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Remote-sensing, telemetric and computer-based technologies for investigating insect movement: a survey of existing and potential techniques

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Abstract

This paper provides an overview of the recent literature on electronic, remote-sensing and computer-based techniques for observing and monitoring insect movement in the field and in the laboratory. Topics (such as entomological radar) which are covered in detail elsewhere in this Special Issue are deliberately omitted. Techniques which have been used, or which have potential for use, in monitoring insects in the field, include optical and opto-electronic devices, videography, thermal imaging, radio frequency identification (RFID), radio-telemetry, X-ray radiography and computed tomography, sodar and sonar. The discussion includes optical sensors and insect trapping, instrumented beehives, acoustic detection of insects in grain, fruit and soil, and various laboratory methods for studying insect movement, such as actographs, treadmills, automatic flight mills, and the video recording and analysis of movement in wind tunnels and in indoor arenas. Airborne and satellite imaging of insect habitats is mentioned, but only in the context of the use of these techniques to deduce changes in population distribution in some migratory species. Finally, some of the main constraints to progress in the sensing of insect movement, and areas where rapid advances seem possible, are discussed. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

The objective of this paper is to provide a comprehensive overview of the literature on technologies that have been used to observe insect movement, but which are not described elsewhere in this Special Issue. Many of the technologies, we discuss can be classified under ‘remote sensing’ in its widest sense, i.e. the observation of objects and features without making physical contact with them. Although far removed from what is usually understood by the term remote sensing, laboratory-based actographs where the insect is very close to but does not actually touch the sensor, are included under this heading (Chesmore, 1995). Where a sensor is actually in contact with the animal, or embedded in it, the technique is usually classified as biotelemetry (e.g. see Kutsch, 2002).

Advances in ‘wildlife telemetry’, that is the transmission of information from a device fixed to a free-ranging animal, have revolutionised ecological studies of vertebrates. The information most commonly obtained is the animal’s location, but other data on the animal’s physiological status (e.g. body temperature, respiration rate) or local environmental conditions may also be acquired. Various telemetry techniques (e.g. VHF radio, the ‘Argos’ satellite tracking system, acoustic tagging, etc) are described in Kenward (1987), Priede and Swift (1992), Wolcott (1995), and in abstracts from the International Symposia on Biotelemetry and similar conferences. The weight and size of the transmitting devices prevent most of this technology being applied to entomological studies, but recently some simple radio transmitters have been made light enough to be carried by large insects (e.g. Kutsch, 2002 and Hedin and Ranius, 2002).

All remote sensing or wildlife telemetry depends on the propagation of either electromagnetic or acoustic energy between the target and a sensor. Within the electromagnetic spectrum, UV through visible to near IR, thermal IR, the microwave region and the radio frequencies have all been utilised for entomological purposes. In this paper, we deal first with electromagnetic remote sensing and telemetry techniques that have been used to monitor insect movement in the field, or which appear to have potential to do so. Brief reference is then made to the satellite and airborne imaging of insect habitats, but only where techniques can be used to infer directly that changes in population distribution due to movement must have occurred. A review of all aspects of the remote sensing of the physical environments of insects is beyond the scope of this paper. We then cover ‘active’ and ‘passive’ acoustic detection of insects, and finally describe some techniques for investigating movement-related behaviour in the laboratory. We have not attempted to summarise the general literature on computer simulations and modelling of the population consequences of insect movement (e.g. metapopulation models, cellular automata, incidence function models), but we do include a section on the use of databases, geographical information systems (GIS) and expert systems which store and use information particularly on highly-mobile insects (see references in Woiwod et al., 2001). The use of new biochemical and molecular biology techniques to investigate insect movement and gene flow (e.g. Loxdale and Lushai, 1998, 2001) falls outside the scope of the paper.

We have concentrated on developments that have occurred since Riley reviewed remote sensing applications to entomology in 1989 (Riley, 1989). In the intervening period, some uses of electronic and computing technology in entomology have been summarised by Chesmore (1995), but with a wider focus than just movement studies. Also, a survey of techniques for quantifying a particular class of insect movement, namely migration, has been provided by Reynolds et al. (1997) and Room et al. (1998) have outlined some recent computer-based technologies which have proven or potential uses in insect ecology and pest management, particularly focusing on plant-insect interactions. Our paper subsumes the relevant material in these reviews, and seeks to present an up to date perspective of the subject. Most of technologies mentioned here are operationally proven and widely used, but others have yet to be applied in entomology and their utilisation is much more speculative.

2. Observing and monitoring insect movement in the field

In this section, we consider the electromagnetic remote-sensing methods used for monitoring the free movement of insects outdoors under natural or semi-natural conditions, but excluding various types of entomological radar that are covered in other papers in this Issue (Chapman et al., 2002; Drake et al., 2002a,b; Riley and Smith, 2002).

2.1. Visual methods

At their simplest, observations may consist of watching insects with the naked eye or through binoculars, and scoring movement activities on handheld electronic event recorders or on portable (often 'notebook' or 'palmtop') computers (Wyatt, 1997). Commercial packages for the collection and management of observational data are now available (e.g. The Observer® from Noldus Information Technology, Wageningen, The Netherlands). Improvements in computer voice recognition will soon allow simplified observations and comments to be entered into a voice data collection system while the observer is following a flying insect on foot or in a vehicle.

For insects that fly in short 'hops', stopping points can be marked by flags, and the ground locations of these later surveyed with an electronic theodolite connected to a data logger (Wiens et al., 1993). Large day-flying insects, such as butterflies, can sometimes be tracked for short distances by taking frequent simultaneous fixes of an individual's bearing and elevation with two theodolites equipped with an electronic means of recording angles and times. This data can then be used to reconstruct the three-dimensional track of the insect (Zalucki et al., 1980). The analysis of individual tracks is discussed by Bell (1991), Young et al. (1993), Varley et al. (1993), Turchin (1998) among others.

Aluja et al. (1989) devised a method of quantifying the foraging movements of insects in shrubs or small trees. First, the tree was pruned somewhat, then each remaining part (branch, leaf, fruit) was labelled with its three-dimensional co-ordinates as measured with respect to an imaginary cube surrounding the tree. The parts on which the test insect was seen to land could then be identified from the labels, recorded (along with times and other information on behaviour) and the movements later analysed by computer. Recording of the three dimensional structure of insect habitats can be considerably automated: for example, magnetic transducing technology (e.g. the FASTRAK, Polhemus Inc., Colchester, Vermont) can be used instead of rulers to determine the co-ordinates of tree parts (e.g. Smith et al., 1996), or of the surface of any other relatively small (a few metres) object, over which the test insect is likely to move. Scientists at the Centre for Plant Architecture Informatics in Brisbane, are currently using a GTCO Freepoint 3D sonic digitizer (GTCO CalComp Inc., Columbia, Maryland) to measure plant co-ordinates for virtual plant/insect models (http://www.cpai.uq.edu.au/), and various other new measurement technologies may be applicable in the future (Room et al., 1998).

2.2. Night vision devices

At night, human vision can be augmented with night-vision (image intensification) binoculars and telescopes, used with or without supplementary near infrared illumination. In these devices the available light is focussed onto a photocathode which then releases electrons: the numbers of these are greatly multiplied by some form of high voltage cascade, and the resulting electron flux is used to produce an image on a phosphor screen. Technical developments, conventionally divided into three stages or 'Generations', have enormously increased the sensitivity, reduced the distortion, and extended the operational life of night-vision devices. In Generation II devices, a Micro-Channel Plate (MCP) is used to multiply the electrons produced by the photocathode, rather than the multistage cascade used in first generation equipment. Generation III equipment is characterised by a gallium-arsenide photocathode and an ion barrier coating on the MCP which increases image tube life. First generation devices are now inexpensive (~ £500), while devices incorporating superior Generation II+ (an enhanced version of the earlier second Generation devices, capable of operating further into the infrared spectrum) or Generation III technology, can be obtained for ~ £1500–2000. Auxiliary illumination can be conveniently provided by fitting suitable filters to the very powerful (1 million candlepower) spotlights which are now readily available. Some entomological uses of image intensification devices are described in Lingren et al. (1986, 1995) and Fitt and Boyan (1991). For example, individual *Helicoverpa zea* moth flights near the ground were followed by observers equipped with night-vision goggles and infrared illuminators riding in a 4-wheel drive vehicle. Tests showed that an observer could follow an ascending moth up to heights of 100 m, when viewed against the night sky (Lingren et al., 1995).

2.3. Videographic techniques

The use of video equipment to observe flying insects in the field has been reviewed in detail by Riley (1993). One major problem with the technique is maintaining a reasonable field of view whilst producing a video image distinct enough to be detectable at more than a few metres. The other major problem, common to most remote sensing methods, is that of identifying the target. Thus it is not surprising that outdoor flight studies been concerned with insects either approaching traps or sources of odour plumes, or other situations where identifiable species are expected to pass through a rather restricted sensing volume. The range of detection can be increased by improving the contrast between the insect and the background, in particular by viewing the target against the night sky using some form of artificial illumination. Illuminators in the near infrared region (750–900 nm) appear to be most suitable because they do not perturb insect behaviour (Riley, 1993), although in the case of *Heliothis virescens*, illumination can be extended down to 600 nm without producing any reaction in the moths' orientation to pheromone plumes (Vickers and Baker, 1997). Other ways of increasing the visibility of insects on video include (for day-time studies) the use of artificial low-reflectivity (cloth) backgrounds (Gibson and Brady, 1985; Willis et al., 1994; Hardie and Powell, 2002), and applying fluorescent powders (David et al., 1983). At low illumination levels, the tracks of hawkmoths were made more distinct by attaching pads of the chemilumescent material, Cyalume, to the insects (Spencer et al., 1997). Quite small insect species (*Nephotettix* leafhoppers, c. 4 mm long) could be seen on video in the dark and against a background of foliage if infrared illumination was used and tiny pieces of 'Reflexite' microprism retroreflecting tape were attached to the thorax of the insect (J. Riley and A. Edwards, 1994 unpublished). Reflective plastic strips have been attached to gypsy moths, *Lymantria dispar*, in order to make clear the precise orientation of the body axis during video studies, although these observations were made in a laboratory wind-tunnel rather than in the field (Zanen and Cardé, 1999).

Most field studies have used one video camera, often looking downwards onto the area of interest (David et al., 1983; Willis et al., 1994; Vickers and Baker, 1997) and resulting in a two-dimensional record of the insect flight-path. By contrast, Okubo et al. (1981) were able to reconstruct the three-dimensional position of cecidomyid midges swarming over a marker, by using the relation of the midges to their shadows. The 'shadow' method has also been used in studies of the flight behaviour of solitary wasps near their nests (Zeil, 1993; Voss and Zeil, 1995), and of landing by honeybees (Srinivasan et al., 2000).

Stereoscopic views of a scene can be obtained by using mirrors with a single camera, but difficulties in obtaining a large field of view (i.e. deploying a large enough mirror) and problems with distracting reflections seem to have restricted mirror methods to the laboratory (see below). Generally, a two-camera viewing system is necessary to obtain three-dimensional tracks of flying insects in the field. Details of various experimental configurations are given by Dahmen and Zeil (1984), Riley et al. (1990), Riley (1993), Voss and Zeil (1995), Baker and Haynes

(1996) and Hardie and Powell (2002). The two cameras must either be very precisely aligned with respect to each other (Baker and Haynes (1996) fixed them to a flatbed cart), or a system of reference markers must be used (e.g. Riley et al., 1990).

Reconstructing the three-dimensional tracks of swarms of similar-looking insects by stereoscopy is made difficult by the need to identify which target in one view corresponds to the same individual in the other view (the matching problem). To overcome this problem in the case of mosquitoes swarming over a marker, Ikawa et al. (1994) used three synchronised 35 mm cameras, and then employed a rather sophisticated probabilistic model to reconstruct the tracks of the insects. Their model had the additional benefit that it recovered the camera alignment angles from the three-view imagery, so there was no need for reference markers or elaborate alignment procedures.

Most video studies of insect flight trajectories under natural conditions have employed manual digitisation of the target position in sequential video frames—an extremely tedious and time-consuming procedure. Automatic position digitisation is now becoming more common where clean video images are acquired under carefully controlled laboratory conditions (see below), but applying this process to recordings of freely-flying insects seen against natural backgrounds is a much more challenging task. These backgrounds are highly variable in contrast and brightness, illumination levels may change (e.g. if the sun is obscured by clouds), an insect may fly out of the field of view and then reappear at a different location, or more than one insect might appear in the frame. The formidable technical problems of automatic digitisation under these circumstances are discussed by Voss and Zeil (1995), who developed a tracking system which compared well with human performance in determining the flight path and body orientation of flying wasps, and which requested human supervision when it detected ambiguous situations.

The future of video recording of insect flight trajectories may lie in the use of video cameras equipped with pan, tilt and zoom drives to enable the cameras to automatically follow moving objects. The control signals for the drives would be derived from sophisticated image processing software, using motion detection and target recognition algorithms. Fry et al. (2000) describe the use of automatic pan and tilt video tracking to follow insects in either two or three dimensions, albeit in the laboratory. The use of telephoto allowed close-up images of the insect's body attitude, but the corresponding narrow field of view did not constrain the angular range over which the system operated, because this was limited only by the pan and tilt ranges. Three-dimensional analysis of insect flight tracks in wind tunnels, flight chambers and other indoor arenas is discussed below.

2.4. Thermal infrared imaging

Thermal IR imaging technology (sometimes referred to as Forward-Looking Infrared) is designed to detect objects in conditions of obscured visibility (darkness, smoke, dust, haze) by utilising the long-wave infrared (heat) radiation emitted from the objects rather than the light reflected off them. Although thermal viewers have poorer resolution than image intensification devices, unlike the latter they can 'see' in complete darkness. Light-weight, high-resolution thermal viewers and cameras are now available (e.g. from FLIR Systems Inc., Portland, Oregon, or Raytheon Company, Lexington, Massachusetts), but these devices are still rather expensive (> £9000) and as far as we know they have not been used to observe flying insects in the field. Thermal imaging cameras are now used commercially as a non-invasive way of detecting active termite infestations in buildings (e.g. Thermographic Surveys Pty Ltd., Melbourne, Australia).

2.5. Optical sensors and insect trapping

Optical methods can provide a method of recording the time of entry of insects to traps, for example, by the interruption of an infrared beam (Hendricks, 1989; Skatulla and Fiecht, 1995; Waddington et al., 1996). Hobbs and Hodges (1993) were additionally able to assign captured insects to body-size categories, by passing the insects individually through an illuminated detection volume, and measuring the amount of light scattered during the transit. It may even prove possible to replace traps altogether in some instances, for example the function of pitfall traps for catching small cursorial invertebrates could be achieved with digital cameras. Images of the animals crossing the camera's field of view would be transferred to a computer, identified by automatic image processing techniques, and the results transmitted back to the laboratory (Dr D. Chesmore, University of Hull, pers. comm.). For larger animals, at least, commercial systems exist which automatically trigger digital cameras mounted inside weatherproof housings, either at regular intervals or when movement is detected by a motion sensor (e.g. 'TrailCam' system, Erdman Video Systems, Miami). An archive of the images can be maintained on a dedicated computer, and/or they can be uploaded to the Internet. In the context of trapping and telemetry, we also mention that infrared telemetry has been used to transfer data from pheromone traps (these used a piezoelectric detection mechanism) and from meteorological sensors in cotton fields, to a base station computer situated in the farm office (Schouest and Miller, 1994).

2.6. Specialist opto-electronic devices

Among the more specialised insect-monitoring electro-optical devices are Farmery's (1981) crossed-beam infrared detectors and Schaefer and Bent's (1984) IRADIT. In the Farmery system, the field of view of the photomultiplier sensor intersected the illuminator beam at a selected height above ground level. Insects passing through this intercept volume could be detected, and their wing-beat frequencies recorded. We have used this system to monitor *Spodoptera exempta* and *Helicoverpa armigera* moths flying below radar cover (i.e. under about 20–30 m) (Farmery, 1982; Riley et al., 1983, 1992; Rose et al., 1985). The Farmery device (like many night-time video and infrared illuminator combinations) is ineffective in twilight and daytime when the luminance of the sky greatly lowers its sensitivity to insect targets. Schaefer and Bent (1984) overcame this limitation by using a very bright xenon flash lamp, working in the near infrared, and a video camera equipped with a gated image intensifier which provided high-contrast images even of small flying insects against the mid-day sky. This sophisticated device has been used for the calibration of light-traps and suction traps (Schaefer and Bent, 1984; Schaefer et al., 1985) but, perhaps due to its complexity, it has not been taken up by other research groups.

3. Instrumented beehives

The constant comings and goings of honey bees at a hive entrance represents an obvious opportunity for automatic monitoring. Dr J. Bromenshenk and colleagues at the University of Montana have developed experimental beehives with an array of electronic and chemical probes, which provide continual real-time monitoring of colony activities and conditions within and outside the hive. Of particular interest here, is a system of bi-directional entrance counters which monitor bees entering and leaving the hive. The bees pass through a system of channels, each of which is fitted with an infrared emitter and two infrared detectors. By determining which detector is activated first, the computer software can distinguish incoming from outgoing bees. The entrance structure is designed to ensure that virtually every bee passes through in an upright position so that it can be reliably and individually counted. The Bromenshenk automated hive is notable for its operational reliability and the degree of development of its computerised analysis and data handling systems which allow hive activity and conditions to be interrogated over the internet. Activity levels can be assessed at a glance with the aid of computer graphics on a remote terminal—'hot' colours (yellow and red) indicate high numbers of bees passing the detectors while 'cool' colours (blue and violet) indicate low rates of passage. Much of this work has not been published in the open literature, but more information can be found at http://biology.dbs.umt.edu/bees/default.htm.

Bar code technology, like that used in supermarkets, has been explored as a means of recording the foraging schedules of individual bees (Sasaki, 1989; Dr Stephen Buchmann, unpublished). The bar code labels themselves had to be custom-made to be small enough to fit onto the thorax of a bee, and they were read by an off-the-shelf laser scanner, and the information fed to a computer (Sandford, 1989). This initiative was apparently not successful enough to be widely taken up. It is convenient to mention here a laboratory use of a bar code system used by McKibben and colleagues to record the distance over which boll weevils moved in response to various odours in a glass tube olfactometer which had bar code markings at set intervals along its length. The effect of an attractant was measured by manually scanning the bar code nearest to the responding insect, thus quickly recording its position and time-stamping the data (G. McKibben, pers. comm.).

4. Radio frequency identification (RFID)

RFID technology may have potential for monitoring and tracking insects moving over distances of less than a metre up to some tens of metres (for instance, in a warehouse-sized indoor arena, or a similar-sized outdoor cage). RFID devices currently have an enormous variety of applications and can be used to identify and track almost any object to which an appropriate transponder or tag can be attached. Transponders range from simple, passive anti-theft tags on merchandise in shops, through implantable devices for marking animals, up to active (battery-powered) read/write units on railway cars or on containers in large warehouses. For general descriptions of the various technologies, and current and potential applications, see websites such as http://rapidttp.com/transponder/index.html; http://www.ettm.com/news/rfid.html. RFID systems which are of most interest in the present context, transmit a radio signal from fixed 'scanners' and this signal is received by any tags within range. These tags reply with a coded signal, and this allows the objects to which they are attached to be uniquely identified. Object position can be inferred either because the tag must be in close proximity to the sensor, or else by signal transit times in more sophisticated systems like the '3D-iD' referred to below. Frequencies used in RFID systems range from 30–500 kHz for short-range, low-cost equipment up to 900 MHz–2.5 GHz for high-performance, longer range, high-cost devices. Systems operating below 135 kHz do not need to be licensed in many countries.

4.1. Passive tags

Passive transponders have no battery of their own but contain a capacitor which is charged inductively or radiatively by transmissions from the scanner, and they use the stored energy to transmit their unique alphanumeric code on an appropriate frequency. Having no battery, these tags have unlimited endurance, but the range at which they can be detected is extremely limited (centimetres to a few metres at most). A major wildlife application of RFID devices is the so-called PIT (Passive Integrated Transponder) tag designed for implanting beneath the skin or in the body cavity of vertebrate animals and used, for example, to census salmonid fish as they pass scanners mounted in fish ladders around dams. Boarman et al. (1998) describe a PIT tag system to automatically monitor movements of a terrestrial vertebrate, viz. a desert tortoise, by siting solar-powered scanners in culverts through which the animals passed in order to cross a highway. Some PIT tags may be just about small and light enough for entomological applications. In the smallest currently available, the antenna, capacitor and coded microchip are encased in a glass capsule about 11 mm in length and weighing about 0.06 g (e.g. the TX1400L tag from Biomark Inc., Boise, Idaho). These have a read range of about 7–15 cm at the operating frequency of 125 kHz. This type of tag has apparently been used in an unpublished pilot study of cockroach movement carried out by The Clorox Company (Mark Owens, Biomark, pers. comm.). Similar devices could perhaps be used for recording the transit of large-bodied wasps and bees (e.g. bumble bees) in and out of their nests (Dr S. Buchmann, pers. com.). Finally, we note in passing that entomological harmonic radars (see Riley and Smith, 2002) use a form of passive transponder tag. Compared with 'normal' passive RFID tags, these have a very large detection range (up to 900 m), but they do not return a uniquely identifiable signal.

4.2. Active tags

Active RFID tags contain an internal battery, and are typically read/write devices. They can in principle communicate over substantial ranges, but there is obviously a severe trade-off between the transmission power (and hence range), operational lifetime, and battery size. The size and weight of all commercially available active RFID tags preclude entomological applications, but recently some battery-operated radio transmitters have been miniaturised sufficiently to work as conventional radio tracking tags on large walking insects, and on one large flying insect (the hermit beetle) albeit over relatively short ranges (see Hedin and Ranius, 2002). The lightest transmitter actually used in an insect radio tracking study appears to be the LB-2 made by Holohil Systems Ltd., Carp, Ontario, Canada, which weighs between 0.47 and 0.52 gm (Hedin and Ranius, 2002; www.holohil.com/index.htm). This is a crystal controlled 'two stage' (amplified oscillator) device, pulsed by a multivibrator, and operating in the 142–235 MHz frequency range. The tiniest 'one-stage' (non-amplified oscillator) transmitter that we are aware of weighs about 350 mg, and measures $12 \times 5 \times 2.5$ mm (without the trailing wire aerial) (Titley Electronics, Ballina, NSW, Australia. www.titley.com.au). This device is said to have maximum trackable ranges of 1–2 km from ground receivers, but 12–15 km from the air. Hopefully, commercial opportunities generated by the market for a radio-tracking capability for small bats or birds, for example, will result in further miniaturisation.

Although the signal is considerably attenuated, active radio tags can be used in relatively shallow fresh water (with the receiver antennae in the air above the water surface), and large aquatic insects viz. corydalid Megaloptera larvae have been tracked by this means (Hayashi and Nakane, 1988, 1989). Radio-tagging is ineffective in (conductive) saline water (Wolcott, 1995).

A possible avenue for tracking many big insects within very large cages may be through systems like the 3D-iD indoor location and tracking system developed by PinPoint Corporation of Billerica, MA. The area to be monitored is divided up into cells each handled by a Cell Controller. The controllers cause a low-power radio signal at 2.4 GHz to be sent to the (active) tags, via an array of up to 16 antennas positioned around each cell. The tags (up to a maximum range of 75 m away) receive the transmission, and reply with a 5.8 GHz signal that includes a unique tag serial number. The Cell Controller calculates the distances between the tags and antennas from the time-delay between the initial and returned signals, and hence is able to calculate the tag positions. Data from at least three antennas is needed, and location accuracy is about 3 m. The system can continuously track the position of hundreds of tags in real-time (a new location can be calculated every 0.5 s) and display and manipulate information on various standard software platforms. Further miniaturisation and customisation of the tags would be essential for entomological applications, but there is strong commercial pressure to achieve small tags for other applications. Further information on continuous indoor tracking systems, and the technical problems overcome in designing the 3D-iD system, can be found in Werb and Lanzl (1998).

5. X-rays

X-ray radiography has been used since the 1950s to detect insects in wood, soil and grain (see references in Southwood and Henderson, 2000). A movement-orientated example is provided by the radiography of successive positions of elateridae and scarabeid beetle larvae as they moved around in specially-prepared soil blocks (Villani and Gould, 1986; Villani and Wright, 1988). The more powerful technique of X-ray computed tomography (where the X-ray absorption along intersecting ‘slices’ through an object is quantified and then, through a process of intensive computation, is transformed into a display of the spatial distribution of regions of different relative absorption), was used to study the burrowing activity of the 4th-instar larvae of the pecan weevil *Curculio caryae* (Harrison et al., 1993). The X-ray CT scans clearly showed the vertical tunnels of the burrowing larvae in both natural and artificial soil cores. Other types of biomedical scanner (e.g. magnetic resonance imaging) may have similar uses, if entomologists can gain access to these very costly imaging technologies.

6. The application of space- and airborne technologies to movement investigations

Monitoring condition of the habitat of some insects, particularly highly-mobile species adapted to ephemeral habitats, can provide strong indications of the likelihood of migration events. The classic example is that of forecasting changes in the distribution and size of desert locust (*Schistocerca gregaria*) populations. These forecasts require data on rainfall and green vegetation over the whole geographical range of the species, and similar requirements apply to some other locusts like the Australian plague locust (*Chortoicetes terminifera*), and to migratory grasshoppers such as *Oedaleus senegalensis*. Another use of wide area vegetation monitoring in insect movement studies relies on the detection of changes in tree or crop foliage due to insect-induced damage. These changes may, in some cases, be indicative of population movements. This section describes how space- and airborne technology, combined with more conventional entomological survey and monitoring, is playing an increasingly important part in both of these types of habitat assessments. The use of GPS systems is also mentioned.

6.1. Satellite remote sensing in the 'optical' spectrum

Visual imagery from satellites cannot detect individual insects, and although military satellites could presumably detect locust swarms and bands, their images are not available for civilian use. Images from satellite-borne sensors are, however, increasingly used to detect the effects of insects on their host plants (usually damage to crops or forests) or to monitor environmental factors (e.g. weather and habitat condition) which may affect insect populations (Riley, 1989; Hay et al., 1997). Changes in, for example, vegetation type and quality, ground temperature, rainfall, soil moisture or degree of inundation in certain geographical areas, can indicate that population movements are likely to occur or have occurred in highly-mobile species such as locusts or armyworm moths. These movements can then be confirmed by ground surveys or trapping records. Earth observation satellites, primarily intended for land-use studies (e.g. Landsat, SPOT, IRS) pass over a location too infrequently to be used in routine forecasting of migratory pests (although the instruments on the SPOT satellites are steerable to either side of the ground track, and this can provide a more frequent 're-visit' facility). High spatial resolution images from earth observation satellites have, however, been useful for detailed mapping of potential locust habitats (Bryceson, 1993; Dumayac et al., 1996; Voss and Dreiser, 1997).

The coarse spatial (1–5 km), but high temporal, resolution images from meteorological satellites are routinely used for migratory pest forecasting, particularly products from the Advanced Very High Resolution Radiometer (AVHRR) instrument on the NOAA series, and the multispectral radiometers on the European Meteosat and Japanese GMS series (Hielkema, 1990; Tappan et al., 1991; Bryceson et al., 1993). The polar-orbiting, sun-synchronous NOAA satellites have a repeat frequency of 12 h (or 6 h if a pair of satellites is used) while the geostationary Meteosat and GMS give new images every 30 min. Data can be downloaded very conveniently and at low cost through small, locally-situated receiver systems and processed on desk-top computers (Bryceson and Cannon, 1990; Perryman, 1996).

Desert locust forecasting: forecasters at FAO use the Africa Real Time Environmental Monitoring using Imaging Satellites system (ARTEMIS), a dedicated satellite data acquisition and processing system, to detect areas of rainfall or green vegetation in the desert where *S. gregaria* outbreaks can be expected to occur (Hielkema, 1990; Cherlet et al., 1991). Rainfall estimation is based on 10-day and monthly cumulated 'cold cloud duration' (ccd) data obtained from the Meteosat thermal infrared images which register the temperature of cloud tops (Milford and Dugdale, 1990). Deep convective clouds with very cold tops (-50 to -70 °C) often produce heavy rain in the form of thunderstorms, but interpretation of ccd products can be far from straightforward. For example, high-level cirrus clouds which never give rise to rain may be picked-up, while warmer clouds which do produce rain (e.g. near the Red Sea in winter) are not, and it is also difficult to take account of run-off which may greatly increase soil moisture in wadis far from the areas where the rain has fallen (Dr K. Cressman, FAO, pers. comm.). Vegetation greenness is assessed from composite maps of the NDVI (normalised difference vegetation index) derived from reflectance in the AVHRR near-infrared and visible channels (Hielkema, 1990). Recently, however, forecasters have also used imagery from the low-resolution vegetation monitoring instrument on the SPOT satellites (Dr K. Cressman, pers. comm.). Again, interpretation of imagery can be problematic. For example, soil or rock in some areas may mimic green vegetation, or some types of sparse tufted vegetation may comprise a low percentage of ground cover and be difficult to distinguish from bare soil, but can still provide a favourable habitat for desert locusts. A range of other vegetation indices, apart from the standard NDVI, could be used to identify ephemeral areas of green vegetation (Cherlet and Di Gregorio, 1993; Bonifacio and Ouladichir, 1996), and forecasters may have to develop special procedures applicable to each geographical area.

Desert locust and environmental information (e.g. vegetation and rainfall) is now incorporated into a specially-developed ARC/INFO-based GIS known as Schistocerca WARning Management System (SWARMS) and compared with historical information (collected over a 60-year period) which can provide useful analogues to help predict how a current locust situation will evolve (Cressman, 1997; Magor and Pender, 1997). As well as modules to input and edit data, to interrogate the databases, and to output maps of results, SWARMS also contains a locust migration trajectory model, and an egg and nymphal development period model.

African armyworm forecasting: the aerial concentration of migrating African armyworm moths (*Spodoptera exempta*) by wind convergence in the vicinity of convective rainstorms, followed by moth deposition, egg-laying, and the subsequent development of larvae on the flush of grass produced by the rain, can lead to serious high-density outbreaks in East Africa (Rose et al., 2000). This association between rainstorms and larval outbreaks, particularly following dry periods at the beginning of the armyworm season, has led to the use of satellite imagery to help predict the likely position of new infestations (Tucker, 1997; Tucker and Holt, 1999). Rainstorms tend to be associated with the edges of cold (e.g. below -50 °C) cloud clusters identified from Meteosat infrared images. These are used to produce maps of maximum ccd which together with other meteorological information and trap catches greatly reduce the areas needing to be surveyed for armyworm infestations.

New earth observation satellites are being launched every year (the commercial 'Ikonos' satellite, for example, can produce 1-m resolution panchromatic and 4-m resolution multispectral images), and thus there are good prospects that many current technical limitations will presently be overcome. It remains to be seen whether the availability and the cost of satellite products will still be a serious constraint to many entomological applications.

6.2. Airborne digital photography and videography

The habitats of migratory insects can of course be surveyed from aircraft using conventional, large format, aerial photography. This is now rapidly being superseded for many aerial survey purposes by digital camera technology which is much more compatible with computer storage and manipulation of images, and has other advantages (such as immediate viewing), although spatial resolution is currently less good than high-quality conventional film (House et al., 1999). Airborne surveys often use colour infrared (CIR) digital cameras which are very sensitive to vegetation type, age and condition (e.g. pest-induced stress).

CIR and conventional colour aerial photography, as well as a three-camera, multispectral, digital video imaging system integrated with a GPS system, were all used to detect infestations of the western pine beetle in ponderosa pine forests in Texas (Everitt et al., 1997). Infested pines could be detected on the video imagery due to their pinkish white or yellowish gray response, and the integration of the GPS with the video imagery permitted the latitude and longitude of the infestations to be printed on each image.

Geo-referenced airborne videography has also been used to map infestations of *Aleurocanthus woglumi* in orchards (Everitt et al., 1994) and *Bemisia* sp. on cotton (Everitt et al., 1996); both of these whiteflies are detectable because deposits of sooty mould fungus associated with the insects alters plant reflectance on colour-infrared and black-and-white near-infrared imagery.

6.3. New developments in airborne optical imaging

High-resolution airborne hyperspectral (tens to hundreds of narrow contiguous bands) imaging systems (see list at http://www.geo.unizh.ch/~schaep/research/apex/is_list.html) may well replace satellite-borne systems for many agricultural and ecological applications, and some of this technology may find more frequent application in monitoring the habitats of insects, or detection of their presence through defoliation, vegetation damage, etc (e.g. Franklin et al., 1995). However, some of these advanced imaging spectrometers have to be carried in large or highly specialised aircraft (e.g. high-flying U2-type planes) while others, for example, CASI—the Compact Airborne Spectrographic Imager, although mountable in light aircraft, are still very expensive (>£200 000) by entomological standards. The challenge is thus to develop digital video systems which have multispectral capabilities, but are small and flexible enough to be deployed in locally-hired light aircraft, and cheap enough be used in entomological projects. The approach is illustrated by the sequence of airborne remote sensing systems developed by J.H. Everitt and colleagues at the USDA unit at Weslaco, Texas (http://webpages.acs.ttu.edu/smaas/asa2000/everitt.htm). For example, their twelve-camera digital video imaging system (ADVIS) generates four real-time digital false colour composite images from any selectable three-band combination among the twelve cameras, and this allows multiband imagery of a scene to be rapidly assessed during the flight as well as stored for later processing (Escobar et al., 1998).

6.4. Synthetic aperture radar

Unlike the sensors which use the 'optical' spectrum, synthetic aperture radars (SAR) are 'active' devices which both transmit and receive radiation, in this case in the microwave region. This imaging technique has the advantage that it is unaffected by differences in illumination, haze, smoke and most types of cloud. SARs utilise the motion of the radar platform (satellite or aircraft) and data processing to obtain a fine azimuth resolution which would normally require a very large aperture (i.e. an antenna several hundred meters long). Microwave penetration of the soil is partly dependent on its moisture content, and thus SAR images may provide another method for routine monitoring of locust habitats by directly sensing the soil moisture content of the top few centimetres of arid/semi-arid soils. Work is currently in progress at the Natural Resources Institute to assess the usefulness of products from the C-band (5.3 GHz) SAR instrument on the ERS-2 satellite, and the Advanced Synthetic Aperture Radar (ASAR) on the soon-to-be launched Envisat satellite (W. Crookes and D. Archer, pers. comm.). The project particularly aims at monitoring Brown Locust (*Locustana pardalina*) habitats in the Karoo region of South Africa, although the principle could also be used for Desert Locust and *Oedaleus sengalensis* habitat monitoring. The ASAR instrument will have an increased potential for soil moisture estimation due to the dual polarisation modes and variable incidence angle of the sensor. However, image processing procedures still have to be developed to allow for the effects of surface roughness, and local soil and vegetation types, which may otherwise mask any soil moisture response. The operational use of SAR for soil moisture assessment in Africa would require the installation, near the locust control headquarters, of a small, relatively cheap and easily transportable ground receiving station capable of acquiring high-resolution satellite data (for example, the RAPIDS system with its trailer-mounted 2.7 m diameter antennae; Downey, 2000).

Aircraft-mounted SAR has also been used for entomological surveys. Pope et al. (1992) used this technique to assess the flooding status of depressions (known as dambos) which form favourable breeding sites for *Culex* mosquitoes, vectors of Rift Valley fever (RVF). The radar could operate at X-, C- and L-band wavelengths, and in the following polarisation modes: transmit and receive in the horizontal plane (HH mode), transmit in the vertical and receive in the horizontal (VH mode), and transmit and receive in the vertical plane (VV mode). L-band HH was found to be the best channel for discriminating between flooded and non-flooded sites under various vegetation conditions. Airborne SAR had the advantage over the then-extant satellite systems of being able to resolve the smaller dambos. However, frequent airborne surveying of large areas for the assessment of RVF risk would be costly and logistically difficult, especially in developing countries, so a high-resolution satellite-borne SAR would be the best solution for routine monitoring.

6.5. Global positioning systems

Outdoor sampling or observational points can now be conveniently and very precisely located by the use of hand-held GPS (global positioning systems) equipment. The worldwide GPS navigation system is based on extremely accurate measurement of the time taken for signals from a constellation of earth-orbiting satellites to reach the hand-held receiver. The US Defence Department, owner of the system, until recently imposed an accuracy constraint on the civilian system (known as 'Selective Availability'), but this has now been switched off. Currently, inexpensive 'civilian grade' GPS receivers (using a single frequency) can provide an accuracy of roughly ± 5 m in horizontal position, and ± 50 m in altitude (error estimates refer to 95 percentiles). Accuracy and precision can be improved by using as many satellites as possible to calculate locations (overdetermination), and by post-processing of data using the 'differential GPS' or 'relative GPS' techniques (Rempel and Rodgers, 1997; Hurlbert and French, 2001). Even if the resulting increases in accuracy are not considered worthwhile, these procedures may identify significant sources of error which were previously masked by Selective Availability (Hurlbert and French, 2001).

GPS coordinates can be imported into a GIS on a portable computer, and can thus be integrated in the field with maps of vegetation and soil type, and other habitat information. Examples of an insect movement-related use of GPS include accurate 'ground truthing' of information on the habitats of migratory insect pests (e.g. locusts: Cherlet and Di Gregorio, 1993; Dumayac et al., 1996; Voss and Dreiser, 1997) obtained by satellite remote sensing, or by airborne photographic or videographic surveys. Other examples include the routine ground surveys carried out by locust control organisations. In eastern Australia, accurate locations of *Chortoicetes terminifera* populations and habitat characteristics, obtained by GPS, are automatically recorded on a palmtop computer in the field officer's vehicle. These data are then relayed to a main computer at Australian Plague Locust Commission headquarters several times a day via a high-frequency radio link (Deveson and Hunter, 2000; and APLC web site). Numerous descriptions of the use of GPS and GIS systems for various purposes can be found on the Internet—some of these, particularly procedures in agriculture and forestry, may have applicability to insect surveys.

Some wildlife telemetry technologies use devices carried by the animal (e.g. in the form of a collar) which locate themselves by means of the GPS satellites. The location can then be transmitted directly to the user or a number of fixes can be stored in the device's memory for later downloading, either when the device is physically recovered from the animal, or by some form of remote interrogation by a special receiver. This GPS-based system is not to be confused with the 'Argos' Platform Terminal Transmitters (PTTs) (although GPS transmitters can use the Argos system to download their data). Argos PTTs transmit a signal to a package on certain polar-orbiting satellites, which in turn relay the message in real-time to ground receiving stations, or store and download it each day when the satellite passes over the station (see www.argosinc.com). The latitude and longitude of the animal are calculated from the Doppler shift in frequency of the PTT transmission as satellite passes over. Argos tracking accuracy is much more limited (150–1000 m) than most GPS-based systems.

Not surprisingly, both the GPS and PTT devices are far too large and heavy to be carried by insects. This is true of even in cases where size reduction has been energetically pursued. For example, the miniaturised GPS and data logging device recently developed to track homing pigeons weighed 33 g without the harness (von Hünerbein et al., 2000), and the smallest PTT transmitter weighs about 15 gm (www.argosinc.com/system_overview.htm)

7. Acoustic detection

Detection of insects by sound waves is the exception to the otherwise invariable rule that remote sensing involves the propagation of electromagnetic waves between the target and sensing device. In this section, we describe how active acoustic devices have been used to monitor the aerial environment in which insects fly, and how airborne insects can be detected by these devices. We also describe the use of sounders to detect the movement of aquatic larvae, and then discuss how insects can be detected from the sounds that they themselves generate.

7.1. Atmospheric sounders

High-frequency sound devices are routinely used to investigate the structure of the lower atmosphere and to determine vertical and horizontal wind components, and these acoustic sounders or 'sodars' (SOund Detection And Ranging) have occasionally been used to obtain complementary meteorological information during insect migration studies. Drake et al. (1994) evaluated two types of sounder, a doppler acoustic wind profiler and a radio-acoustic sounding system (RASS) which measured temperature, for use alongside a vertical-looking insect monitoring radar. The intention was to obtain simultaneous height profiles of meteorological and insect data, but it was found that both acoustic devices had rather limited vertical range (~ 500 m). They also noted that the high-intensity sound pulses would probably preclude night-time operations near any human habitation.

Riley et al. (1995) used a simple monostatic non-doppler sodar to determine the height of the nocturnal temperature inversion and thus to ascertain the best height for aerial netting.

Theoretical consideration of acoustic back-scattering from insects shows that at least large species such as grasshoppers and hawkmoths will register as individual 'point' targets at ranges of several hundred metres on many acoustic sounders, and dense concentrations of small insects may appear as solid layers (Riley, 1994; Riley and Edwards, 1997). However, as far we are aware, Cronenwett et al. (1972) is the only published study where a named insect was detected by an acoustic sounder; they reported that discrete targets on a 1.5 kHz sounder were probably due to migrating *Neoconocephalus robustus*, a long-horned grasshopper.

Hendricks (1980) developed a low-power, 40 kHz sodar for detecting moths approaching close (within 1 m) of a sex pheromone source. The device counted over twice as many *Heliothis virescens* than were actually taken in a pheromone trap.

It has been suggested that a 'phased array' ultrasonic system may be useful in short-range tracking of small insects (e.g. aphids) in flight close to a crop canopy (Isard and Gage, 2001, p. 137). A grid of 15 ultrasonic transmitters would emit 42 kHz pulses which are phase delayed to enable the system to sweep across the sensed volume (2.5 m long $\times$ 1.5 m wide $\times$ 2 m high). The return echoes from insects would by be picked up by eight receivers, amplified, and passed to a digital signal processor and its associated computer system. The position of insects within the tracking volume, and their rate and direction of movement, could thus be calculated and displayed in near-real time. A prototype device was tested but, as far we know, a full system has not yet been operated under field conditions to determine how it copes with multiple targets and background noise.

7.2. Hydroacoustics

The aquatic larvae of *Chaoborus* spp. (Diptera: Chaoboridae), sometimes called phantom midges, can be a major faunal component of certain lakes. Some larval instars, and the pupae of *Chaoborus* undertake diurnal vertical and transverse 'migrations' between the bottom of the lake and surface waters, and these movements have been studied with the aid of high-frequency (70–200 kHz) echosounding (Northcote, 1964; Franke, 1987; Eckmann, 1998; Malinen et al., 2001). *Chaoborus* larvae are thought to provide good sound scattering compared with other zooplankton due to their air sacs, but the identification of the targets forming the scattering layers has to be confirmed by vertical or horizontal net sampling. The timing of observations is also important: echosounding is best carried out when as few of the larvae as possible are in the sediment or near the water surface. Portable scientific echosounding systems are now commercially available which use dual- or split-beam transducers (MacLennan and Simmonds, 1992) that can be mounted on a small boat or on a towed body. These commercial systems have considerable processing power, for example, in integrating echo intensities over specified time periods using dedicated algorithms, displaying the results on a computer screen, and storing the data for further analysis by special post-processing software. Obtaining realistic quantitative estimates of *Chaoborus* densities can still be very difficult if the larvae always occur with larger targets. However, Eckmann (1998) describes a method of attributing echo integrator values produced by two clearly distinct size classes of target (viz. *Chaoborus* and juvenile fish).

7.3. 'Passive' acoustic detection of insects

There has been much research on developing 'passive' acoustic methods for detecting and monitoring pest insects hidden in a range of media, particularly stored grain (where there is a need to grade samples for regulatory purposes) but also in fruits, timber, living plants and soil (see Table 1). The insects are detected by the low-intensity incidental sounds (in the range c. 0.5–150 kHz), that they make while moving and feeding in the medium. The feasibility of using acoustic detection depends on factors such as the signal-to-noise ratio, the amount of distortion and attenuation of the sound as it travels through the medium, the distinctiveness of sound patterns from target and non-target organisms, and the fraction of the measurement period during which signals are generated (Mankin et al., 1998).

Sensing elements can comprise acoustic transducers (condenser microphones, piezoelectric microphones) attached to special sample holders, or vibration transducers (piezoelectric disks, accelerometers) fixed to or embedded in solid media such as wood or soil. The more evolved systems often have an array of sensors in an acoustically shielded enclosure, and the outputs are fed through suitable amplifiers and band pass filters, before being processed by sophisticated signal processing software, including neural networks. Some of the recent technical developments are described in a special issue of Applied Acoustics (volume 50, no. 4). Systems such as ALFID (Acoustic Location 'Fingerprinting' Insect Detector) do not merely detect insects, but can quantify the infestation by automatically determining the number of live larvae in a sample of grain (Mankin et al., 1997b; Shuman et al., 1997; Weaver et al., 1997). Some progress has also been made in distinguishing acoustically between different insect species on the basis of the intensity, duration and spectral characteristics of their incidental sounds (Hagstrum and Flinn 1993; Mankin et al., 1997a), but this remains a difficult task particularly where non-target species may be present (as in the soil) (Mankin et al., 2000). Schmidt et al. (1995) found that a neural network program was necessary for practicable automatic detection of wood-boring beetle larvae in house beams.

Mankin (1994) investigated the possibility of using the acoustic detection of flying mosquito swarms or individuals, in very quiet environments, as an automatic surveillance technique. For *Aedes taeniorhynchus* in remote salt marshes, he found that swarms flying several tens of metres away from the microphone

Table 1
Acoustical detection of hidden insect infestations

Medium	Examples of insect taxa involved	References
Stored grain: wheat	*Sitophilus oryzae* (rice weevil) *Tribolium castaneum* (red flour beetle) *Ryzopertha dominica* (lesser grain beetle) *Cryptolestes ferrugineus* (rusty grain beetle) *Oryzaephilus surinamensis* (saw-toothed grain beetle)	Vick et al., 1988; Hagstrum & Flinn, 1993; Hagstrum et al., 1996; Shuman et al., 1997; Mankin et al., 1997a,b, 1999
Fruit: papya, grapefruit, mango	*Dacus dorsalis* (oriental fruit fly) *Anastrepha suspensa* (Caribbean fruit fly)	Hansen et al., 1988 Calkins and Webb, 1988; Webb et al., 1988; Sharp et al., 1988
Cotton bolls	*Pectinophora gossypiella* (pink bollworm)	Hickling et al., 1994; Schneider, 1995
Living plants: wheat stems	*Cephus cinctus* larvae (wheat stem sawfly)	Mankin and Weaver, 2000
Lumber, wooden structures	Termites *Hylotrupes bajulus* (house longhorn beetle)	Scheffrahn et al., 1993; Matsuoka et al., 1996; Lemaster et al., 1997; Weissling and Thoms, 1999; Schmidt et al., 1995
Soil	*Phyllophaga* (white grubs (Scarabaeidae)) *Diaprepes abbreviatus* (root weevil larvae) *Otiorynchus sulcatus* (black vine weevil larvae) *Scapteriscus* (mole crickets)	Mankin et al., 1998, 2000

could be detected and distinguished from background noises. However, the sound pressure level of individuals was low, and an attractant would probably be necessary to bring the insects close to the microphone.

7.4. Acoustic traps

Another acoustic technique which can be used to monitor movement is the use of sound to attract insects to traps; taxa include mosquitoes, mole crickets and field crickets and their ormiine tachinid parasitoids, and galleriine moths (wax moths). Reviews of the history, operation and limitations of sound-baited traps are given by Service (1993) for mosquitoes and Walker (1988, 1996) for a variety of insects. Sound traps have mainly been used in (apparently rather futile) control campaigns, and to monitor populations, but they can also give useful information on migration and local movements (e.g. of mole crickets; Walker and Fritz, 1983). Service (1993) concludes that sound traps are unlikely to be widely used for trapping mosquitoes as they mainly attract males, have a short attraction range and usually have to be supplemented with host odours. Audio-frequency sound, combined with light, was thought to have potential for control of chironomid midges (Hirabayashi and Ogawa, 1999; Hirabayashi and Nakamoto, 2001).

8. Laboratory techniques for the study of insect movement

Very many types of device have been designed to investigate 'activity' and movement behaviour in the laboratory, and we attempt to summarise only the key techniques here. A useful and complementary compendium can be found on an Oklahoma State University website (http://psychology.okstate.edu/museum/ratus).

8.1. Actographs

These are devices used to measure the gross activity of an animal or a group of animals confined in a cage or container. They are particularly useful for studies of the temporal pattern of activity over longish periods (e.g. circadian rhythms) but they generally do not distinguish between types of movement (e.g. mate-finding, foraging for food, etc.). Movements within actographs have been detected by a variety of means, e.g. capacitance discharge between floor elements (Chabora and Shukis, 1979), changes in resistance of an artificial substrate (carbon-covered paper) (Wheater, 1988), vibration of floor or walls (Leppla et al., 1979; Racette et al., 1990; Kaneko et al., 1995), changes in ultrasonic standing waves (Luff et al., 1979; Johnson et al., 1986), variations in the light falling on photoelectric cells (Eaton, 1980; Kaneko et al., 1995), microwave interference or doppler devices (Buchan and Moreton, 1981; Renou et al., 1999; Knoppien et al., 2000) and by video recording (Allemand et al., 1994; Noldus et al., 2002). Some of the earlier of the above-mentioned actographs used pen and chart recording methods, but virtually all of the devices can now be automated by linking the sensor to a computer via an analogue-to-digital converter card (Wyatt, 1997).

8.2. Physiological and neuro-mechanical studies of walking and running

Various physiological and neuro-mechanical processes (such as metabolic capacity, leg kinematics and biomechanics, muscle activity, neural control of movement, etc.) have been studied in pedestrian insects by using combinations of miniaturised mechanical force plates (Full and Tu, 1991), gelatin tracks (Full et al., 1995), miniature treadmills and 3-D image-motion analysis (see, for example, work at the PolyPEDAL Laboratory at Berkeley (Worthington, 1998; http://polypedal.berkeley.edu). Typically, the test insect is enclosed in a transparent box and is allowed to run freely on a treadmill. Kinematic parameters are usually derived from an analysis of a high-speed videographic record taken in either lateral view, or (via a mirror) ventrally as well (Kram et al., 1997). Points on the subject's limbs or body are marked with white paint so that they show up more clearly on the video. Variations in experimental regime include making the enclosure an airtight respirometer in order to measure oxygen consumption (Full et al., 1990), or simultaneously recording electromyograms (EMGs) by implanting fine electrodes into specific leg muscles (e.g. Watson and Ritzmann, 1998). Rather than running on a treadmill, the insect may be induced to move across a photoelastic gelatin track placed between crossed-polarising filters and illuminated from below: the resulting stress-induced optical signals are recorded on high speed video, and insect leg forces can be derived from the size and skew of these optical patterns (Full et al., 1995). Other workers have used tethered preparations. Theophilidis and Burns (1990) tethered a locust on a balsawood platform fixed to its metathorax and one metathoracic femur, and allowed it to walk on a treadmill. The movement of the opposite femur was monitored with a capacitance movement detector, and motor nerve impulses were recorded from the fixed femur. Tryba and Ritzmann (2000) studied leg kinematics (by videotaping) and motor control (by EMGs) in tethered cockroaches running on a slippery glass plate.

In many of these applications it is clear that the increasing affordability of very high-speed (hundreds or even several thousands of frames per s) digital video systems (from manufacturers such as Redlake Imaging, Morgan Hill, California, or NAC Inc., Tokyo) is a great boon, and coupled with commercial motion analysis packages (e.g. Peak Performance Technologies Inc., Englewood, Colorado) provide powerful tools in studies of very rapid limb motion or other body movements (Worthington, 1998; and references quoted above). A running *Periplaneta americana* cockroach, for example, can cover 50 body lengths per s, and the leg cycling frequency (25 Hz) is comparable to the wingbeat frequencies used in flight (Full et al., 1990). Another example of the high-speed video/microscope documentation of a movement far too fast to be followed by the naked eye, is the prey capture technique of a small rove-beetle (see www.iwf.de/iwfeng/4projekt/44/highspeed_in.html).

8.3. Laboratory studies of the movement paths of pedestrian insects

The detailed paths (e.g. searching patterns) of walking insects can be conveniently recorded in the laboratory with a form of treadmill called the 'servosphere' locomotion compensator (Kramer, 1976; Bell, 1991). Here, the movement of an insect walking freely on top of a sphere is detected by a sensor (such as a video-tracker) and a negative feedback system rotates the sphere (via a pair of computer-controlled servo-motors) so that the insect is maintained on top. The movements of the sphere are fed to a data-analysis computer, where various track parameters can be calculated. A sophisticated recent version of the servosphere is described by Sakuma (2002). To study the extremely rapid turning and running movements of cockroach (*P. americana*) escape reactions, Ye et al. (1995) *tethered* the test insect on top of a air-floated hollow styrofoam sphere using a mounting device which allowed insect to make turning movements in the horizontal plane. Rotational movements of the sphere were picked up by two plastic wheels, converted to electrical signals by a shaft-angle encoders, and fed to a computer. The reconstructed movements of the cockroach and the activity of the interneurones mediating the escape reactions (simultaneously recorded via implanted electrodes) could be correlated over very fine time scales.

Another approach is allow the insect to move around in an small arena within the field of view of a video camera, and use a computerised digitisation program or better still, an image-processing package to track the insect. Some general principles involved in this type of video experiment are discussed by Varley et al. (1993), and recent applications include: the behavioural responses of insects to chemical attractants (Bakchine-Huber et al., 1992; Roberts and Chambers, 1993), chemical insecticides (Watson et al., 1997), entomopathogenic fungi (Lacey et al., 1997) and soil types (Kindvall et al., 2000), and the characteristics of host searching activity of female parasitoids (Vigneault et al., 1997a; Wajnberg and Colazza, 1998; Drost et al., 2000). Recently, there have been significant advances on the development of semi-automatic or automatic systems for capturing video images of insects walking in laboratory arenas, and for reconstruction and analysis of movement paths (Bakchine-Huber et al., 1992; Varley et al., 1993; Allemand et al., 1994; Vigneault et al., 1997a,b; Drost et al., 2000; Noldus et al., 2002). Originally, the reflectance of the arena floor had to be more-or-less uniform, and considerably different from the reflectance of the insect (e.g. dark insect on white floor). It is now possible to track animals against more heterogeneous backgrounds and more variable light conditions, more than one individual can be tracked in each arena, and several arenas can be observed with a single camera. Allemand et al. (1994) automatically analysed parasitoid movement in a large array (60 or more) of small circular arenas: a single camera made computer-controlled horizontal movements over the array, scanning a group of arenas at each successive position. Future prospects for simultaneously following the individual tracks of large numbers (potentially hundreds) of small insects such as ants in an arena is illustrated by the work of Balch et al. (2001). Their image processing procedure first classified pixels by their colour in order to quickly identify regions which might contain an ant, then operationallyslower image differencing algorithms were used to look for movement of ant-sized objects within these regions, and finally other algorithms were used to associate the positions of individual ants in consecutive frames. The average difference in number of ants recognised by a human observer and by the machine vision system was 11%, but there was scope for reducing sources of error.

Strauss et al. (1997) studied the processing of locomotion-induced visual feedback of a freely walking *Drosophila melanogaster* fruit fly in a sophisticated 'virtual reality' simulator. The position and orientation of the fly in a circular arena was continuously evaluated by a video tracking system, and this information was used to update a computerised 360° panorama composed of 5760 LEDs around the arena. The system allowed, for example, the suppression of visual feedback arising from the fly's own motion, without interfering with its mechano-sensory system (conditions that the authors term 'virtual open-loop'). In other experiments, on leg co-ordination during turning movements, Strauss's group employed a further level of sophistication in the experimental arena in order to record the precise kinematics of leg placement. A thin layer of red laser light was projected over the glass plate on which the fly walked, and when the fly's leg tarsi came in contact with the glass, they were illuminated so each step could be videoed from underneath the apparatus. Meanwhile the orientation and position of the fly's body could be tracked from above, and combined by the computerised analysis system with the reconstructed leg actions (www.biozentrum.uni-wuerzburg.de/bericht/wng2/abb2_en.html).

8.4. Flight studies in the laboratory

Laboratory techniques for the assessment of insect flight can be divided into those where the subject is tethered and those where it is free flying (albeit in a rather limited 'arena'). Among the tethering techniques we have static tethering, flight balances, roundabouts and mills (see reviews by Hardie, 1993; Cooter, 1993; Dingle, 1996; Reynolds et al., 1997). Recent descriptions of computer-monitored flight mills are given in Taylor et al. (1992), Weber et al. (1993), Beerwinkle et al. (1995), and Schumacher et al. (1997). Static mounts sometimes incorporate force transducers to sense some combination of thrust, lift and yaw of a test insect flying in a wind tunnel. The measured forces can be used to modulate the air flow so that it accurately simulates the in-flight air speed (Zarnack and Wortmann, 1989; Preiss and Spork, 1993). Preiss and Kramer (1984) developed a sophisticated flight mill which presented the test insects with a moving visual environment of the type which they might experience in free flight, and thus allowed them to adjust their flight speeds. It was used for investigating the sensory-motor mechanisms underlying wind-drift compensation and the control of ground speed in flying gypsy moths, *Lymantria dispar*. A sophisticated 'virtual-reality' flight simulator has also been developed for small insects by M.H. Dickinson and his colleagues (Dickinson and Lighton, 1995; Lehmann and Dickinson, 1997). A tethered fruit fly experiences visual stimuli as if under free-flight conditions because the angular velocity of a vertical stripe on the walls is actively controlled by changes in the relative stroke amplitude of the fly's wings. Total flight force and torsional turning forces are measured by a tiny laser and mirror torque detector, while wingbeat kinematics are measured by optically tracking the shadows of the wings cast by an infrared light source. Complex visual panoramas can be created around the fly by a cylindrical array of computer-controlled LEDs.

In their classic studies of aphid flight behaviour, the late John Kennedy and his collaborators designed and used a vertical wind tunnel in which the rate of climb of a freely-flying insect towards a light source was just counteracted by a manually-controlled downward air flow, thus maintaining the insect at a particular height in the flight chamber (Kennedy and Ludlow, 1974). Frequency of take-off, flight duration and the propensity for landing could be investigated under various experimental conditions (for example, different coloured 'leaves' could be periodically presented to the test insect). This flight chamber has been considerably developed and automated through video recording, automatic tracking and data collection as well as computerised feedback to control the air flow in the wind tunnel (Young et al., 1993; Hardie and Powell, 2002). Kennedy-type vertical flight chambers have also been employed in studies on other small insects which have a phototactic flight phase, e.g. the nitidulid beetle, *Carpophilus hemipterus* (Blackmer and Phelan, 1991) and the whitefly, *Bemisia tabaci* (Blackmer and Byrne, 1993).

The detailed spatial tracking of paths of free-flying insects in the laboratory often requires the subject to orientate into an airflow in a horizontal wind tunnel which constrains it from quickly traversing the working section of the tunnel. Wind tunnels of this type have been used to investigate orientation towards a visual stimulus (Isaacs et al., 1999), but much more frequently the studies are of behaviour in plumes of pheromone or other odours (for recent examples, see Schofield and Brady, 1997; Mafra-Neto and Cardé, 1998; Zanen and Cardé, 1999; Cardé and Knols, 2000). Insects flying upwind to an odour source often require visual feedback from features on the ground below or to the side of them (the optomotor response) and this is often provided by patterns on the floor of the wind tunnel. Movement of these patterns (by a moving conveyor-belt floor or by film projections on a static floor) can, therefore, be used to influence the insect's flight speed and direction, and help to retain it within the working section of the tunnel (Young et al., 1993). In the 'barber's pole' tunnel, the optomotor effect is produced by the movement of an outer tube marked with a helical stripe pattern which rotates around a transparent inner tube containing the insects (David, 1982). In each of the above cases, detailed flight manoeuvres in the wind tunnel can then be recorded by video camera and the flight path reconstructed. General principles and useful practical suggestions for setting up video studies of this type are described in Young et al. (1993): for example, infrared light is often used to provide illumination for the camera, while 'visual' wavelength light can be manipulated according to the behavioural requirements of the insects being studied. The resultant flight paths are usually two-dimensional (in the horizontal (yawing) plane), but a smaller number of wind tunnel/flight chamber studies have employed two video cameras with an overlapping field of view, thus enabling a three-dimensional analysis of flight tracks (Young et al., 1993; Mankin and Hagstrum, 1995; Hardie and Young, 1997; El-Sayed et al., 2000; Fry et al., 2000; Hardie and Powell, 2002).

As mentioned above in connection with walking insects, there has been considerable commercial development of automatic systems for capturing and analysing video images of movement in the laboratory. Optical motion capture systems used in the reconstruction of three-dimensional insect flight paths include: the Trackit 3D system from Biobserve, Bonn, Germany (Fry et al., 2000; www.biobserve.com/software/trackit/index.html), the EthoVision system (Takken et al., 1996 and at www.noldus.com/applications/ index.html; Noldus et al., 2002), the MacReflex from Qualisys Inc, Glastonbury, Connecticut (Marden et al., 1997), and several video tracking systems from OKK Inc., Tokyo (www. okk-inc.com; Sakuma, 2002). The Trackit 3D system was successfully used to study the phonotactic flight of females of the parasitoid fly *Ormia ochracea* towards synthetic cricket songs in a laboratory arena. Three-dimensional flight trajectories were recorded by the active tracking system using two infrared cameras with computer-controlled pan-tilt optics, while the sound stimulus was controlled on-line as a function of the fly's position in space (Fry et al., 2000; Müller and Robert, 2001). It was shown that the flies were able to accurately gauge the direction and distance of the sound source and, subsequently, to find it in darkness and silence.

Some small insects with good vision and flight control (e.g. fruit flies) will fly semi-continuously within a limited arena, making sharp, saccade-like turns when they approach the walls. Dickinson and colleagues have developed an automatic tracking arena (the 'Fly-o-rama') to study flight control in *Drosophila melanogaster* (http://socrates.berkeley.edu/ ~ flymanmd). Behaviour was recorded with two gen-locked CCD infrared-sensitive video cameras, looking down on a circular arena with an infrared absorbent floor and lit by a ring of infrared LEDs. The cameras were connected via digital signal processors to video recorders. Three-dimensional trajectories were reconstructed by dedicated software.

The spatial resolution and frame rate of video systems were, at the time, considered inadequate to measure the body orientation during flight of the blowfly *Calliphora vicina* in a $40 \times 40 \times 40$ cm cage, due to the insect's relatively fast movement and very sharp turns (several thousand degrees per s) (Schilstra and van Hateren, 1998). These authors, therefore, recorded the position and thorax orientation of the flies using a variation of the induction coil technique often used for measuring head and eye movements in humans and other animals (cf. magnetic motion capture systems like the Polhemus FASTRAK mentioned above). A time-varying magnetic field was produced around the experimental cage with three orthogonal pairs of field coils, carrying sinusoidal currents at frequencies of 50, 68, and 86 kHz, respectively. Each pair of field coils induced a voltage at the corresponding frequency in each of three tiny orthogonal sensor coils mounted on the insect. The sensor coils were connected via very fine (12 μm) wires to a set of nine lock-in amplifiers, each locking to one of the three field frequencies (Schilstra and van Hateren, 1998). It was possible to measure orientation with a typical accuracy of ~ 0.5 degrees, and position accuracy to 1 mm. The maximum weight of the sensor coils and leads was approximately 5.7 mg, and this apparently did not hinder normal flight in an insect weighing about 80 mg.

Among other techniques for studying the biomechanics and physiology of insect flight, and associated areas such as bio-robotics, we might mention: high-speed video recording of insect wing motions (Willmott and Ellington, 1997); large, dynamically scaled-up, mechanical models of insect wings (Ellington et al., 1996; Dickinson et al., 1999); flow visualisation of the pattern of vortices produced by tethered insects and by dynamic models (e.g. by particle image velocimetry—video recording and computerised analysis of bubble motion; Dickinson et al., 1999); and supercomputer simulation of the two-dimensional fluid motion around wings (Wang, 2000).

9. Future prospects

It will be clear from this review that studies of insect movement have benefited greatly from recent developments in sensor and computer technologies. This is particularly evident in the case of small computers, night-vision devices, GPS and digital image capture, where military or commercial pressures have produced quite extraordinary advances. Further improvements in hardware seem highly probable, especially in videography, where very high frame rates combined with large pixel arrays and extensive spectral sensitivity range can be found in remarkably small digital video cameras. Although costly at the moment, these cameras should eventually become available at affordable prices.

Due to widespread applications in engineering, robotics, medicine, sport, ergonomics, and entertainment animation, notable progress is being made in commercial software development for motion tracking and image analysis, which combine video (or specialised opto-electronic devices) and computer technology. While fully automatic tracking may not be feasible for field-recorded imagery, partially automated processes of the type described by Voss and Zeil (1995) should soon be commonplace.

Numerous companies are competing to develop 3-D scanning and representational systems operating on optical, magnetic, acoustic, mechanical principles (see web pages such as perso.club-internet.fr/dpo/numerisation3d), and further progress is also likely in this area. Although some of these scanners are very expensive, entomologists may be able to use equipment bought for other purposes (e.g. by other departments of a university).

Growth of the RFID industry worldwide, driven by the development of technologies combining electronic article surveillance and bar code replacement systems, as well as by an increasing number of other applications (see http://rapidttp.com/transponder/trendfut.html), is leading to smaller, 'smarter', but still inexpensive, passive transponders. These devices consist of a single microchip and surface printed antenna, and if they can be made to have reasonable range of detection (a few metres, say), they may prove to be a useful resource in laboratory studies of insect movement.

The main and long standing barrier to miniaturisation of 'active' transponders is the (relatively) large size and weight of even the smallest batteries. Battery technology has been able to advance only slowly, in spite of huge incentives, and is clearly up against fundamental constraints. Some of the latest developments relevant to wildlife telemetry are described by R. Sheldon in the final discussion at the 1997 Snowmass Forum (see www.npwrc.usgs.gov/resource/tools/telemtry/transcpt.htm). Special-purpose batteries (silver oxide, zinc–air, and some lithium cells, e.g. lithium–manganese dioxide) are readily available in very small (~ 5 mm diameter button or coin cells) and lightweight (~ 0.1 g) configurations, but they generally have low capacities (a few milliamp hours). A silver oxide button cell weighing about 0.12 g was, however, found to be an adequate power source for the transmitter used in the hermit beetle dispersal study (Jonas Hedin, pers. comm.).

Lithium thionyl chloride cells have the highest power density of any primary cell, and they operate at a higher voltage than most (open circuit voltage is 3.65 V, compared with a silver oxide button cell's 1.5 V), have a long service life and other advantages. Miniature configurations of these cells are not routinely produced, and must be manufactured to order. The smallest lithium thionyl chloride cell available on the market was designed by the Electrochem Battery Division of Wilson Greatbatch Ltd (Clarence, New York) to power a transmitter for tracking fish fry: it measured 8.4 mm long $\times$ 7 mm diameter and weighed 1.2 gm (www.batteryeng.com/cust_products.htm # Fish).

It will be clear from the above that a dramatic improvement in battery power-to-weight ratios is essential if insect telemetry is to be applied to any but the largest species. The very small fuel cells like those under development by Motorola Inc./Los Alamos National Laboratory, the Case Western Reserve University, and others (e.g. www.howstuffworks.com/news-item7.htm) may provide the necessary breakthrough, but devices currently under development are still very large (1×1 cm) compared with the chip-sized batteries needed for insect tags.

Dudley (2001) estimates that the average body length of the North American insect fauna is only about 7 mm, so most insect species are far beyond the reach of currently envisaged telemetry techniques that rely on batteries. This position seems unlikely to change in the absence of some radical breakthrough.

It is possible to use tiny solar cells to build active devices which are small enough, at least in principle, to be carried by a large insect (Falter et al., 1990), but solar-powered transmitters have not yet actually been used in any entomological study.

In contrast to technologies with mass market applications, complex one-off electronic devices developed purely for entomological use (e.g. Schaefer and Bent's IRADIT system) seem unlikely to be widely adopted due to the cost and specialised expertise involved in equipment construction and maintenance. Consequently these devices, although ingenious, may have very limited application in entomological studies. Entomological radar is a partial but important exception to this rule, probably because it was made economically feasible by the widespread availability of inexpensive marine radar equipment. Even in this case, we note that early radar entomology depended on long-term funding by government organisations (the Overseas Development Administration in UK, CSIRO in Australia, and USDA in the USA), a resource rarely available today.

Lastly, and in the broader context of the interaction between entomology and technology, we mention the very active ongoing collaborations between robotic engineers and insect biologists to develop insectoid walking or flying robots (e.g. Ritzmann et al., 2000; papers in Chang and Gaudiano, 2000). Examples include the small flying robots under development by the Micromechanical Flying Insect (MFI) project at U.C. Berkeley (http://robotics.eecs.berkeley.edu/ ~ ronf/mfi.html), the 'Entomopter' mechanical insect project at the Georgia Tech Research Institute (http://gtresearchnews.gatech.edu/reshor/rh-spr97/microfly.htm), a range of walking robots (http://polypedal.berkeley.edu/Bioinspire/Robotics.html) and robots which, although wheeled, are guided by the principles of insect vision (Srinivasan et al., 1999; http://cvs.anu.edu.au/bioroboticvision). Another area of overlap between engineers and biologists concerns a form of Artificial Intelligence (namely 'Swarm Intelligence'), which is based on aspects of behaviour of social insects (Bonabeau et al., 2000): models of movement-related behaviour, particularly pheromone-trail following in ants (Ant Colony Organisation and Ant Colony Routing techniques), have lead to progress in a series of important optimisation and control problems. Knowledge flows both ways—robotics and computer engineering are providing insights into insect biomechanics, neural control, neuroethology, and foraging behaviour. For example: how information from sensory processing and central pattern generators is integrated to achieve neuromuscular control of insect locomotion (Ritzmann et al., 2000); how an autonomous blimp-like flying robot can be used to investigate vision-based mechanisms of navigation in flying insects (Iida, 2001); and how studies of the group behaviour in multi-robot systems without any direct communication or robot differentiation, can provide models for co-operative transport in foraging ants (Kube and Bonabeau, 2000).

References

Allemand, R., Pompanon, F., Fleury, F., Fouillet, P., Bouletreau, M., 1994. Behavioural circadian rhythms measured in real-time by automatic image analysis: applications in parasitoid insects. Physiol. Entomol. 19, 1–8.

Aluja, M., Prokopy, R.J., Elkinton, J.S., Laurence, F., 1989. Novel approach for tracking and quantifying the movement pattern of insects in three dimensions under seminatural conditions. Environ. Entomol. 18, 1–7.

Bakchine-Huber, E., Marion-Poll, F., Pham-Delègue, M.H., Masson, C., Soussaline, F., 1992. Real-time detection and analysis of the exploratory behavior of small animals. Naturwissenschaften 79, 39–42.

Baker, T.C., Haynes, K.F., 1996. Pheromone-mediated optomotor anemotaxis and altitude control exhibited by male oriental fruit moths in the field. Physiol. Entomol. 21, 20–31.

Balch, T., Khan, Z. Veloso, M., 2001. Automatically tracking and analyzing the behavior of live insect colonies. In: The fifth International Conference on Autonomous Agents, Montreal, Canada, 28 May–1 June, 2001. (See http://www.cs.cmu.edu/ ~ trb/papers/agents01ants.pdf)

Beerwinkle, K.R., Lopez, J.D. Jr, Cheng, D., Lingren, P.D., Meola, R.W., 1995. Flight potential of feral *Helicoverpa zea* (Lepidoptera: Noctuidae) males measured with a 32-channel, computer-monitored flight mill system. Environ. Entomol. 24, 1122–1130.

Bell, W.J., 1991. Searching Behaviour: The Behavioural Ecology of Finding Resources. Chapman and Hall, London.

Blackmer, J.L., Phelan, P.L., 1991. Behavior of *Carpophilus hemipterus* in a vertical flight chamber: transition from phototactic to vegetative orientation. Entomol. Exp. Applic. 58, 137–148.

Blackmer, J.L., Byrne, D.N., 1993. Behavior of *Bemisia tabaci* in a vertical flight chamber: effect of time of day, sex, age and host quality. Physiol. Entomol. 18, 223–232.

Bonabeau, E., Dorigo, M., Theraulaz, G., 2000. Inspiration for optimization from social insect behaviour. Nature 406, 39–42.

Bonifacio, R., Ouladichir, A., 1996. Use of NOAA/AVHRR data in desert locust control in the Algerian Sahara. In: Power, C.H., Rosenberg, L.J., Downey, I. (Eds.), Remote Sensing and GIS for Natural Resource Management. Natural Resources Institute (NRI), Chatham, UK.

Boarman, W.I., Beigel, M.L., Goodlett, G.C., Sazaki, M., 1998. A passive integrated transponder system for tracking animal movements. Wildlife Soc. Bull. 26, 886–891.

Bryceson, K.P., 1993. Locust survey and drought monitoring—two case studies of the operational use of satellite data in Australian government agencies. ITC J. 1993 (3), 267–274.

Bryceson, K.P., Cannon, R., 1990. Acquisition and use of low-cost meteorological satellite data in the Australian plague locust commission. Comput. Electronics. Agric. 5, 47–64.

Bryceson, K.P., Hunter, D.M., Hamilton, J.G., 1993. Use of remotely sensed data in the Australian Plague Locust Commission. In: Corey, S.A., Dall, D.J., Milne, W.M. (Eds.), Pest Control and Sustainable Agriculture. CSIRO, Melbourne, pp. 435–439.

Buchan, P.B., Moreton, R.B., 1981. Flying and walking of small insects (*Musca domestica*) recorded differentially with a standing-wave radar actograph. Physiol. Entomol. 6, 149–155.

Calkins, C.O., Webb, J.C., 1988. Temporal and seasonal differences in movement of the Caribbean fruit fly larvae in grapefruit and the relationship to detection by acoustics. Florida Entomol. 71, 409–416.

Cardé, R.T., Knols, B.G.J., 2000. Effects of light levels and plume structure on the orientation manoeuvres of male gypsy moths flying along pheromone plumes. Physiol. Entomol. 25, 141–150.

Chabora, P.C., Shukis, A.A., 1979. The automated recording of insect activity: the house fly. Ann. Entomol. Soc. Am. 72, 287–290.

Chang, C., Gaudiano, P. (Eds), 2000. Biomimetic robotics (special issue). Robotics and Autonomous Systems 30 (issue 1–2).

Chapman, J.W., Smith, A.D., Woiwod, I.P., Reynold, D.R., Riley, J.R., 2002. Development of vertical-looking radar technology for monitoring insect migration. Comput. Electron. Agric. 35, 95–110.

Cherlet, M., Di Gregorio, A., 1993. Calibration and integrated modelling of remote sensing data for desert locust habitat monitoring. RSC Series no. 64, FAO, Rome.

Cherlet, M., Di Gregorio, A., Hielkema, J.U., 1991. Remote-sensing applications for desert-locust monitoring and forecasting. Bull. OEPP 21, 633–642.

Chesmore, D., 1995. Electronic and computing technology in entomology: time for a special interest group. Antenna 19, 59–64.

Cooter, R.J., 1993. The Flight Potential of Insect Pests and its Estimation in the Laboratory: Techniques, Limitations and Insights. The Gooding Memorial Lecture, given to The Central Association of Bee-Keepers, 13 September 1992. The Central Association of Bee-Keepers, Hadleigh, Essex, UK.

Cressman, K., 1997. SWARMS: a geographic information system for desert locust forecasting. In: Krall, S., Peveling, R., Ba Diallo, D. (Eds.), New Strategies in Locust Control. Birkhäuser Verlag, Basel, pp. 27–35.

Cronenwett, W.T., Walker, G.B., Inman, R.L., 1972. Acoustic sounding of meteorological phenomena in the planetary boundary layer. J. Appl. Meteorol. 11, 1351–1358.

Dahmen, H.-J., Zeil, J., 1984. Recording and reconstructing three-dimensional trajectories: a versatile method for the field biologist. Proc. Roy. Soc. Lond. B 222, 107–113.

David, C.T., 1982. Compensation for height in the control of groundspeed by *Drosophila* in a new, 'barber's pole' wind tunnel. J. Comp. Physiol. A 147, 485–493.

David, C.T., Kennedy, J.S., Ludlow, A.R., 1983. Finding of a sex pheromone source by gypsy moths in the field. Nature 303, 804–806.

Deveson, E.D., Hunter, D.M., 2000. Decision support for Australian plague locust management using wireless transfer of field survey data and automatic internet weather data collection. In: Laurini, R., Tanzi, T. (Eds), TeleGeo2000-Proceedings of the second Annual Conference on Telegeoprocessing, 10–12 May 2000, Nice-Sophia Antipolis. École des Mines de Paris, Sophia Antipolis, Nice, pp. 103–110.

Dickinson, M.H., Lighton, J.R.B., 1995. Muscle efficiency and elastic storage in the flight motor of *Drosophila*. Science 268, 87–90.

Dickinson, M.H., Lehmann, F.O., Sane, S.P., 1999. Wing rotation and the aerodynamic basis of insect flight. Science 284, 1954–1960.

Dingle, H., 1996. Migration: the Biology of Life on the Move. Oxford University Press, Oxford, UK.

Downey, I., 2000. Data feast, information famine: operational remote sensing in developing countries. GeoInformatics 3, July/August 2000 issue pp. 24–27.

Drake, V.A., Harman, I.T. Bourne, I.A., Woods, G.J.C., 1994. Simultaneous entomological and atmospheric profiling: a novel technique for studying the biometeorology of insect migration. In: Proceedings of 21st Conference on Agricultural and Forest Meteorology-11th Conference on Biometeorology, 7–11 March, San Diego, California. American Meteorological Society, Boston, pp. 444–447.

Drake, V.A., Harman, I.T., Wang, H.K., 2002a. Insect Monitoring Radar: stationary-beam operating mode. Comput. Electron. Agric. 35, 111–137.

Drake, V.A., Wang, H.K., Harman, I.T., 2002b. Insect Monitoring Radar: remote and network operation. Comput. Electron. Agric. 35, 77–94.

Drost, Y.C., Qiu, Y.T., Posthuma-Doodeman, C.J.A.M., Van Lenteren, J.C., 2000. Comparison of searching strategies of five parasitoid species of *Bemisia argentifolii* Bellows and Perring (Hom., Aleyrodidae). J. Appl. Entomol. 124, 105–112.

Dudley, R., 2001. The biomechanics and functional diversity of flight. In: Woiwod, I.P., Reynolds, D.R., Thomas, C.D. (Eds.), Insect Movement: Mechanisms and Consequences. CAB International, Wallingford, UK, pp. 19–41.

Dumayac, M.N., Crisostomo, B., Cayabyab, B.F., Ebuenga, M.D., Candelaria, E.D., 1996. Geographic Information System (GIS) and remote sensing: important tools in managing migratory locust infestation. In: Dizon, T.O., Eusebio, J.E., Mabbayad, M.O., Duenas, J.N., Palis, F.V. (Eds), 27th Anniversary and Annual Scientific Meeting of the Pest Management Council of the Philippines, Inc. Davao City, Philippines, 7–10 May 1996. Pest Management Council of the Philippines, College, Laguna, Philippines.

Eaton, J.L., 1980. An infrared LED-based electronic actograph for monitoring insect flight activity. Ann. Entomol. Soc. Am. 73, 744–746.

Eckmann, R., 1998. Allocation of echo integrator output to small larval insect (*Chaoborus* sp.) and medium-sized (juvenile fish) targets. Fisheries Res. 35, 107–113.

Ellington, C.P., van den Berg, C., Willmott, A.P., Thomas, A.L.R., 1996. Leading-edge vortices in insect flight. Nature 284, 626–630.

El-Sayed, A.M., Godde, J., Arn, H., 2000. A computer-controlled video system for real-time recording of insect flight in three dimensions. J. Insect Behav. 13, 881–900.

Escobar, D.E., Everitt, J.H., Noriega, J.R., Cavazos, I., Davis, M.R., 1998. A twelve-band airborne digital video imaging system (ADVIS). Rem. Sens. Environ. 66, 122–128.

Everitt, J.H., Escobar, D.E., Summy, K.R., Davis, M.R., 1994. Using airborne video, global positioning system, and geographical information system technologies for detecting and mapping citrus blackfly infestations. Southwest Entomol. 19, 129–138.

Everitt, J.H., Escobar, D.E., Summy, K.R., Alaniz, M.A., Davis, M.R., 1996. Using spatial information technologies for detecting and mapping whitefly and harvester ant infestations in South Texas. Southwest Entomol. 21, 421–432.

Everitt, J.H., Richerson, J.V., Karges, J., Alaniz, M.A., Davis, M.R., Gomez, A., 1997. Detecting and mapping western pine beetle infestations with airborne videography, global positioning system and geographic information system technologies. Southwest Entomol. 22, 293–300.

Falter, D.D., Alley, G.T., Falter, K.G., Rochelle, J.M., Valentine, K.H., Westbrook, R.D. Jellison, G.E., Fleming, P.H., 1990. Development of a solar-powered infrared injection laser microminiature transmitting system. In: Harris, D.G., Shay, T.M. (Eds.), Proceedings of the International Conference on Lasers '89, New Orleans, 3–8 December 1989. STS Press, McLean, Virginia, pp. 1081–1087.

Farmery, M.J., 1981. Optical studies of insect flight at low altitude. Ph.D. Thesis University of York, York, UK.
Farmery, M.J., 1982. The effect of air temperature on wingbeat frequency of naturally flying armyworm (*Spodoptera exempta*). Entomol. Exp. Applic. 32, 193–194.
Fitt, G.P., Boyan, G.S., 1991. Methods for studying behaviour. In: Zalucki, M.P. (Ed.), Heliothis: Research Methods and Prospects. Springer, New York, pp. 122–150.
Franke, C., 1987. Detection of transversal migration of larvae of *Chaoborus flavicans* (Diptera, Chaoboridae) by the use of a sonar system. Arch. Hydrobiol. 109, 355–366.
Franklin, S.E., Bowers, W.W., Ghitter, G., 1995. Discrimination of adelgid damage on single balsam fir trees with aerial remote sensing data. Int. J. Rem. Sens. 16, 2779–2794.
Fry, S.N., Bichsel, M., Müller, P., Robert, D., 2000. Tracking of insects using pan-tilt cameras. J. Neurosci. Methods 101, 59–67.
Full, R.J., Tu, M.S., 1991. Mechanics of a rapid running insect: two-, four- and six-legged locomotion. J. Exp. Biol. 156, 215–231.
Full, R.J., Zuccarello, D.A., Tullis, A., 1990. Effect of variation in form on the cost of terrestrial locomotion. J. Exp. Biol. 150, 233–246.
Full, R.J., Yamauchi, A., Jindrich, D.L., 1995. Single leg force production: cockroaches righting on photoelastic gelatin. J. Exp. Biol. 198, 2441–2452.
Gibson, G., Brady, J., 1985. Anemomtatic' flight paths of tsetse flies in relation to host odour: a preliminary video study in nature of the response to loss of odour. Physiol. Entomol. 10, 395–406.
Hagstrum, D.W., Flinn, P.W., 1993. Comparison of acoustical detection of several species of stored-grain beetles (Coleoptera: Curculionidae, Tenebrionidae, Bostrichidae, Cucujidae) over a range of temperatures. J. Econ. Entomol. 86, 1271–1278.
Hagstrum, D.W., Flinn, P.W., Shuman, D., 1996. Automated monitoring using acoustical sensors for insects in farm-stored wheat. J. Econ. Entomol. 89, 211–217.
Hansen, J.D., Webb, J.C., Armstrong, J.W., Brown, S.A., 1988. Acoustical detection of oriental fruit fly (Diptera: Tephritidae) larvae in papaya. J. Econ. Entomol. 81, 963–965.
Hardie, J., 1993. Flight behaviour in migrating insects. J. Agric. Entomol. 10, 239–245.
Hardie, J., Young, S., 1997. Aphid flight track analysis in three dimensions using video techniques. Physiol. Ent. 22, 116–122.
Hardie, J., Powell, G., 2002. Video analysis of aphid flight behaviour. Comput. Electron. Agric. 35, 229–242.
Harrison, R.D., Gardner, W.A., Tollner, W.E., Kinard, D.J., 1993. X-ray computed tomography studies of the burrowing behavior of fourth-instar pecan weevil (Coleoptera: Curculionidae). J. Econ. Entomol. 86, 1714–1719.
Hay, S.I., Packer, M.J., Rogers, D.J., 1997. The impact of remote sensing on the study and control of invertebrate intermediate hosts and vectors for disease. Int. J. Rem. Sens. 18, 2899–2930.
Hayashi, F., Nakane, M., 1988. A radio-tracking study on the foraging movements of the dobsonfly larva, *Protohermes grandis* (Megaloptera, Corydalidae). Kontyû (Tokyo) 56, 417–429.
Hayashi, F., Nakane, M., 1989. Radio tracking and activity monitoring of the dobsonfly larva, *Protohermes grandis* (Megaloptera, Corydalidae). Oecologia 78, 468–472.
Hedin, J., Ranius, T., 2002. Using radio telemetry to study dispersal of the beetle *Osmoderma eremita* an inhabitant of tree hollows. Comput. Electron. Agric. 35, 171–180.
Hendricks, D.E., 1980. Low-frequency sodar device that counts flying insects attracted to sex pheromone dispensers. Environ. Entomol. 9, 452–457.
Hendricks, D.E., 1989. Development of an electronic system for detecting *Heliothis* sp. moths (Lepidoptera: Noctuidae) and transferring incident information from the field to a computer. J. Econ. Entomol. 82, 672–684.
Hickling, R., Lee, P., Wei, W., Geyer, M.W., Pierce, D., Staten, R., Henneberry, T., 1994. Multiple acoustic sensor system for detecting pink bollworm in bolls. In: Proceedings of 1994 Beltwide Cotton Conferences, 5–8 January, San Diego, California. National Cotton Council of America, Memphis, Tennessee. vol. 2, pp. 1134–1136.
Hielkema, J.U., 1990. Satellite environmental monitoring for migrant pest forecasting by FAO: the ARTEMIS system. Phil. Trans. Roy. Soc. Lond. B 328, 705–717.

Hirabayashi, K., Ogawa, K.I., 1999. The efficiency of artificial wingbeat sounds for capturing midges in black light traps. Entomol. Exp. Applic. 92, 233–238.

Hirabayashi, K., Nakamoto, N., 2001. Field study on acoustic response of chironomid midges (Diptera: Chironomidae) around a hyper-eutrophic lake in Japan. Ann. Entomol. Soc. Am. 94, 123–128.

Hobbs, S.E., Hodges, G., 1993. An optical method for automatic classification and recording of a suction trap catch. Bull. Entomol. Res. 83, 47–52.

House, J., Koh, A., Edwards, E., Hall, D., 1999. Revolutionising remote sensing. Biologist 46, 123–128.

Hurlbert, I.A.R., French, J., 2001. The accuracy of GPS for wildlife telemetry and habitat mapping. J. Appl. Ecol. 38, 869–878.

Iida, F., 2001. Goal-directed navigation of an autonomous flying robot using biologically inspired cheap vision. In: Proceedings of the Thirtysecond ISR (International Symposium on Robotics), 19–21 April 2001, Seoul, Korea, pp. 1404–1409.

Ikawa, T., Okabe, H., Mori, T., Urabe, K., Ikeshoji, T., 1994. A method for reconstructing three-dimensional positions of swarming mosquitoes. J. Insect Behav. 7, 237–248.

Isaacs, R., Willis, M.A., Byrne, D.N., 1999. Modulation of whitefly take-off and flight orientation by wind speed and visual cues. Physiol. Entomol. 24, 311–318.

Isard, S.I., Gage, S.H., 2001. Flow of Life in the Atmosphere: An Airscape Approach to Understanding Invasive Organisms. Michigan State University Press, East Lansing, Michigan.

Johnson, M.W., Toscano, N.C., Jones, V.P., Bailey, J.B., 1986. Modified ultrasonic actograph for monitoring activity of lepidopterous larvae. Proc. Hawaiian Entomol. Soc. 27, 141–146.

Kram, R., Wong, B., Full, R.J., 1997. Three dimensional kinematics and limb kinetic energy of running cockroaches. J. Exp. Biol. 200, 1919–1929.

Kramer, E., 1976. The orientation of walking honeybees in odour fields with small concentration gradients. Physiol. Entomol. 1, 27–37.

Kaneko, S., Ino, M., Takamizawa, Y., 1995. Three sensitive actographs for cockroaches. Jpn. J. Appl. Entomol. Zool. 1995 (3), 65–73.

Kennedy, J.S., Ludlow, A.R., 1974. Co-ordination of two kinds of flight activity in an aphid. J. Exp. Biol. 61, 173–196.

Kenward, R., 1987. Wildlife Radio Tracking: Equipment, Field Techniques and Data Analysis. Academic Press, London.

Kindvall, O., Nordlander, G., Nordenhem, H., 2000. Movement behaviour of the pine weevil *Hylobius abietis* in relation to soil type: an arena experiment. Entomol. Exp. Applic. 95, 53–61.

Knoppien, P., van der Pers, J.N.C., van Delden, W., 2000. Quantification of locomotion and the effect of food deprivation on locomotor activity in *Drosophila*. J. Insect Behav. 13, 27–43.

Kube, C.R., Bonabeau, E., 2000. Cooperative transport by ants and robots. Robotics Autonom. Syst. 30, 85–101.

Kutsch, W., 2002. Transmission of muscle potentials during free flight of locusts. Comput. Electron. Agric. 35, 181–199.

Lacey, L.A., Mesquita, A.L.M., Mercadier, G., Debire, R., Kazmer, D.J., Leclant, F., 1997. Acute and sublethal activity of the entomopathogenic fungus *Paecilomyces fumosoroseus* (Deuteromycotina: Hyphomycetes) on adult *Aphelinus asychis* (Hymenoptera: Aphelinidae). Environ. Entomol. 26, 1452–1460.

Lehmann, F.O., Dickinson, M.H., 1997. The changes in power requirements and muscle efficiency during elevated force production in the fruit fly *Drosophila melanogaster*. J. Exp. Biol. 200, 1133–1143.

Lemaster, R.L., Beall, F.C., Lewis, V.R., 1997. Detection of termites with acoustic emission. For. Prod. J. 47, 75–79.

Leppla, N.C., Hamilton, E.W., Guy, R.H., Lee, F.L., 1979. Circadian rhythms of locomotion in six noctuid species. Ann. Entomol. Soc. Am. 72, 209–215.

Lingren, P.D., Raulston, J.R., Henneberry, T.J., Sparks, A.N., 1986. Night-vision equipment, reproductive biology, and nocturnal behaviour: importance to studies of insect flight, dispersal, and migration. In: Danthanarayana, W. (Ed.), Insect Flight: Dispersal and Migration. Springer, Berlin, pp. 253–264.

Lingren, P.D., Raulston, J.R., Popham, T.W., Wolf, W.W., Lingren, P.S., Esquivel, J.F., 1995. Flight behaviour of corn earworm (Lepidoptera: Noctuidae) moths under low wind speed conditions. Environ. Entomol. 24, 851–860.

Loxdale, H.D., Lushai, G., 1998. Molecular markers in entomology. Bull. Entomol. Res. 88, 577–600.

Loxdale, H.D., Lushai, G., 2001. Use of genetic diversity in movement studies of flying insects. In: Woiwod, I.P., Reynolds, D.R., Thomas, C.D. (Eds.), Insect Movement: Mechanisms and Consequences. CAB International, Wallingford, UK, pp. 361–386.

Luff, M., Molyneux, L., Ball, S., 1979. An ultrasonic insect movement detector. Physiol. Entomol. 4, 147–153.

MacLennan, D.N., Simmonds, E.J., 1992. Fisheries Acoustics. Chapman & Hall, London.

Mafra-Neto, A., Cardé, R.T., 1998. Rate of realized interception of pheromone pulses in different wind speeds modulates almond moth orientation. J. Comp. Physiol. A 182, 563–572.

Magor, J.I., Pender, J., 1997. Desert locust forecasters' GIS: a researchers' view. In: Krall, S., Peveling, R., Ba Diallo, D. (Eds.), New Strategies in Locust Control. Birkhäuser-Verlag, Basel, pp. 21–26.

Malinen, T., Horppila, J., Liljendahl-Nurminen, A., 2001. Langmuir circulations disturb the low-oxygen refuge of phantom midge larvae. Limnol. Oceanogr. 46, 689–692.

Mankin, R.W., 1994. Acoustical detection of *Aedes taeniorhynchus* swarms and emergence exoduses in remote salt marshes. J. Am. Mosq. Contr. Assoc. 10, 302–308.

Mankin, R.W., Hagstrum, D.W., 1995. Three-dimensional orientation of male *Cadra cautella* (Lepidoptera: Pyralidae) flying to calling females in a windless environment. Environ. Entomol. 24, 1616–1626.

Mankin, R.W., Weaver, D.K., 2000. Acoustic detection and monitoring of *Cephus cinctus* sawfly larvae in wheat stems. In: Abstracts of XXI International Congress of Entomology, Foz do Iguassu, Brazil, Book 1. Embrapa Soja, Londrina, Brazil, Abstract number 0800 p. 202.

Mankin, R.W., Shuman, D., Coffelt, J.A., 1997a. Acoustic counting of adult insects with differing rates and intensities of sound production in stored wheat. J. Econ. Entomol. 90, 1032–1038.

Mankin, R.W., Sun, J.S., Shuman, D., Weaver, D.K., 1997b. Shielding against noise interfering with quantitation of insect infestations by acoustic detection systems in grain elevators. Appl. Acoust. 50, 309–324.

Mankin, R.W., Crocker, R.L., Flanders, K.L., Shapiro, J.P., 1998. Acoustic detection and identification of insects in soil. In: Kuhl, P.K., Crum, L.A. (Eds), Proceedings of the 16th International Congress of Acoustics and the 135th Annual Meeting of the Acoustical Society of America, pp. 685–686.

Mankin, R.W., Shuman, D., Weaver, D.K., 1999. Thermal treatments to increase acoustic detectability of *Sitophilus oryzae* (Coleoptera: Curculionidae) in stored grain. J. Econ. Entomol. 92, 453–462.

Mankin, R.W., Brandhorst-Hubbard, J., Flanders, K.L., Zhang, M., Crocker, R.L., Lapointe, S.L., McCoy, C.W., Fisher, J.R., Weaver, D.K., 2000. Eavesdropping on insects hidden in soil and interior structures of plants. J. Econ. Entomol. 93, 1173–1182.

Marden, J.H., Wolf, M.R., Weber, K.E., 1997. Aerial performance of *Drosophila melanogaster* from populations selected for upwind flight ability. J. Exp. Biol. 200, 2747–2755.

Matsuoka, H., Fujii, Y., Okumura, S., Imamura, Y., Yoshimura, T., 1996. Relationship between the type of feeding behavior of termites and the acoustic emission (AE) generation. Wood Res. 83, 1–7.

Milford, J.R., Dugdale, G., 1990. Monitoring of rainfall in relation to the control of migrant pests. Phil. Trans. Roy. Soc. Lond. B 328, 705–717.

Müller, P., Robert, D., 2001. A shot in the dark: the silent quest of a free-flying phonotactic fly. J. Exp. Biol. 204, 1039–1052.

Noldus, L.P.J.J., Spink, A.J., Tegelenbosch, R.A.J., 2002. Computerised video tracking, movement analysis and behaviour recognition in insects. Comput. Electron. Agric. 35, 201–227.

Northcote, T.G., 1964. Use of a high-frequency echosounder to record distribution and migration of *Chaoborus* larvae. Limnol. Oceanogr. 9, 87–91.

Okubo, A., Bray, D.J., Chiang, H.C., 1981. Use of shadows for studying the three-dimensional structure of insect swarms. Ann. Entomol. Soc. Am. 74, 48–50.

Perryman, A., 1996. Introduction to Remote Sensing and the LARST Systems. Natural Resources Institute, Chatham, UK.

Preiss, R., Kramer, E., 1984. Control of flight speed by minimization of the apparent ground pattern movement. In: Varju, D., Schnitzler, H.U. (Eds.), Localisation and Orientation in Biology and Engineering. Springer, Berlin, pp. 140–142.

Preiss, R., Spork, P., 1993. Flight-phase and visual-field related optomotor yaw responses in gregarious desert locusts during tethered flight. J. Comp. Physiol., A 172, 733–740.

Priede, I.G., Swift, S.M., 1992. Wildlife Telemetry: Remote Monitoring and Tracking of Animals. Ellis Horwood, Chichester, UK.

Pope, K.O., Sheffner, E.J., Linthicum, K.J., Bailey, C.L., Logan, T.M., Kasischke, E.S., Birney, K., Njogu, A.R., Roberts, C.R., 1992. Identification of central Kenyan Rift Valley fever virus vector habitats with Landsat TM and evaluation of their flooding status with airborne imaging radar. Rem. Sens. Environ. 40, 185–196.

Racette, G., Hill, S.B., Vincent, C., 1990. Actographs for recording daily activity of plum Curculio (Coleoptera: Curculionidae). J. Econ. Entomol. 83, 2385–2392.

Rempel, R.S., Rodgers, A.R., 1997. Effects of differential correction on accuracy of a GPS animal location system. J. Wildl. Manage. 61, 530–539.

Renou, M., Berthier, A., Desbarats, L., Van der Pers, J., Guerrero, A., 1999. Actographic analysis of the effects of an esterase inhibitor on male moth responses to sex pheromone. Chem. Senses 24, 423–428.

Reynolds, D.R., Riley, J.R., Armes, N.J., Cooter, R.J., Tucker, M.R., Colvin, J., 1997. Techniques for quantifying insect migration. In: Dent, D.R., Walton, M.P. (Eds.), Methods in Ecological and Agricultural Entomology. CAB International, Wallingford, UK, pp. 111–145.

Riley, J.R., 1989. Remote sensing in entomology. Ann. Rev. Entomol. 34, 247–271.

Riley, J.R., 1993. Flying insects in the field. In: Wratten, S.D. (Ed.), Video Techniques in Animal Ecology and Behaviour. Chapman & Hall, London, pp. 1–15.

Riley, J.R., 1994. Acoustic sounding, atmospheric structure and insects. Int. J. Rem. Sens. 15, 293–297.

Riley, J.R., Edwards, A.S., 1997. Airborne insects as potential sources of acoustic reflectivity. J. Atmos. Oceanic. Tech. 14, 538–542.

Riley, J.R., Smith, A.D., 2002. Design considerations for an harmonic radar to investigate the flight of insects at low altitude. Comput. Electron. Agric. 35, 151–169.

Riley, J.R., Reynolds, D.R., Farmery, M.J., 1983. Observations of the flight behaviour of the armyworm moth, *Spodoptera exempta*, at an emergence site using radar and infra-red optical techniques. Ecol. Entomol. 8, 395–418.

Riley, J.R., Smith, A.D., Bettany, B.W., 1990. The use of video equipment to record in three dimensions the flight trajectories of *Heliothis armigera* and other moths at night. Physiol. Entomol. 15, 73–80.

Riley, J.R., Armes, N.J., Reynolds, D.R., Smith, A.D., 1992. Nocturnal observations on the emergence and flight behaviour of *Helicoverpa armigera* (Lepidoptera: Noctuidae) in the post-rainy season in central India. Bull. Entomol. Res. 82, 243–256.

Riley, J.R., Reynolds, D.R., Mukhopadhyay, S., Ghosh, M.R., Sarkar, T.K., 1995. Long-distance migration of aphids and other small insects in northeast India. Eur. J. Entomol. 92, 639–653.

Ritzmann, R.E., Quinn, R.D., Watson, J.T., Zill, S.N., 2000. Insect walking and biorobotics: a relationship with mutual benefits. BioScience 50 (1), 23–33.

Roberts, G.T., Chambers, J., 1993. System for laboratory investigation of insect behaviour. In: Proceedings of the Working Group Meeting on Use of Pheromones and other Semiochemicals in Integrated Control, Chatham, UK, 11–14 May 1993. IOBC/WPRS Bulletin vol. 16 (10) pp. 29–35.

Room, P.M., Hanan, J.S., Clarke, A., 1998. 3D dynamics, scientific visualisation, VR and PPM in entomology. In: Zalucki, M.P., Drew, R.A.I., White, G.G (Eds), Pest Management—Future Challenges. Proceedings of the Sixth Australasian Applied Entomological Research Conference Brisbane, 29 September–2 October 1998 vol. 2. University of Queensland Press, Brisbane, pp. 279–288.

Rose, D.J.W., Page, W.W., Dewhurst, C.F., Riley, J.R., Reynolds, D.R., Pedgley, D.E., Tucker, M.R., 1985. Downwind migration of the African armyworm moth, *Spodoptera exempta*, studied by mark-and-capture and by radar. Ecol. Entomol. 10, 299–313.

Rose, D.J.W., Dewhurst, C.F., Page, W.W., 2000. The African Armyworm Handbook: The Status, Biology, Ecology, Epidemiology and Management of *Spodoptera exempta* (Lepidoptera: Noctuidae), second ed. Natural Resources Institute, Chatham, UK.

Sakuma, M., 2002. Virtual reality experiments on a digital servosphere: guiding male silkworm moths to a virtual odour source. Comput. Electron. Agric. 35, 243–254.
Sandford, M.T., 1989. Bar codes on bees and honey, APIS-Apicultural Information and Issues 7 (5) 1989.
Sasaki, M., 1989. A trial of the micro-bar-code system for monitoring honeybee behaviour. Honeybee Sci. (Mitsubachi-Kagaku) 10, 182–183.
Schaefer, G.W., Bent, G.A., 1984. An infra-red remote sensing system for the active detection and automatic determination of insect flight trajectories (IRADIT). Bull. Entomol. Res. 74, 261–278.
Schaefer, G.W., Bent, G.A., Allsopp, K., 1985. Radar and opto-electronic measurements of the effectiveness of Rothamsted Insect Survey suction traps. Bull. Entomol. Res. 75, 701–705.
Scheffrahn, R.H., Robbins, W.P., Busey, P., Su, N.-Y., Mueller, R.K., 1993. Evaluation of a novel, hand-held, acoustic emissions detector to monitor termites (Isoptera: Kalotermitidae, Rhinotermitidae) in wood. J. Econ. Ent. 86, 1720–1729.
Schilstra, C., van Hateren, J.H., 1998. Using miniature sensor coils for simultaneous measurement of orientation and position of small, fast-moving animals. J. Neurosci. Methods 83, 125–131.
Schmidt, R., Göller, S., Hertel, H., 1995. Computerized detection of feeding sounds from wood boring beetle larvae. Mater. Org. 29, 295–304.
Schneider, K., 1995. Acoustical detection of pink bollworms in cotton bolls. In: Proceedings 1995 Beltwide Cotton Conference, San Antonio, TX, vol. 2, pp. 1054–1057.
Schofield, S., Brady, J., 1997. Effects of carbon dioxide, acetone and 1-octen-3-ol on the flight responses of the stable fly, *Stomoxys calcitrans*, in a wind tunnel. Physiol. Entomol. 22, 380–386.
Schouest, L.P., Miller, T.A., 1994. Automated pheromone traps show male pink bollworm (Lepidoptera: Gelechiidae) mating response is dependent on weather conditions. J. Econ. Entomol. 87, 965–974.
Schumacher, P., Weyeneth, A., Weber, D.C., Dorn, S., 1997. Long flights in *Cydia pomonella* L. (Lepidoptera: Tortricidae) measured by a flight mill: influence of sex, mated status and age. Physiol. Entomol. 22, 149–160.
Service, M.W., 1993. Mosquito Ecology: Field Sampling Methods, second ed. Elsevier Applied Science, London.
Sharp, J.L., Thalman, R.K., Webb, J.C., Masuda, S., 1988. Flexible acoustical device to detect feeding sounds of Caribbean fruit fly (Diptera: Tephritidae) larvae in mango, cultivar Francis. J. Econ. Ent. 81, 406–409.
Shuman, D., Weaver, D.K., Mankin, R.W., 1997. Quantifying larval infestation with an acoustical sensor array and cluster analysis of cross-correlation outputs. Appl. Acoust. 50, 279–296.
Skatulla, U., Fiecht, E., 1995. Observations of the flight behaviour of *Lymantria monacha* L. (Lep., Lymantriidae) to pheromone baited traps. J. Appl. Entomol. 119, 17–19.
Smith, G.S., Curtis, J.P., Habib, R., Blaise, P., 1996. A fast and effective method of measuring tree structure in 3 dimensions. Acta Hortic. 416, 15–20.
Southwood, T.R.E., Henderson, P.A., 2000. Ecological Methods, third ed. Blackwell Science, Oxford, p. 575.
Spencer, J.L., Gewax, L.J., Keller, J.E., Miller, J.R., 1997. Chemiluminescent tags for tracking insect movement in darkness: application to moth photo-orientation. Great Lakes Entomol. 30, 33–43.
Srinivasan, M.V., Chahl, J.S., Weber, K., Venkatesh, S., Nagle, M.G., Zhang, S.W., 1999. Robot navigation inspired by principles of insect vision (review). Robotics Autonom. Syst. 26, 203–216.
Srinivasan, M.V., Zhang, S.W., Chahl, J.S., Barth, E., Venkatesh, S., 2000. How honeybees make grazing landings on flat surfaces. Biol. Cybern. 83, 171–183.
Strauss, R., Schuster, S., Götz, K.G., 1997. Processing of artificial visual feedback in the walking fruit fly *Drosophila melanogaster*. J. Exp. Biol. 200, 1281–1296.
Takken, W., Huisman, P.W.T., Buma, M.O.S., Noldus, L.P.J.J., 1996. Three-dimensional video tracking and analysis of the flight of nocturnal anopheline mosquitoes. In: Measuring Behavior'96, International Workshop on Methods and Techniques in Behavioral Research, 16–18 October 1996, Utrecht, The Netherlands.
Tappan, G.G., Moore, D.G., Knausenberger, W.I., 1991. Monitoring grasshopper and locust habitats in Sahelian Africa using GIS and remote sensing technology. Int. J. Geogr. Inform. Syst. 5, 123–135.

Taylor, R.A.J., Nault, L.R., Styer, W.E., Cheng, Z.B., 1992. Computer-monitored, 16-channel flight mill for recording the flight of leafhoppers (Homoptera: Auchenorrhyncha). Ann. Entomol. Soc. Am. 85, 627–632.

Theophilidis, G., Burns, M.D., 1990. The firing pattern of the locust (*Schistocerca gregaria americana*) mesothoracic femoral motor axons in resistance reflexes and during walking on a treadmill. J. Insect Physiol. 36, 513–522.

Tryba, A.K., Ritzmann, R.E., 2000. Multi-joint coordination during walking and foothold searching in the *Blaberus* cockroach. I. Kinematics and electromyograms. J. Neurophysiol. 83, 3323–3336.

Tucker, M.R., 1997. Satellite-derived rainstorm distribution as an aid to forecasting African armyworm outbreak. Weather 52, 204–212.

Tucker, M.R., Holt, J., 1999. Decision tools for managing migrant insect pests. In: Grant, I.F., Sear, C. (Eds.), Decision Tools for Sustainable Development. Natural Resources Institute, Chatham, UK, pp. 97–128.

Turchin, P., 1998. Quantitative Analysis of Movement. Sinauer Associates, Sunderland, MA.

Varley, M.J., Copeland, M.J.W., Wratten, S.D., Bowie, M.H., 1993. In: Wratten, S.D. (Ed.), Video Techniques in Animal Ecology and Behaviour. Chapman & Hall, London, pp. 33–63.

Vick, K.W., Webb, J.C., Weaver, B.A., Litzkow, C., 1988. Sound detection of stored-product insects that feed inside kernels of grain. J. Econ. Ent. 81, 1489–1493.

Vickers, N.J., Baker, T.C., 1997. Flight of *Heliothis virescens* males in the field in response to sex pheromone. Physiol. Entomol. 22, 277–285.

Vigneault, C., Founier, F., Hui, K.P.C., Boivin, G., 1997a. Systèm d'analyse d'images adapté pour l'étude du comportement de trichogrammes. Cahiers Agric. 6 (4), 289–292.

Vigneault, C., Panneton, B., Cormier, D., Boivin, G., 1997b. Automated system to quantify the behaviour of small insects in a four-pointed star olfactometer. Appl. Eng. Agric. 13, 545–550.

Villani, M.G., Gould, F., 1986. Use of radiographs for movement analysis of the corn wireworm, *Melanotus communis* (Coleoptera: Elateridae). Environ. Entomol. 15, 462–464.

Villani, M.G., Wright, R.J., 1988. Use of radiography in behavioural studies of turf-grass scarab grub species (Coleoptera: Scarabaeidae). Bull. Entomol. Soc. Am. 34, 132–144.

von Hünerbein, K., Hamann, H.J., Rüter, E., Wiltschko, W., 2000. A GPS-based system for recording the flight paths of birds. Naturwissenschaften 87, 278–279.

Voss, R., Zeil, J., 1995. Automatic tracking of complex objects under natural conditions. Biol. Cybern. 73, 415–423.

Voss, F., Dreiser, U., 1997. Mapping of desert locust habitats using remote sensing habitats. In: Krall, S., Peveling, R., Ba Diallo, D. (Eds.), New Strategies in Locust Control. Birkhäuser, Basel, pp. 37–45.

Waddington, K.D., Esch, H., Burns, J.E., 1996. The effects of season, pretraining, and scent on the efficiency of traps for capturing recruited honey bees (Hymenoptera: Apidae). J. Insect Behav. 9, 451–455.

Wajnberg, E., Colazza, S., 1998. Genetic variability in the area searched by a parasitic wasp: analysis from automatic video tracking of the walking path. J. Insect Physiol. 44, 437–444.

Walker, T.J., 1988. Acoustic traps for agriculturally important insects. Florida Entomol. 71, 484–492.

Walker, T.J., 1996. Acoustic methods of monitoring and manipulating insect pests and their natural enemies. In: Rosen, D., Bennet, F.D., Capinera, J.L. (Eds.), Pest Management in the Subtropics: Integrated Pest Management—a Florida Perspective. Intercept, Andover, UK, pp. 245–257.

Walker, T.J., Fritz, G.N., 1983. Migratory and local flights in mole crickets, *Scapteriscus* sp. (Gryllotalpidae). Environ. Entomol. 12, 953–958.

Wang, Z.J., 2000. Two dimensional mechanism for insect hovering. Phys. Rev. Lett. 85, 2216–2219.

Watson, J.T., Ritzmann, R.E., 1998. Leg kinematics and muscle activity during treadmill running in the cockroach, *Blaberus discoidalis*. I. Slow. running. J. Comp. Physiol. A 182, 11–22.

Watson, E., Barson, G., Pinniger, D.B., Roberts, G., Ludlow, A.R., 1997. Evaluation of the behavioural responses of *Anthrenus verbasci* adults and larvae to permethrin using a computerized tracking system. J. Stored Prod. Res. 33, 335–346.

Webb, J.C., Slaughter, D.C., Litzkow, C.A., 1988. Acoustical system to detect larvae in infested commodities. Florida Entomol. 71, 492–504.

Weber, D.C., Ferro, D.N., Stoffolano, J.G., 1993. Quantifying flight of Colorado potato beetles (Coleoptera: Chrysomelidae) with a microcomputer-based flight mill system. Ann. Entomol. Soc. Am. 86, 366–371.

Weaver, D.K., Shuman, D., Mankin, R.W., 1997. Optimizing and assessing the performance of an algorithm that cross-correlates acquired acoustic emissions from internally feeding larvae to count infested wheat kernels in grain samples. Appl. Acoust. 50, 297–308.

Weissling, T.J., Thoms, E.M., 1999. Use of an acoustic emission detector for locating Formosan subterranean termite (Isoptera: Rhinotermitidae) feeding activity when installing and inspecting aboveground termite bait stations containing hexaflumuron. Florida Entomol. 82, 60–71.

Werb, J., Lanzl, C., 1998. Designing a positioning system for finding things and people indoors. IEEE Spectr. 35 (9), 71–79.

Wheater, C.P., 1988. Measurement of the activity of mesofauna using an actograph-microcomputer system. Pedobiologia 31, 219–222.

Wiens, J.A., Crist, T.O., Milne, B.T., 1993. On quantifying insect movements. Environ. Entomol. 22, 709–715.

Willis, M.A., David, C.T., Murlis, J., Cardé, R.T., 1994. Effects of pheromone plume structure and visual stimuli on the pheromone-modulated upwind flight of male gypsy moths (*Lymantria dispar* L.) in a forest. J. Insect Behav. 7, 385–409.

Willmott, A.P., Ellington, C.P., 1997. The mechanics of flight in the hawkmoth *Manduca sexta*. I. Kinematics of hovering and forward flight. J. Exp. Biol. 200, 2705–2722.

Woiwod, I.P., Reynolds, D.R., Thomas, C.D., 2001. Introduction and overview. In: Woiwod, I.P., Reynolds, D.R., Thomas, C.D. (Eds.), Insect Movement: Mechanisms and Consequences. CAB International, Wallingford, UK, pp. 1–18.

Wolcott, T.G., 1995. New options in physiological and behavioural ecology through multichannel telemetry. J. Exp. Mar. Biol. Ecol. 193, 257–275.

Worthington, S.L.S., 1998. Video cameras and high speed imaging detect insect locomotion, Vision Systems Design, 30–37.

Wyatt, T.D., 1997. Methods in studying insect behaviour. In: Dent, D.R., Walton, M.P. (Eds.), Methods in Ecological and Agricultural Entomology. CAB International, Wallingford, UK, pp. 27–56.

Ye, S., Dowd, J.P., Comer, C.M., 1995. A motion tracking system for simultaneously recording of rapid locomotion and neural activity from an insect. J. Neurosci. Methods 60, 199–210.

Young, S., Hardie, J., Gibson, G., 1993. Flying insects in the laboratory. In: Wratten, S.D. (Ed.), Video Techniques in Animal Ecology and Behaviour. Chapman & Hall, London, pp. 17–32.

Zalucki, M.P., Kitching, R.L., Abel, D., Pearson, J., 1980. A novel device for tracking butterflies in the field. Ann. Entomol. Soc. Am. 73, 262–265.

Zanen, P.O., Cardé, R.T., 1999. Directional control by male gypsy moths of upwind flight along a pheromone plume in three wind speeds. J. Comp. Physiol. A 184, 21–35.

Zarnack, W., Wortmann, M., 1989. On the so called constant-lift reaction of migratory locusts. J. Exp. Biol. 147, 111–124.

Zeil, J., 1993. Orientation flights of solitary wasps (Cercis; Sphecidae; Hymenoptera). I. Description of flight. J. Comp. Physiol. A 172, 189–205.