), closed with wheat culicular wax extract (comparing with control solvent alone), and given vertical grooves in the wax to simulate leaf veins (or left without grooves). One of each stimulus combination was present in the simultaneous test with a single female. Black boxes indicate the first cue at each pair is present. The main effects of each stimulus and the higher order interactions were of significant. (From Harris and Foster, 1995, data from Harris and Rose, 1990; reproduced with permission from Entomological Society of America.) However, later experiments showed the effect of colour (green) was due to its effect in increasing landing (Harris et al., 1993).
3.4. Investigating Behaviour

The decision to investigate a species is usually made on the basis of its potential to provide insight into an ecological or evolutionary question. For example, studies of birds have helped us understand the evolution of flight, while studies of insects have helped us understand the evolution of communication.

Laboratory experiments can be an effective way to study the effects of a stimulus on a species. For example, studies of insect communication have shown that the presence of a pheromone can alter the choice of partner in a mate selection experiment.

In conclusion, laboratory experiments can be a powerful tool for studying the effects of stimuli on a species. However, they should be used in conjunction with field studies to ensure that the results are ecologically relevant.

Fig 3.2: Schematic diagram of a test chamber for studying the effects of a pheromone on mating behavior. The test chamber consists of a mating arena and a pheromone release chamber. The pheromone is released into the mating arena, and the behavior of the insects is observed.


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if you are investigating responses to resource stimuli it may be worth investigating factors such as habitat structure, patch size and resource distribution (Prokopy, 1986). Ultimately, the goal is to test the predictions in the field.

3.4.2. Field observation

Laboratory experiments may allow for easier replication of experiments but they raise the question: do animals really behave in the same way in the wild? This can only be answered by observing animals in their natural environment, in the field.

Important new subjects such as the role of learning in entomophagous parasitoids (see Section 3.3.4) can grow up without a firm base of studies showing its significance in the field (Papaj, 1993). Similarly, almost all studies on the feeding patterns of herbivorous insects have been laboratory based, with a range of plant choices determined by the experimenter. Rauenthaler and Bernays (1993) heroically followed individual marked female grasshoppers (Locomela sparsi) for the whole day (sunrise to sunset) in Arizona. Using a hand-held electronic event recorder (see Section 3.2.3) they recorded all the feeding bouts, their duration and marked the plants for later identification as the insects moved around the habitat. For this species, perhaps reassuringly, many parameters such as the feeding rate of the insects feeding events into bouts, were very similar to laboratory studies of other arachnids although there were some differences which highlighted the need for equivalent laboratory studies of this species. Similar field techniques have been applied to other insects. For example, Aluja et al. (1989) labelled every twig on trees to allow the 3-D movement of apple maggot flies, Rhagoletis pomonella, to be followed. Near-focusing binoculars to follow insects may be useful in field studies. Nocturnal insects have been observed in the field by using night vision equipment, for example, the behaviour of moths flying to pheromone traps (see Riley 1994; also this volume, Chapter 5, Opp and Prokopy 1986) discuss other aspects of field experiments. For example, you may need to mark your animals (see Chapter 5).

Much of the classic work on ant navigation has been done in the field (see e.g. Wehner et al., 1996) as was Tinbergen’s pioneering work with the digger wasps. In each case experimental manipulation was combined with observation. Placing models or test arenas in the field so animals encounter them naturally can be very effective (e.g. Judd and Borden’s, 1991, experiments on ocean fly, Dolichopus antiguus). A major advantage of field experiments is that the internal state of the animals can be assumed to be natural, but with the disadvantage that it might not be known or necessarily repeatable. Another reason for studying animal behaviour in the field is when important factors, especially stimuli, might be altered by moving the experiment into laboratory. For example, cutting, plants to provide leaves for feeding choices could alter wilting leaves and imitate wound responses by the leaves, all factors now known to affect insect feeding behaviour (Bernays and Chapman, 1994). When it is impossible to reproduce field conditions in the laboratory, for example the range and activity of predators, field experiments may be the only way of investigating topics such as the effectiveness of parental care. For example, by elegant in situ exclusion experiments Tallamy and Deno (1982) showed that eggplant lace bug, Desepseiy solani, females were able to successfully defend their broods against arthropod predators.

While there are many advantages in doing field experiments there are also good reasons why many experimenters attempt to do at least part of their work through laboratory experiments. The principal problem in temperate regions is the unpredictability of the weather. On cool or rainy days there may be no insect activity. Low animal densities may also be a problem. With field behavioural work on some species (especially for pests – not chosen for their case of study) the problem is not being able to identify species or their sex accurately at a distance (Finch, 1986). In these cases you will need to be able to catch the individual after the experiment.

Where field conditions are difficult or the animals are difficult to rear, a compromise may be to use field collected animals in laboratory experiments where you can better control the conditions. It is possible to discover much about the field behaviour of insects by the use of traps as an indirect way of testing stimuli, for example colours or odours, rather than watching individual animals. Conversely, behavioural observations of individuals can be used to improve traps. Small differences in design can have large effects on trap catch (Phillips and Wyatt, 1992). Yale and co-workers used electroradiating grids to show the numbers of tsette flies approaching and going into different trap designs (e.g., Vale, 1982).

Testing pheromone identifications based on laboratory biossays is one important use of traps. Cardé and Elkinson (1984) discuss the design and interpretation of field trials, including trap interactions (Bayes, 1992; see also this volume, Chapter 7). The design of field trials still presents a major practical problem (e.g., Sanders, 1989; Wyatt, 1997). 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. This reinforces the need to be able to do realistic tests of pheromone blends and above rates before field trials.

3.4.3. Visual stimuli

Visual stimuli are important in the lives of all insects. Their influence has been extensively investigated in both host-finding by phytophagous insects (see this volume, Chapter 6; Prokopy, 1986; Bernays and Chapman, 1994) and by pollinators (this volume, Chapter 9). Finch (1986) gives a good review of features to consider in bioassay of colour responses of insects. Among the most difficult problems are producing standard colours changing in hue (dominant wavelength) but not in brightness (intensity of reflected light). Colour saturation (spectral purity) is another variable. For
3.4.4. Chemical signals

Chemical signals are important in terms of animal behaviour from communication to host plant selection. This very small number of olfactory molecules is able to elicit complex responses, often governed by the interaction between chemical signals and visual orientation. When considering brightness, an important factor is the light sources available. Brighter signals can appear brighter, and therefore more conspicuous. Brighter signals are more likely to be detected by the insect's sensory receptors, thus increasing the likelihood of successful communication.

For example, Sancisi and Scherer (1984) demonstrated that缇光強度 affects the attractiveness of nectar to bees. They showed that bees are more likely to be attracted to nectar that is brighter. Similarly, Hull and Scherer (1982) were able to show that the effect of light intensity on nectar attractiveness is similar to that of chemical signals.

The background on which targets are presented can also affect visual responses. For example, Hull and Scherer (1982) found that black backgrounds are more effective than white backgrounds in attracting bees to nectar.

In conclusion, the effectiveness of chemical signals is determined by the interaction between chemical signals and visual orientation. Brighter signals are more likely to be detected by insect sensory receptors, thus increasing the likelihood of successful communication.

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anemotaxis (for an explanation of terms see Table 3.1). Y-tubes and four-arm olfactometers share the problem of sharp boundaries to the odour plume which allow the insects to use chemosensory cues in ways that could not be done at a distance from the source. Bioassays that allow control of the way the insect contacts the pheromone, for example by a catwalk for walking at right angles to the gradient of odour, are preferred. However, bioassays also allows one to identify active components it can be useful even when the orientation mechanism are not revealed.

Behavioural bioassays in assess fractions as they come direct from a gas chromatograph (GC) have been developed (e.g. Leaf et al., 1994; Nazzal et al., 1996). A combined GC/EEG/behavioral bioassay using associative learning of a sugar reward and odour, which exploits the bee’s tongue extension behaviour, has been used by Wadhams et al. (1994) to investigate honey bee responses to flower odours. However, searching for synergy (below) remains difficult when fractions are only tested as they come from the GC columns in a linear time sequence.

Most insect pheromones appear to be composed of more than one synergistic component acting together. Each synergist alone may have little activity, but presented together at appropriate concentrations they are bioactive. This poses problems for isolating the active compounds from an insect extract as sub-fractions will not show activity unless the other synergists are also present. As the number of major fractions rises the complexity of bioassaying the potential combinations increases as a power. Byers (1992) compares the efficiency of different bioassay strategies and firmly advocates 'subtractive combination' (fractions containing active synergists are revealed when removing the fraction reduces the activity of the whole extract). De Jong (1987) provides a method for efficiently determining the optimum blend if the compounds are known.

Apart from the design of the bioassay, additional questions for work with olfactory bioassays include the type of substrate used to disse the chemicals, the strength of the stimulus, and the way in which two or more chemicals should be mixed (Baker and Cardé, 1984). Most experiments release chemical stimuli from filter paper or rubber septa. Sherlock (1979) suggests using diffusion from open tubes may be particularly appropriate for field experiments or when high release rates are required (Byers, 1988).

Bioassays for investigating glandular sources of the pheromones of social insects and their chemical characteristics have been critically reviewed by Travassol and Robson (1995) in particular citing the failure of many bioassays to distinguish between recruitment and orientation which are distinct behaviours in trail communication and foraging organization in both ants and termites. The extreme sensitivities of insects to their semiochemicals dictates extreme cleanliness in the laboratory to avoid contamination (solvent controls are a safeguard). The soaking of all glassware in detergents such as Decone® 90 between experiments is recommended.
Feeding is a central part of any insect’s behaviour and has important consequences for plant and pest management. This chapter reviews the feeding behaviour of blood-sucking insects such as mosquitoes, blackflies, and sandflies. It discusses the role of feeding in the biology of these species, including their feeding strategies, host preference, and the factors that influence feeding behaviour. The chapter also examines the role of feeding in the transmission of diseases such as malaria, dengue fever, and leishmaniasis.

Some software packages can also be used for manipulating the signals by modifying, adding, or removing certain stimuli. Signal playback through a loudspeaker or eyes is also possible using commercial electronic equipment. One can also design and build experimental setup to create a specific environment and record the feeding response of the insect. This can be done using a variety of techniques such as artificial hosts, laboratory rearing, and exposure to natural host cues. The chapter also discusses the use of feeding deterrents and repellents to control feeding behaviour and reduce disease transmission.

The final stage is testing the sounds and analyzing them. Each insect's behaviour and development are influenced by the environmental conditions, which may be critical in determining whether or not it will feed. Therefore, it is essential to understand the factors that influence feeding behaviour and develop strategies to exploit them for effective pest management.
3.4.9. Reproductive behaviour

Over the last 25 years the emphasis of research on insect reproductive behaviour has been increasing. Much of this research has been motivated by the potential of understanding the mechanisms of reproductive processes in animals, leading to the development of effective strategies for the manipulation of insect populations. Recent studies have focused on the role of pheromones in controlling insect reproduction, and the potential of these molecules for pest control.

3.5. Conclusions

Although it is clear that more experimental design is needed, the high technology involved in this type of research is likely to reveal new insights into the mechanisms of reproductive behaviour. Future research should focus on a better understanding of the complex interactions between males and females.

3.6. References

see www.online.ox.ac.uk/pheromones for reviews and downloads from Wyatt, TD (2003) Pheromones and animal behaviour. Cambridge University Press


see www.online.ox.ac.uk/pheromones for reviews and downloads from


