INAUGURAL LECTURE SERIES

Riding on the Wind: A Radar Perspective of Insect Flight

by

Joe Riley
Professor of Radar Entomology
Natural Resources Institute

5th May 1999

the
UNIVERSITY
of
GREENWICH

RIDING ON THE WIND: A RADAR PERSPECTIVE OF INSECT FLIGHT

by
Joe Riley
Professor of Radar Entomology
Natural Resources Institute

An Inaugural Lecture Delivered at the University of Greenwich
5th May 1999

ISBN 1 86166 129 0

First published in 1999 by the Procurement and Business Services Department, University of Greenwich.

University of Greenwich, a charity and company limited by guarantee, registered in England (reg. no. 986729). Registered office: Bexley Road, Eltham, London SE9 2PQ.

Dr Joseph R. Riley

Joe Riley excelled at chemistry at school, but his predilection for making explosive compounds led to his being banned from the chemistry laboratory, and he went on to Oxford to read physics instead. There, owing to a misunderstanding with his tutors, he found that he had an unexpected opportunity to spend a year in industry, but as this led to the award of a patent to his new employers and a scholarship for him, his remaining two years at Oxford proved less impecunious than they might have been. Immediately after taking his degree, and newly married, he took up a year's lectureship in physics at the Middle East Technical University, in Ankara. On his return to the UK, while working as a senior research fellow at the Royal Military College of Science in Shrivenham, he registered for a D.Phil. at Oxford, and spent the next four years investigating non-linear interactions between high power microwaves and gaseous plasmas. In 1970, he left Shrivenham to join the Centre for Overseas Pest Research (a precursor of NRI), and set up a unit at the Royal Radar Establishment in Malvern to develop radar for entomological purposes. Apart from a year spent in the USA working as National Academy of Sciences Senior Research Associate at the NASA Flight Centre at Wallops Island, Virginia, he has been working in Malvern ever since.

The COPR Radar Unit quickly developed the capacity to carry out observations of the high altitude migration of insects, and subsequently worked in nine developing countries in Africa, and the Far and Middle East, as well as collaborating in studies in Australia and the USA. Funded mainly under the crop protection programmes of the Overseas Development Administration (now the Department for International Development), the Radar Unit investigated the long-range movement of a series of insect pests, and over the years it acquired the reputation of being the leading radar entomology group in the world. In 1992, Joe was presented with the Friendship Medal of the Government of China by Premier Li Peng, for the outstanding contributions made to Chinese agriculture by his team, and in 1996, the Radar Unit achieved world-wide publicity for their development of harmonic radar able to track insects in low-level flight.

He is a Fellow of the Institution of Electrical Engineers, and is the author or co-author of over 90 papers, book chapters and conference publications.

RIDING ON THE WIND: A RADAR PERSPECTIVE OF INSECT FLIGHT

Joe Riley
Professor of Radar Entomology
Natural Resources Institute

PROLOGUE

And the Lord brought an east wind upon the land...
And the east wind brought the locusts... over all the land of Egypt Exodus 10:13–14

In the ancient world, the sudden appearance of plagues of flying locusts, apparently out of nowhere, was so mysterious and dramatic that it was often seen as a direct manifestation of divine displeasure. With the passage of time, this explanation gradually came to seem less plausible, but nevertheless, the locust mystery remained more or less intact until Boris Uvarov, a Russian entomologist, established his 'phase theory' (Uvarov 1921). He found that an inconspicuous and normally innocuous species of solitary grasshopper (known as *Locusta danica*) had a Jekyll and Hyde capacity to transform itself into the much feared Migratory Locust (*Locusta migratoria)*, with gregarious habits, increased activity, rapacious appetite and accelerated reproduction. What had previously been thought of as two species, was in fact one, but with the ability to change its appearance and behaviour dramatically when individuals became crowded together.

While this discovery partially resolved the ancient enigma of how locusts originated, it did not explain why they sometimes appeared so suddenly in such large numbers. Then in the 1920s, the British Government became concerned about serious locust plagues in the colonies, especially those of the Desert Locust (*Schistocerca gregaria*) and Uvarov (now in the UK and working at the Imperial Bureau of Entomology) was asked to investigate. His subsequent cartographic work, and that of his colleagues (especially Zena Waloff), showed that under certain circumstances, locusts could fly astonishingly long distances, both in their gregarious and solitary forms (Pedgley 1981; Ritchie & Pedgley 1989). This led to the realization that airborne movement played a vital part in locust population dynamics, and it was gradually recognized that this was probably true for some other insect pests too. Thus the aerial migration of insects in general came to be seen as a subject worthy of serious study for economic as well as for academic reasons.

Even in daylight, individual airborne insects are very hard to see for more than a few tens of metres. Worse, many fly at night when they are even more difficult to observe, so studying long-range insect migration was to be no simple task. Much hinged on painstakingly acquired circumstantial and indirect evidence, and conclusions were often tentative and subject to dispute. Then in the 1950s, Reg Rainey FRS, a distinguished pioneer in locust migration studies (Rainey 1951), became convinced that radar could be used to resolve *by direct observation* many of the uncertainties about what insects did in the sky (e.g. Rainey 1955). The technique had, after all, been originally developed specifically to detect unwelcome airborne invaders, and locusts fell into this class rather nicely.

I hope to show in this presentation how Rainey was entirely justified in his conviction, and how the bulk of our current knowledge about insect migratory flight behaviour at high altitude has come directly from the application of radar to entomology.

INTRODUCTION

In 1945, the Anti-Locust Research Centre (ALRC) emerged as an independent entity from within the Imperial Bureau of Entomology. I was 5 years old at that time, so it was not immediately obvious that this event held any particular personal significance for me. But it turned out otherwise, because 24 years later I responded to a newspaper advertisement by ALRC for a new and temporary post of radar entomologist. In hindsight this seems to have been a rather rash thing to do, as I knew next to nothing about insects and had never even seen a radar. But the advertisement mentioned the prospect of overseas travel and, like many post-doctoral students, I was full of largely unwarranted confidence, and wanted a change of topic for a year or two. To my surprise, the application was successful, and I was precipitated from the calm and temperate atmosphere of laboratory physics into the helter-skelter world of field work in the developing countries, which I discovered to my alarm, was neither calm nor temperate. Another matter for concern was that ALRC (an antecedent of NRI) had an excellent reputation in its field, with a tradition of distinguished scientists on its staff, including Boris Uvarov, who had received a knighthood, and Dr Reg Rainey, both Fellows of the Royal Society, so there were some very hard acts to follow. Fortunately for me, the fledgling science of radar entomology turned out to be a more sturdy infant than many thought, and now, some 27 years later, I have the privilege of being able to outline its development in this inaugural lecture.

PRE-RADAR STUDIES OF INSECT MIGRATION

The need to control locusts proved a major stimulus (and source of serious funding) for research into their migration, and this helped to promote a greater awareness of migration studies on other insects. Probably because they fly during the day, usually at low altitude and so are relatively easy to spot, butterflies had been one of the first insects to attract attention – European records of their mass movements date back to the 12th century (Williams 1965). More recent studies collated sightings reported by numerous and widespread amateur observers (e.g. Williams 1930, 1965), or used mark-recapture experiments – the classic example being that of Urquhart (1960, 1987) on the Monarch butterfly (*Danaus plexippus*) in North America, which over the years has involved thousands of collaborators.

Studying migration at altitude was obviously more problematic, but by the late 1920s and early 1930s, Coad and Glick in the USA, and Berland in France, were flying around in aircraft with sampling nets attached, and finding insects flying at altitudes up to 4 km above ground level (Johnson 1969). Similar research was carried out in the UK, although characteristically, with more modest equipment: nets on kites (Hardy & Milne 1938), on wireless station masts (Freeman 1945) and on ships' mastheads (Hardy & Milne 1937; Hardy & Cheng 1986). This work led to C. G. Johnson's studies of aphid migration using nets and suction traps suspended at altitude from barrage balloons (Johnson 1969); to the development of suction traps as standardized instruments for the quantitative monitoring of small migratory insects by Johnson and L. R. Taylor; and to the establishment (in the 1960s) of the Rothamsted Insect Survey's network of suction traps designed to routinely monitor aerial fauna at 12 m above ground level (Taylor 1985; Woiwod & Harrington 1994).

Although aerial sampling provided intriguing glimpses of insect activity aloft, obtaining information on even the basic features of faunal distribution within the lower atmosphere was very difficult and costly, and the technique yielded little or no information on flight behaviour (air speed and orientation, rate of climb) or how this is related to small-scale atmospheric phenomena. Clearly, another technique was required if research was to progress – but which?

THE BEGINNINGS OF RADAR ENTOMOLOGY

The first application of radar to observe biological targets was made by ornithologists whose experience of wartime radar operations had alerted them to the potential of the technique as a means of studying flying birds (Lack & Varley 1945). Their subsequent development of radar ornithology (Eastwood 1967) vastly increased the range and accuracy of observations of bird migration, and led to new and detailed descriptions of their migratory behaviour.

The exciting possibility of detecting targets as small as individual insects was demonstrated by Crawford in the USA in 1949, and almost coincidentally in 1950, serious proposals were being made to use radar to study locust flight (Rainey 1955). Rainey was unaware of Crawford's work, but deduced from a consideration of the water content of locusts, that meteorological radars should be able to detect swarms of these insects as least as easily as they detected heavy precipitation. In the event, the first locust swarm detection was made by chance, by a 10-cm wavelength naval radar in the Persian Gulf (Rainey 1955). Evidence continued to accumulate that radar had real potential as an entomological tool (summarized in Riley 1980), and in 1968 ALRC decided to sponsor an attempt to use a specially assembled, mobile radar to study the flight behaviour of solitary Desert Locusts. This pioneering study was lead by Dr Glen Schaefer of Loughborough University, who already had experience of using radar to track birds, and it turned out to be a resounding success (Roffey 1969; Schaefer 1969). The modified 3.2-cm marine radar displayed parts of the flight trajectories of individual locusts out to ranges of 2 km by day and night, and provided a measure of their aerial density, height of flight (up to 1.2 km) and ground speed, as well as showing dramatic increases in aerial density at nocturnal windshift lines. It was from this point that radar entomology was to grow into a discipline that found application round the world.

THE ESTABLISHMENT OF RADAR ENTOMOLOGY

The role of NRI and its antecedents

The 1968 experiments were so promising that ALRC (later renamed the Centre for Overseas Pest Research, COPR) decided to set up a temporary in-house radar capability, and this resulted in the advertisement that brought me into the picture. I was uncomfortably aware before taking up the post that the technical resources required to build and test radars were very specialized and expensive – well beyond the budget allocated to the 2-year project which I had been hired to run. However, by good fortune I had contacts at the Royal Radar Establishment (RRE), the UK's main centre for radar research, and it was agreed that the new COPR Radar Entomology Unit would be set up on one of the RRE sites in Malvern, Worcestershire, with access to such test and measurement facilities as were needed. With this excellent technical base we were well placed to play a leading role in the development and application of radar techniques to entomology, and as a result, the 2-year project eventually came to be a permanent fixture of COPR and, on its change of name, of NRI. The achievements of the Radar Unit are summarized in later sections of this presentation, but to put them in context, I briefly outline other initiatives in radar entomology which began at about the same time.

Developments elsewhere

Britain

Schaefer continued to make major contributions to radar entomology, independently of COPR, and mounted a radar field expedition in Australia for CSIRO in March 1971 (Schaefer 1976; Roffey 1972). In October–November of that year, and in October of 1973 and 1974, he also undertook radar observations of moths and grasshoppers in the Gezira area of Sudan, under contract to the CIBA-financed Agricultural Aviation Research Unit (AARU) at the Cranfield Institute of Technology (Schaefer 1976), and between 1973 and 1976, he contributed to an ambitious experimental programme for the Canadian Forestry Service. This programme focused on the movements of the Spruce Budworm Moth, *Choristoneura fumiferana*, and used entomological radars specially designed for airborne use, ground-based radar, aircraft-mounted insect sampling nets, and aircraft equipped with Doppler wind-finding equipment (Greenbank, Schaefer & Rainey 1980; Dickison et al. 1986). In 1975, Schaefer established the Ecological Physics Research Group at Cranfield, and worked on the development of radar and other remote sensing techniques for insect observation, until his death in 1986. Schaefer's pioneering contributions to radar entomology are described in an obituary by Rainey (1986).

Australia

In the meantime, CSIRO had established its own capacity to make observations of insect flight, focusing primarily on studies of the Australian Plague Locust, *Chortoicetes terminifera* (Roffey 1972; Reid, Wardhaugh & Roffey 1979), but also mounting investigations of insect migration over the Arafura Sea and across the Torres Strait, with support from the COPR radar group. In 1978, Dr V. A. Drake was appointed to lead their radar entomology effort, and he subsequently made many significant contributions to the radar entomology literature, describing field observations of grasshoppers, locusts and moths, and of atmospheric phenomena influencing their migration (see references in Drake & Farrow 1988). Now at the Australian Defence Force Academy, he continues to play an active role in radar entomology research, particularly in investigating methods for the long-term monitoring of airborne populations using a combination of entomological and meteorological remote-sensing methods (Drake 1993; Drake et al. 1994).

USA

Through the 1960s and 1970s, very small 'point' targets were often inadvertently detected by sensitive meteorological radars in the USA, such as the FMCW radar developed by the Naval Electronic Laboratory in San Diego (Richter et al. 1973) or the high-powered, multi-wavelength radars situated at Wallops Island, Virginia (e.g. Hardy, Atlas & Glover 1966). Studies of these so-called 'dot-angel' echoes showed that they were caused mostly by insects (Glover et al. 1966), but radar entomology nevertheless did not become established in the USA until 1978, when the United States Department of Agriculture (USDA) entered the field. Mr W. W. Wolf, then working at their Western Cotton Research Laboratory, fitted a military radar with a marine transceiver, and carried out radar observations of insect flight over cotton fields in Arizona (Wolf 1979). He later moved to the USDA Insect Biology and Population Management Research Laboratory in Tifton, Georgia, and with colleagues there, engaged in a long-term investigation of the migration of the Corn Earworm, *Helicoverpa zea*, and other moths into southern USA, particularly from sources in the Lower Rio Grande Valley of north-eastern Mexico. Wolf extended the USDA technical capacity to include observations with airborne insect-detecting radar, in collaboration with Dr S. Hobbs of Cranfield University (Wolf et al. 1990; Hobbs & Wolf 1996), and configured his ground-based radars so that they could be moved and set up quickly, allowing observations to be made from sequential sites, at intervals of only an hour or so.

Another USDA radar entomology group was formed at College Station in Texas in 1985, with Dr K. R. Beerwinkle as the principal radar engineer. Besides operating conventional scanning radar, this group took up the idea, originally developed by NRI, of using vertical-looking radar with rotating polarization to monitor overflying insects (Beerwinkle, Witz & Schleider 1993). Using a computerized data logging and processing facility, the College Station group were able to make qualitative records of nocturnal insect flight between 500 and 2400 m above ground, for a whole year in 1990–91 (Beerwinkle et al. 1995). The two USDA groups were combined in 1991, and presently form part of the Areawide Pest Management Research Unit (APMRU), based at College Station. Recent innovative field techniques of the APMRU include long-distance radio tracking of instrumented tetroons (fixed volume balloons which drift at more or less constant altitude) as surrogates for migrating moths (Westbrook et al. 1995), and aerial capture of insects using traps attached to tetroons and to tethered balloons.

Another large American programme was the 1983–85 Illinois 'Pests and Weather' project which was designed to study the migration of aphids and other insect pests into Illinois State. The project used the Illinois State Weather Survey's 'CHILL' high-power S-band Doppler radar and a tracking X-band radar, as well as a helicopter-borne aerial insect sampler (Hendrie et al. 1985).

China

In 1980, the Jilin Academy of Agricultural Sciences in Gongzhuling, Northern China, acquired a Japanese marine radar and re-configured it to make it more suitable for entomological observations (with advice from Schaefer and Rainey who visited Jilin as part of a Royal Society delegation in 1981). The Chinese radar entomology unit was headed by Prof. Chen Rui-lu who had played a leading role in the classic studies of the Oriental Armyworm (*Mythimna separata*) in the early 1960s. The unit concentrated its efforts mainly on studying the migration of the Meadow Moth, *Loxostege sticticalis* (Chen et al. 1992), and the Oriental Armyworm (Chen et al. 1989, 1995). The 1986, 1989 and 1992 *M. separata* studies in Jilin Province were carried out with the assistance of Drs Drake and Farrow from CSIRO. Chen Rui-lu died in 1995, and he was succeeded as head of radar entomology by Prof. Sun Yajie.

Further accounts of the early history of radar entomology are given in Riley (1980), Vaughn (1985), Rainey (1986) and Reynolds (1988). Information on the subject generally, including history, techniques and current activities, is now available on The Radar Entomology Web Site (TREWS) on the Internet (http://www.ph.adfa.edu.au/a-drake/trews/).

BASIC PRINCIPLES AND PRACTICALITIES

Radar (**RA**dio **D**etection **A**nd **R**anging) is based on the very simple concept that radio waves are always reflected to some degree from objects in their path, and that the reflected energy can be used (at least in principle) to infer both the presence and the location of the reflecting objects. Surprisingly, the 'objects' need not necessarily be large metal things, like ships or aircraft, but can be birds, raindrops, insects or even inhomogeneities in the refractive index of the atmosphere (see for example, Skolnik 1990). Radar is unsurpassed as a technique for detecting and tracking airborne objects, and in the case of biological targets, it offers the added great advantage that it *does not perturb their behaviour.* A number of different radar techniques have been applied in entomological studies (Reynolds & Riley 1997), but the pulse technique described below is by far the most commonly used.

Pulse radars

These radars emit short bursts or pulses of radio waves from an antenna designed to focus most of the emitted energy in a defined direction, i.e. into a 'beam'. If the focused pulse intercepts an object, a fraction of its energy is reflected or scattered, and some of this propagates back the way it came. A proportion is collected by the radar antenna, and if the resulting signal is strong enough, it is detected by the radar receiver and the presence of an 'echo' (and, therefore, of a target) is registered. The target's angular position is determined by the direction of the beam, and its range from the speed of radio wave propagation (3×10^5 km s^{-1}) multiplied by half the time elapsing between transmission of the illuminating pulse and reception of an echo. Although the concept is disarmingly simple, its practical realization in the early 1940s required major resources and exceptional scientific and technical ingenuity. The main difficulty was in generating pulses of sufficient power (typically tens of kilowatts) to allow targets to be detected at useful ranges, and to make the pulses short enough (on a scale of millionths of a second) to yield adequate range resolution. This problem was compounded by the need for the pulses to be of centimetric wavelengths, because short wavelengths meant that highly directional beams could be achieved without the use of large unwieldy antennas. However, huge investment ensured that rapid technical progress was maintained, and by the 1960s, 10-cm and 3-cm wavelength radars, with pulse powers of tens of kilowatts and pulse lengths of a fraction of a microsecond, were being routinely mass produced for the marine market. It turns out fortuitously that 3-cm is a particularly good wavelength for insect detection, because large and moderate-sized insects reflect this wavelength reasonably well, and it was the commercial availability of rugged, compact and inexpensive 3-cm marine radars that made radar entomology a viable proposition (Schaefer 1969, 1972, 1976; Riley 1974). Ruggedness and small size were essential in the context of NRI work, which usually entailed deployment of equipment in remote and inhospitable areas, and low cost was necessary too, given the traditional small size of entomological field budgets. Figure 1 shows two early NRI entomological radars being prepared for field work in Kenya.

Insect radar cross-sections

In order to predict how well an object will be detected on radar, it is necessary to know how effectively that object reflects radio waves back towards a transmitter. One of the first technical tasks in radar entomology was, therefore, to measure this property (the *radar back scattering cross-section* or RCS) for insect species of interest, and to determine how it varied with the aspect they presented to the radar (Riley 1973; Schaefer 1976). Water reflects radar waves almost as well as metal, and so insects, whose bodies contain a large percentage of water, turn out to be surprisingly good reflectors (for their size). An example of measurements made by the NRI Radar Unit is shown in Figure 2, from which it can be seen that the RCS (at 3.2-cm wavelength) of medium-sized moths is just over 1 cm^2 when seen from the side, but as little as 10^{-2} cm^2 from the end. Drawing together many such measurements (Riley 1985), we found that the radar cross-section of water droplets provided a rough but convenient guide to the all-aspects average for insects of the same mass, at least in the Rayleigh scattering region where body dimensions are less than a wavelength (Figure 3).

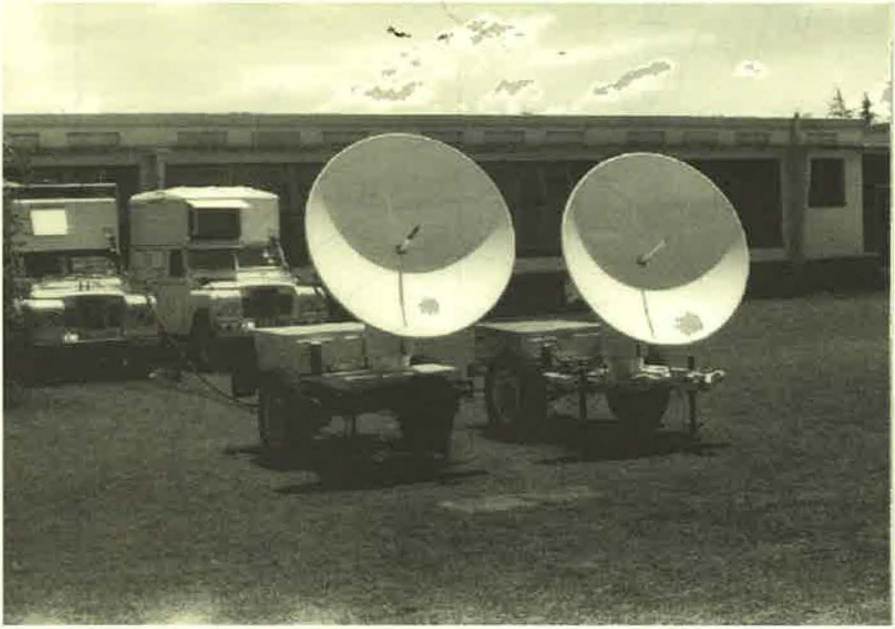
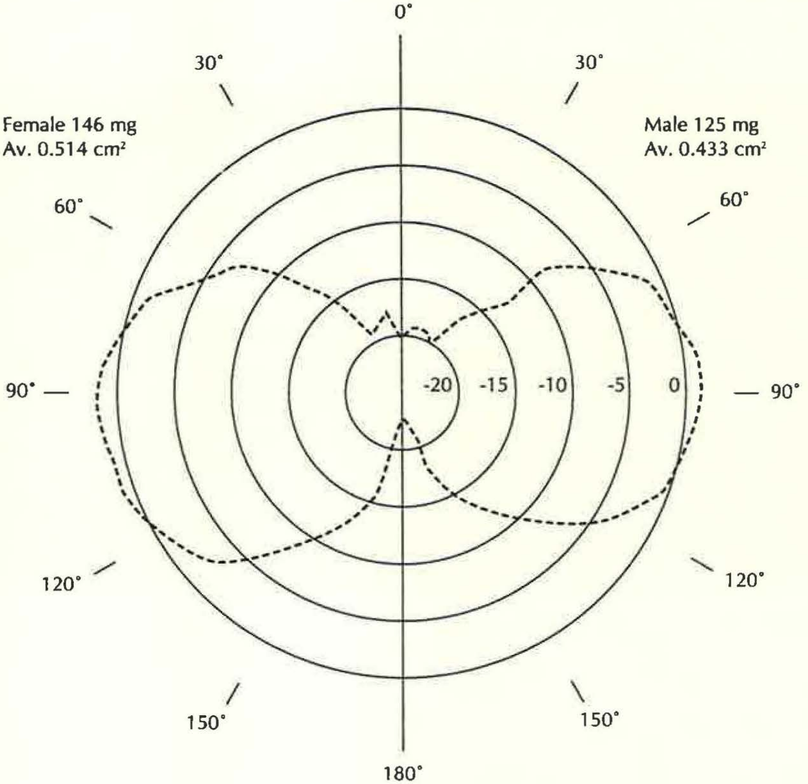


Figure 1 **Two scanning entomological radars built by the NRI Radar Unit, being prepared in Kenya for studies of the migration of the African Armyworm Moth.**

To put insect cross-sections in the context of more familiar radar targets, one notes that a medium-sized passenger aircraft might have a broadside cross-section of typically 30 m^2, i.e. 300,000 times larger than that of a medium-sized insect.

Modulation of radar signals by wing-beating action

It had been known from the earliest days of radar that the action of wing beating by birds modulated the radar signals which they returned (Eastwood 1967), and Schaefer found the same effect in flying insects (Schaefer 1969). The modulation depth for Desert Locusts turned out to be only a few percent (Riley 1973), and even less for moths (Schaefer 1976), but it was nevertheless important, because it allowed the wing-beat frequency of these airborne insects to be determined by radar, and wing-beat frequency was to prove a valuable aid to species identification (Schaefer 1969, 1976; Riley 1974). In a typical entomological radar scanning in azimuth at 20 rpm, the radar beam swings past a point target in only ~ 10^{-2} s, far too short an interval to determine wing-beat frequency. Thus the procedure to measure wing-beat modulation is to stop rotational scanning, and simply let insects fly through the stationary beam: this gives typical transit times of 1 to 3 s which are ample for frequency sampling. It is also necessary to use electronic 'sample and hold' circuitry to separate and capture the wing-beat modulated returns from the insects at different ranges from the radar, plus some form of spectrum analysis to extract the wing-beat frequency from the captured signals.



Notes: Nos on radial scale indicate dB relative to 1 cm²; electric vector and body axis horizontal. Radar wavelength 3.2 cm. Zero elevation angle.

Figure 2 How the radar reflectivity of a medium-sized moth varies with the azimuthal aspect it presents to the radar – 0° degrees indicates head-on aspect, and 180°, tail aspect. Reflectivity is measured as scattering cross-section, and the radial scale is logarithmic. The diagram shows that the reflectivity from the head or tail ends is less than 1% of that from the side.

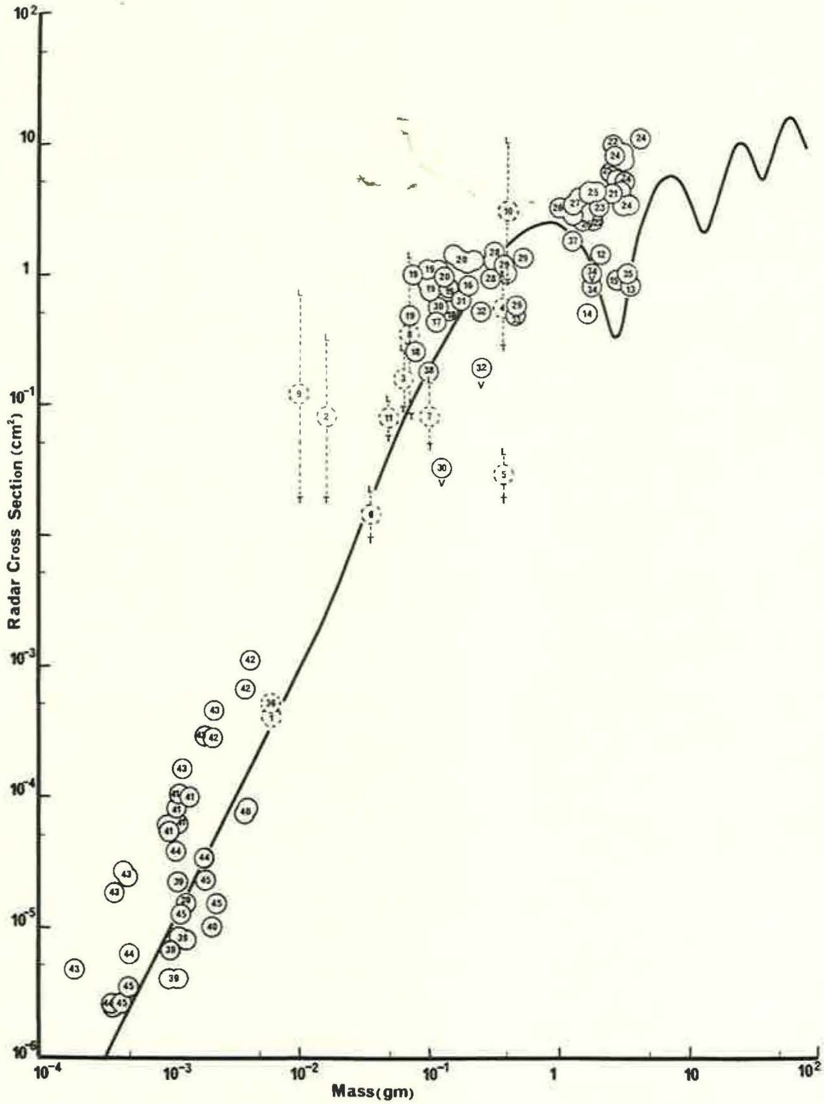


Figure 3 This graph (from Riley 1985) shows how the radar cross-section of a spherical water droplet varies with its mass for a 3.2-cm wavelength radar. The circles represent cross-section measurements made on insects of a wide variety of sizes, and it can be seen that the water droplet model provides a rough estimate of the insects' cross-sections over a mass range covering four orders of magnitude.

Radar target identification

Two levels of identification are required in radar entomology. Firstly, it is necessary to differentiate between echoes returned from insects and those from birds, bats and precipitation, and secondly, it is usually necessary to identify the species of insect detected. There are several clues in the radar signal to target identity: the spatial distribution of the returned echoes, their amplitude and temporal variation, and their response to changes in the polarization of the radar signals.

Insects and precipitation

In the case of low aerial densities of insects (< 10^{-4} m^{-3}) observed at close range (< 3 km) the spatially discrete returns detectable from individual large and medium-sized insects are clearly different from the semi-continuous echoes generated by precipitation and no confusion is likely. Returns from insect concentrations, on the other hand, may be similar to rain echoes and reliable discrimination between the two may be difficult, especially at long range, when supplementary evidence (e.g. rain at the ground) may not be available. If, however, the semi-continuous echo extends up to very high altitudes where it would be too cold for insect flight, it can be safely assumed that precipitation is the cause. It has been suggested that the use of circular polarization, which substantially reduces radar sensitivity to rain echoes should alleviate this difficulty (Schaefer 1976). This seems to be likely, but no supporting measurements have been reported to date.

Insects and birds

Although the radar cross-sections of birds (Edwards & Houghton 1959; Vaughn 1985), and presumably of bats, are in general much larger than those of insects (Riley 1973, 1985; Schaefer 1976), the difference between the average amplitudes of echoes received from the larger species of insects and those from the smallest birds may be very small (or even non-existent) and are certainly not large enough to produce obvious differences on the display of a scanning radar system. On the other hand, reported air speeds of birds (Meinhertzagen 1955) and of bats (Pye 1978) are higher than those of most insects (Johnson 1969), so that differences in flight trajectories might reasonably be expected to provide a reliable means of discriminating between small birds and insects (Riley 1974; Schaefer 1976). This assumption was called into question for a time, when Larkin reported that migrating birds can have air speeds well below the 5 to 6 ms^{-1} characteristic of the fastest insects (Larkin et al. 1979; Larkin & Thompson 1980), but he subsequently concluded that the slowly flying targets which he had detected were actually insects, and not birds (Larkin 1991). It is appropriate here to emphasize the fact that estimates of target flying speeds require simultaneous measurements of wind velocity at the same altitude as the target, and preferably close to it.

The modulation of radar echo amplitude caused by wing beating provides a valuable means of discrimination between birds and insects. Schaefer (1976) points out that although there is a considerable overlap of insect and bird wing-beat frequency in the range 8–30 Hz, only those birds which maintain continuous, rather than intermittent or irregular wing beats, are likely to be confused with insects. The upper wing-beat frequency for these birds is ~ 14 Hz (Schaefer 1976), so the range of overlap is effectively reduced to 8–14 Hz.

In summary, aerial targets found to have flying speeds below 6 to 7 ms^{-1}, and generating continuous wing-beat modulation above 14 Hz will almost certainly be insects. In our studies usually only a small percentage of the targets detected on the radar screen could be attributed to birds, but this may not be the case in other environments (e.g. Larkin 1991).

Resolving insect species

Some degree of 'automatic' discrimination will always occur between species differing substantially in size, larger insects being more readily detected than smaller ones (Riley 1979). In fact, radar thresholds of detection may be adjusted to ensure that small insects are not (individually) detected at all at a selected range of interest. Apart from crude categorizations of this sort, conventional scanning entomological radars make little use of the average amplitude of insect radar echoes, because echo size depends on the insects' aspects (Riley 1973) and on their position in the radar beam, both of which are usually unknown. However, NRI has recently developed a novel type of vertical-looking entomological radar, equipped with rotating linear polarization and a small degree of beam nutation (Riley, Smith & Gregory 1993; Smith, Riley & Gregory 1993), which is able to make comprehensive estimates of the underside back-scattering properties of overflying insects (see below), and this promises to improve substantially discrimination between insects of different size and shape.

In some situations, radar measurements of wing-beat frequency provides an effective means of identifying airborne insects, at least for large species such as Acridoidea (grasshoppers). Species with longer wings tend in general to have lower wing-beat frequencies than those with shorter wings (Greenwalt 1962), and in the case of some Acridoidea this tendency has been found to take the form of a well-defined inverse power relation between wing length and frequency (Schaefer 1976). Spectral analysis of the radar returns from individual acridoids thus allows one to make estimates of the distribution of the wing lengths in the airborne population, and hence, in the special case of a population containing only a few differently sized species, to deduce the species present and even to distinguish the sexes (Schaefer 1976; Riley & Reynolds 1979; Reynolds & Riley 1988). In other insect orders less information may be available about relations between wing length and frequency (but note Oertli 1991), and in any case, it seems probable that the abundance of migrant species of very similar sizes, for example, in noctuid moths, will always make identification from wing-beat frequencies tentative at best.

Thus the wing-beat frequency procedure is normally useful in only the most simple of entomological environments and to date, successful radar entomology studies have been largely confined to areas in which the 'wanted' species were numerically dominant. Even then, ancillary information on insect identity derived from ground observations (e.g. emigration from localized outbreak areas (Riley, Reynolds & Farmery 1983) and/or trapping with nets supported by aircraft (Schaefer 1976; Greenbank, Schaefer & Rainey 1980)) proved essential for confident identification of the species studied. Trapping in nets attached to kites and tethered balloons has also been used in radar studies of larger-sized moths and grasshoppers, but their aerial density is only occasionally high enough to give adequate catch rates (Drake & Farrow 1983, 1985; Riley et al. 1995).

Radar returns from small insect species seem not to contain detectable wing-beat modulation (Riley, Reynolds & Farrow 1987) and in any case, the multitude of species of small insects often found aloft would militate against the use of wing-beat frequencies for identification purposes. However, aerial trapping by nets supported by helium-filled, aerodynamically shaped balloons (kytoons) has proved to be an effective and inexpensive means of identification for smaller species (Figure 4). Trapping works particularly well in this instance, because radar information about the altitudinal distribution of the insects allows the net to be positioned at altitudes where the insect density is at a maximum, and catching rates are often high (Riley, Reynolds & Farrow 1987; Riley et al. 1990, 1991).

Figure 4 **A small (11 m^3) helium-filled blimp being prepared for aerial netting in West Bengal, India. These blimps are shaped to generate aerodynamic lift, and so stay aloft even when flown in winds of up to 50 km h^{-1}.**

ENTOMOLOGICAL RADARS

When Schaefer began looking for suitable equipment from which to derive an entomological radar in the 1960s, marine transceivers were the natural choice. They operated at 3.2-cm wavelength (X-band), had peak transmitted powers of 20 to 25 kW and pulse lengths down to 0.1 μs (corresponding to a spatial resolution of 15 m), and, when fitted with an appropriate antenna, had the capability of detecting *individual* airborne insects of medium to large size at ranges of up to 1 to 2 km. Although this range is very short by normal radar standards, it vastly exceeds that of any other means of observing individual insects, and is adequate for studies of high altitude flight. Marine equipment was also compact, relatively rugged, and spares were readily available, and most importantly, it was orders of magnitude less costly than any other type of radar.

Azimuthally scanning radars

What was *not* suited to entomological observations was the marine radar antenna. This produced a 'fan' beam typically 1 or 2° wide in bearing and 30° in elevation, which rotated in azimuth. The wide vertical beam was used to ensure coverage for surface targets in spite of pitching and rolling by the ship carrying the radar, but what was needed in insect flight studies, was a means of selectively viewing different altitudes. The solution adopted by Schaefer in his original studies (Roffey 1969), and widely copied in entomological radars since then (Riley 1974; Wolf 1979; Drake 1981a), was to use rotating marine antenna mounts, but with the original antenna replaced by a tiltable, parabolic dish and feed. This produced a narrow conical beam, adjustable in elevation, and scanning in azimuth at ~ 20 rpm. Provided airborne insects were separated by distances of 20 m or more, those intercepted by the beam registered as individual 'dots' (Figure 5) on a plan position indicator (PPI) radar display (Eastwood 1967). The dot position gave insect range and azimuth, and altitude could be calculated by multiplying range by the sine of the antenna elevation angle. Time-lapse records of the PPI screen were made on 16 mm ciné film, one frame being exposed for every revolution of the antenna. Sequential interception of an individual insect by the rotating beam produces a string of dots, and these represent position fixes on the insect, made once every 3 s, which provide a measure of its speed and direction of displacement. At low angles of elevation (< 15°), speed and direction can be obtained by direct scaling from the screen, but at higher angles, it is necessary to correct for the geometric distortion produced by plotting signals from the elevated beam on to a plane (Riley 1979).

The vertical profile of wind velocity can be conveniently measured by releasing a helium-filled toy balloon carrying a small piece of aluminium foil. As the balloon drifts away from the radar, ascending slowly, its subsequent trajectory on the radar screen (Figure 5) describes the horizontal velocity of the wind. Subtraction of this from the displacement vectors of individual insects flying at the same height as the balloon then gives the insects' *air speed* and *heading*.

The area density of dots on the radar screen can be interpreted in terms of the volume density of flying insects, but this is not a trivial matter because it requires a knowledge of the RCS of the insects, and of the characteristics and performance of the radar (Riley 1979). Procedures have also been developed to allow density estimation when airborne insects become so numerous that their echoes merge and can no longer be individually counted: this too, requires information on insect RCS and on radar performance (Drake 1981b).

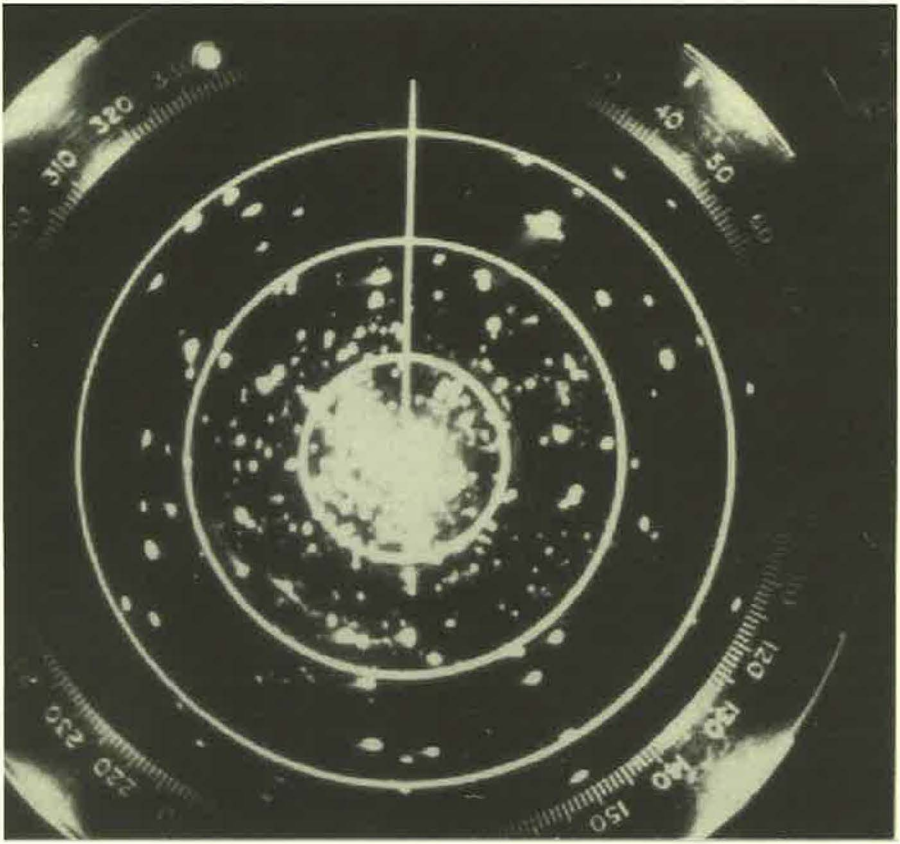


Figure 5 **A conventional entomological radar screen. The distance from the centre to the edge of the radar screen represents 1.4 km, and the vertical line shows the direction of north. Insects appear as individual dots because their aerial density is relatively low (4–5 per $10^7 m^3$). The larger 'blob' in the north-east quadrant is caused by a freely drifting balloon carrying a small piece of aluminium foil, and its position recorded every 3 s on sequential frames of the film record describes the wind velocity at the height of the balloon.**

The dramatic effect of RCS on target visibility was graphically illustrated during the first radar entomology observations, when it was noticed that the density of dots in diametrically opposed quadrants on the screen was often higher than in the intervening quadrants. The explanation for this effect was that, unexpectedly, high-flying nocturnally migrating insects often fly with a degree of common orientation. Because they reflect radio waves most effectively when seen side on, they are more visible to radar from these aspects, and so appeared to be more numerous in the screen quadrants at right angles to their mean direction of orientation (Schaefer 1969; Riley 1975). It was this fortuitous sensitivity of entomological radar to non-random orientation that lead to the discovery of collective orientation in insects migrating at altitude.

Range-height indicator radars

The operation of azimuthally scanning entomological radars at different angles of beam elevation provides information from which the vertical profiles of insect density and climb rate can be determined. However, the process of data extraction is rather tedious, and the alternative method of scanning the radar antenna about a *horizontal* axis provides a much more immediate and graphic picture of motion and of density profiles in the vertical plane. We built a 'nodding' antenna which formed a beam which was fan-shaped in the horizontal plane, and which oscillated up and down (Figure 6) to generate a conventional range height indicator (RHI) scan. This system produced dramatic records of ascending layers of insects in Mali (Figure 7). We later produced a more unconventional 'toppling' antenna system which provided RHI coverage over 180° in the vertical plane, and used this to record the upward motion of African Armyworm Moths (*Spodoptera exempta*) leaving emergence sites in Kenya (Riley, Reynolds & Farmery 1983). Other examples of insect layers on RHI radar displays are shown in Vaughn (1985).

Millimetric radar

In the 3-cm radar band, insects lie predominantly in the Raleigh scattering region where their RCS is approximately proportional to the square of their mass (Riley 1985;Vaughn 1985). Thus the smaller species like planthoppers and aphids present very tiny RCSs, typically 10^{-4} to 10^{-6} cm^2 (Riley 1985), and cannot be individually detected at useful ranges with standard entomological radars. However, in the Rayleigh region, RCS is also inversely proportional to the fourth power of radar wavelength, so using a shorter wavelength offers the prospect of greatly increasing the RCS of smaller insects, and hence, of making them viable radar targets. In order to exploit this effect, NRI designed and built an 8.8-mm wavelength scanning radar (Riley 1989a, 1992), and as a consequence was able to successfully observe the migration of the Brown Planthopper (*Nilaparvata lugens*) and other hemipteran pests of rice (Riley, Reynolds & Farrow 1987; Riley et al. 1990, 1991, 1994). The maximum range for detection of individual *N. lugens* was in excess of 1 km. This high-frequency entomological radar is still the only one of its type, and gave NRI the unique capacity to observe individual flying insects of much smaller body size (*ca* 2 mg in the case of *N. lugens*) than the grasshoppers and noctuid moths which are the usual objects of study with 3-cm radars.

Vertical-looking radar

Scanning entomological radars proved to be powerful tools in the investigation of insect migratory flight and they were widely used (Riley 1989b). The radars suffered, however, from two important limitations: their capacity to identify the species which they detected was limited, and their operation and data analysis were so labour intensive that they could not be sensibly used for long-term monitoring tasks.

Figure 6 A range height indicator (RHI) radar built by the NRI Radar Unit, and deployed in Mali in November 1974. This radar oscillates or 'nods' once every 3 s over a range of 60° in the vertical.

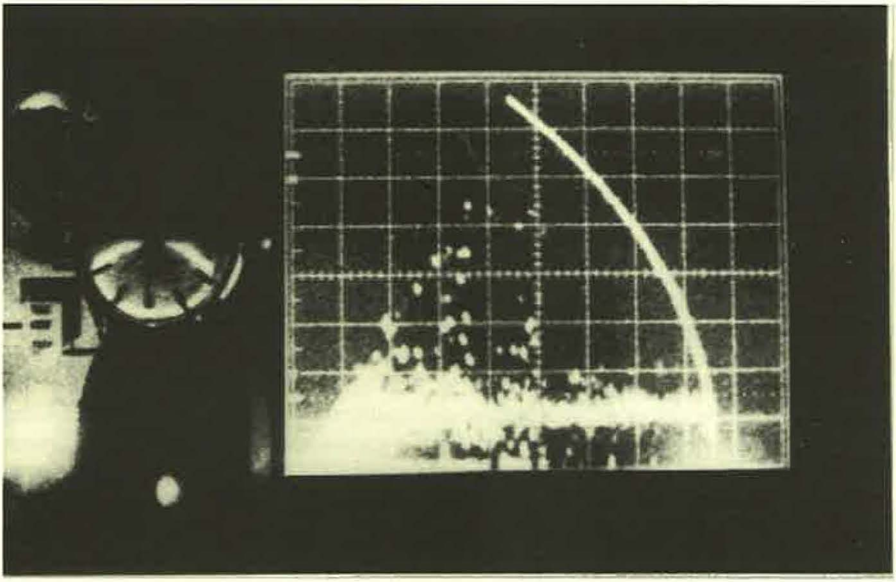


Figure 7 The display of the RHI radar illustrated in Figure 6. The squares represent intervals of 100 m, and the display gives a graphic picture of an insect layer at an altitude of about 120 m.

Polarization rotation

In an attempt to alleviate the first of these constraints, NRI developed a radar which projected a conical beam vertically upwards, and in which the transmissions were linearly polarized, with the plane of polarization rotating at a few rpm (Riley & Reynolds 1979). The idea behind this vertical-looking radar (VLR) was that we expected overflying insects to scatter radar waves like prolate dielectric spheres, so that echoes from species with long, thin bodies would show greater response to polarization rotation than those with short, fat ones. It was hoped that this difference could be used to supplement wing-beat frequency as a means of species identification. Rotating polarization also promised to provide a means of accurately measuring the *alignment* of individual insects, because maxima in the signals scattered back to the radar were expected to occur when the electric vector in the radar waves became parallel to the insect body axis. The transit time of insects moving through the vertical beam would give an indication of their horizontal displacement speed (Atlas, Harris & Richter 1971).

The radar was deployed in Mali in 1975 and 1978, and generated signals of the type expected. Analysis of these signals yielded novel measurements of insect heading distributions (Riley & Reynolds 1979, 1983, 1986), but the extraction of body-shape information was frustrated by inadequate dynamic range in our receiver. Later laboratory measurements of the underside RCS of insects (Riley 1985; Aldous 1990) made it clear that there was a more fundamental problem with the body-shape technique, because polarization dependence was found to be a function of overall body size as well as shape, at least in the case of larger insects. The VLR signals did however yield high-quality wing-beat data, and the main value of the system followed from this, and from its ability to resolve fine scale details of heading distributions (Figure 8). The idea of VLR with rotating polarization was later taken up in the USA, and Beerwinkle et al. (1995) showed how an automated VLR could be used to make long-term, qualitative assessments of the aerial abundance of migrating insects.

Beam nutation

Some years after rotating polarization VLR was first used, Schaefer introduced an important modification to the VLR concept by suggesting that the nutating principle used in tracking radars might be exploited to gain information about the size of targets in the radar beam. Graham Bent later developed Schaefer's idea, and showed that, in principle, nutation should allow measurement of an overflying insect's speed and direction, as well as of its body alignment and two parameters related to its RCS (Bent 1984). The key to using this technique was being able to devise a method of decoding the complex modulations produced by the combination of polarization rotation, beam nutation and target movement. Although the method developed by Bent worked with simulated data, it proved incapable of extracting useful data from real signals, and his prototype radar consequently never reached operational status. Because of the potential value of this form of VLR, NRI took on the formidable problem of signal decoding, and eventually succeeded in producing an analysis algorithm which yielded the target alignment, speed and direction, and *three* RCS parameters related to insect body size and shape (Smith, Riley & Gregory 1993; Riley & Reynolds 1993; Riley 1993). Prototypes of the NRI nutating VLR were tested in India in 1985 and 1986, and in Australia in 1990. The first operational trials were in Mauritania in 1993 and 1994, and we subsequently ran the radar throughout the summer of 1995 in the UK, which yielded the first ever measurements of insect movement at high altitude in England.

This second generation VLR not only promises to improve the capacity of entomological radar to identify the targets which it detects, but because control of the system, *and* the task of data analysis are both performed automatically by personal computer (Smith & Riley 1996), it makes long-term, quantitative monitoring of insect migration a practicable and cost-effective option for the first time.

Harmonic radar

Conventional radar cannot be used to track insects at low altitude, because the small radar echoes from insects are usually swamped by the much larger reflections (*clutter*) from ground features and vegetation. This is a serious limitation because practically all non-migratory flights (e.g. those concerned with feeding and reproduction) and some migration flights, take place near the ground.

The problem of clutter can be overcome if the target to be tracked carries a *transponder*, a device which picks up incoming radar signals and replies with a transmission on a different frequency; the radar receiver is selectively tuned to this new frequency, and clutter signals are then ignored. Conventional active transponders of the type carried in aircraft are far too massive for use on insects, so we began to develop the idea of making a radar system which would work with *passive harmonic* transponders (Vogler, Maguire & Steinhauer 1967). In a passive transponder, energy from incoming signals is captured and part of it is re-radiated at

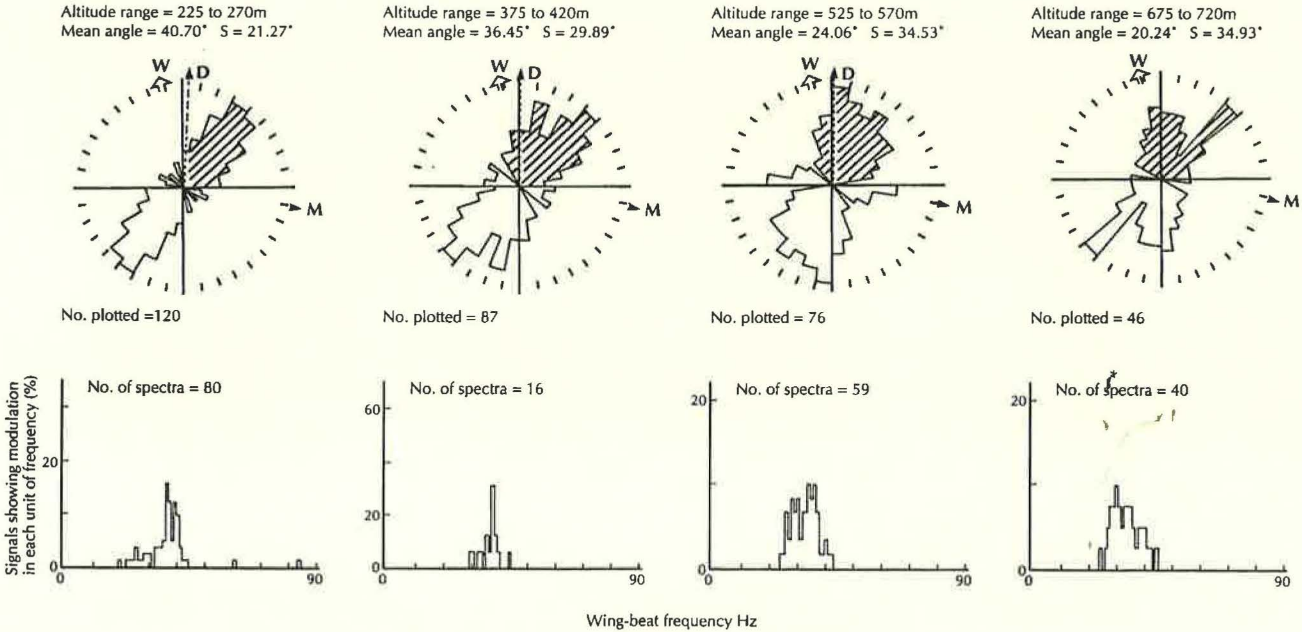


Figure 8 This diagram shows how vertical-looking radar can resolve fine details of the orientation behaviour of overflying insect populations. The circular histograms show that insects flying at 225–270 m above the ground were aligned around 41°, while those at 675–720 m were headed northwards. At intermediate altitudes, alignments overlap and form bimodal distributions which are reflected in the corresponding distributions of wing-beat frequency. The data shows that different species airborne at the same time, in the same aerial environment, sometimes adopt very different mean headings.

twice the original frequency – no battery is needed, and so *extreme* miniaturization is feasible. This concept had already been examined in the late 1970s at the University of North Dakota, with the intention of producing a radar to track flies of the screw-worm, *Cochliomyia hominivorax*, but the initiative failed to produce a working radar. The next application of the harmonic principle for entomological studies was by Mascanzoni & Wallin (1986). These authors used commercially available, hand-held harmonic 'radars' (actually harmonic *direction finders*) which had been developed to locate skiers buried by snow, but they made their own transponders from lengths of wire and microwave diodes. These 'tags' were glued to the elytra of several species of ground-dwelling, nocturnally active carabid beetles, and it was found that the beetles could be located from a range of up to 10 to 12 m. Because the beetles were relatively large (11 to 23 mm in body length), they were apparently unimpeded by the 2.5–5 cm wire aerial, which trailed behind them. The wavelength used by the transmitter/receiver was about 30 cm, and this gave the equipment the ability to penetrate vegetation and soil to some degree: individual beetles could be located down to 20–30 cm below the surface.

The direction-finding equipment was subsequently used in a number of successful studies of pedestrian movements by carabids (e.g.Wallin & Ekbom 1988; Wallin 1991; Kennedy 1994), and for locating settled butterflies (Roland et al. 1996), but it is intrinsically unsuited to tracking the fast translation of insects *in flight*, because its short range of detection (< 50 m) means that the operator must be able to keep up with the tagged insect by walking or running after it. Our efforts were thus focused on achieving a detection range adequate for flight studies (~ 1 km), combined with the instantaneous position-fixing capability characteristic of a true radar. This was not straightforward, but largely as a result of the sustained encouragement of Dr Glyn Vale of the EEC Regional Tsetse and Trypanosomiasis Control Programme (RTTCP) in Zimbabwe, and with support from ODA's Speculative Research Programme, we persisted and eventually succeeded in fielding a working prototype, the first of its kind in the world (Figure 9). This radar, which used 3-mg transponders, immediately proved successful in tracking bumble bees and honey bees (Riley et al. 1996, and in press; Carreck 1996; Osborne et al. in press), and noctuid moths (Riley et al. 1998). Much international interest followed, and the technique seems certain to find wide application in studies of insect flight at low altitude.

THE CONTRIBUTION OF RADAR TO ENTOMOLOGY

Since the emergence of radar entomology as a distinct discipline, there have been close to 250 publications in the field, with NRI making the largest single contribution. By vividly revealing the magnitude and extent of high altitude flight, these papers have gradually produced something of a paradigm shift in thinking about long-range windborne migration, and about the weather systems that influence it. In many species, long-range migrations can no longer be seen as occasional accidental displacements, brought about by freak weather, but rather as a result of specialized and highly adaptive flight behaviour, forming an integral part of the species' life-history strategy (see J.S. Kennedy's classic (1985) paper; also Dingle 1996).

Flight behaviour of migrant insect pests

Prior to the advent of radar in entomology, evidence for the windborne migration of many pest species was fragmentary and circumstantial, and left much room for alternative interpretations and disputes about its importance. The unique ability of radar to observe undisturbed high-altitude movement *while it is in progress*, has allowed unequivocal and graphic demonstrations of the migratory performance of whole populations of a range of important pests (e.g. Sahelian grasshoppers, African Armyworm, Brown Planthopper, Rice Leaf-roller (Reynolds & Riley 1997)), and allowed us to quantify the migrations in terms of the timing of migration, aerial densities, altitudinal distributions, displacement speed and direction, and the migratory flux of insects passing overhead.

Figure 9 **The NRI harmonic radar used to record the low-altitude flight trajectories of bumble bees and honey bees.**

Take-off and ascent

One of the first discoveries of radar studies was the massive scale of emigration by nocturnal migrants at dusk, stimulated by the decreasing illumination. In the case of solitarious locusts, Sahelian grasshoppers and African Armyworm Moths, this take-off occurs when illumination has fallen below the level at which they can be seen by eye, and there is scant indication that it is taking place at all. By contrast, with a typical entomological radar scanning 10 million cubic metres every 3 s, take-off is seen as a spectacular transition from a nearly blank screen to one filled with targets, in the space of about 15 min. Rice planthoppers and leafhoppers start to take off *en masse* before it gets dark, but because of their small size there is again little visible evidence of the scale of the emigration. The radar picture is startlingly different, showing dense concentrations rising steadily in altitude. Rates of climb can be derived from the rate at which the ceiling of the concentrations rise, or alternatively from RHI measurements of individual trajectories, and turns out to be ~ 0.5 ms^{-1} for locusts and grasshoppers, ~0.4 ms^{-1} for medium-sized moths, and 0.2 ms^{-1} for planthoppers.

In some species, e.g. the African Armyworm Moth and some rice planthoppers, there is sometimes another period of mass take-off at dawn, but the resulting flights are usually short compared to those following the dusk take-off.

Cruising altitude and duration of flight

Climbing at about 100 m every 3 min, grasshoppers and solitarous locusts arrive at their cruising altitudes of typically 250 to 900 m in the first 10 to 30 min of flight, and then level off. Radar revealed that in their subsequent flight, they sometimes separate out into distinct layers, separated by 100 m or less. The cues which are used by the insects to select their cruise altitudes remain unknown, but air temperature probably plays a part, because layers sometimes occur near the warmest level in nocturnal temperature inversions. Temperature certainly determines the maximum altitude of the Brown Planthopper flight – a sharp and distinct ceiling can be seen at altitudes corresponding to the lowest temperature at which they can sustain flight.

Because radar range is limited to about 2 km for individual insects, direct observations of *duration* of flight are not possible, but indirect evidence derived from the rate of decline of aerial density with time (after the dusk take-off period) suggests that migration continued for 3 to 7 h in Sahelian grasshoppers, and 6 to 12 h in Brown Planthoppers in China.

Air speed and orientation

As mentioned above, scanning radar data can be used to calculate accurate values for the *air speeds* and *headings* of individual high-flying insects, information that could not be obtained in any other way. This method has shown that the cruising speeds of locusts and grasshoppers are 4–5 ms^{-1}, moths 3–4 ms^{-1} and planthoppers, ~ 1 ms^{-1}, and these results can be used to provide information on the energetic cost of cruising flight (Riley, Downham & Cooter 1997). Irrespective of their capacity to measure individual headings, scanning radars are fortuitously sensitive to the presence of non-random orientation in overflying populations at large (an effect which follows from the azimuthally non-isotropic radar cross-sections of insects). It was this sensitivity which led to the surprising discovery that many insects, migrating at high altitude at night, often adopt a degree of common orientation (Riley 1975;

Schaefer 1976). Vertical-looking radars have shown that different species appear to adopt different mean headings (Riley & Reynolds 1979, 1986), but the function of this phenomenon and the sensory mechanisms by which it is achieved, remain unknown (Riley & Reynolds 1986; Riley 1989c).

Ground speed and range

A very striking result to emerge from radar studies is the speed at which aerial migration often takes place, especially in some areas of the tropics. On calm evenings when there is no wind at ground level, insects a few hundred metres overhead may be travelling at 50–60 km h^{-1}, having climbed into the fast moving air stream known as the low level jet (Riley & Reynolds 1979; Drake 1985). The combination of high ground speed with flight endurances of up to 12 h gives impressive migration ranges of hundreds of kilometres *per night*, even for small insects like planthoppers with very low air speeds (Riley et al. 1991). Migration of this sort is frequently described as *windborne*, but it is important to note that this does *not* mean that migrants are *kept aloft* by the wind. In the absence of lift from thermals (i.e. for all nocturnal flight), an insect as small as an aphid would take only 20 min to sink to earth from 1000 m if it stopped actively flying (Thomas, Ludlow & Kennedy, 1977), and larger ones would presumably descend even faster.

Atmospheric effects

The wind is obviously the major determinant of the speed and direction of high-altitude insect migration, but the degree of *cohesion* of the migrants *en route* clearly plays an important part in their post-migration population dynamics.

Dispersal

Unlike locusts swarming in the daytime, nocturnal migrants cannot see each other and show no signs of interacting *en route* in a way which would prevent them from becoming separated. Although they minimize initial dispersal by setting off in a synchronized manner, small variations in timing of take-off, rates of climb, cruising altitudes, headings and air speeds all accumulate, and add to the dispersal caused by atmospheric turbulence. This is especially the case if there is a strong vertical gradient in the wind speed, and both radar (Riley, Reynolds & Farmery 1983) and numerical simulations show that within the space of less than an hour an airborne population can spread into a zone from ten to over a hundred times the size of its source area.

Concentration

If dispersal during migratory flight continued unabated, many migrant populations of pest species would become so dilute that they would not be noticed. Unfortunately, it sometimes happens that such migrants enter a zone of *horizontal wind convergence*, where, for example, the outflow of cold air from a storm undercuts and flows against a warmer prevailing wind. Radar has shown graphically that this type of strong convergence can rapidly gather initially dispersed airborne insects into dense, linear concentrations, a few hundred metres wide and many kilometres long (Schaefer 1976; Riley, Reynolds & Farmery 1981; Pedgley et al. 1982, Drake 1982; Riley & Reynolds 1990). If these insect concentrations are deposited in vulnerable agricultural areas they have the potential to give rise to serious pest outbreaks. The radar observations of the concentration of African Armyworm Moths by rainstorm outflows, together with other evidence, has eventually led to the routine use of satellite imagery in East Africa to locate convective rainstorms in order to forecast the likely position of new armyworm infestations (Reynolds & Riley 1997; Tucker 1997).

In some cases, convergent wind flows are produced in circulations set up by topographic features, and in these cases, local deposition of insect concentrations can become a regular event (Riley, Reynolds & Farmery 1981; Pedgley et al. 1982).

SUMMING UP

Radar was introduced to entomologists as the method, *par excellence*, of studying in detail the high altitude migratory flight of insect pests. It fulfilled this task so well that it eventually became a victim of its own success – by 1992 research into the flight behaviour of many of the more important migrant pests had been completed, and the future of radar entomology looked uncertain. There remained, however, two areas where there was clear potential for the technique to make major contributions to entomology. The first was in providing a means of inexpensive, *long-term, routine* monitoring of insect migration at altitude, both for pest management purposes and for basic research. The second was in extending radar's unique flight trajectory measurement capability to insects engaged *in low-altitude, non-migratory* flight.

These opportunities presented formidable technical challenges, but my group was fortunate in being uniquely equipped to tackle them, both by virtue of our accumulated expertise in designing and building entomological radars, and because of our access to specialist facilities at the Radar Establishment at Malvern. As a result we were able to successfully develop VLR as a monitoring tool, and harmonic radar for low altitude tracking. Both these achievements were world firsts, and have opened up whole new areas of application. We have just completed a technical design study, funded by the Government of China, for a VLR to monitor the movement of rice pests – an initiative with the long-term objective of deploying a network of such radars as part of the Chinese national management programme for rice pests. In May of this year we will have installed a VLR at IACR-Rothamsted, as part of a BBSRC-funded project to monitor migratory movement of insects over south-central England. The harmonic radar has attracted much international attention and we are currently working with prestigious research groups from the USA, Germany, the UK and Sweden. These collaborative field studies are investigating the neurobiology of learning processes in honey bees; cognitive mapping by honey bees; foraging behaviour and wind compensation by bumble bees; and the disruption of moth flight by artificial pheromones.

All these studies are breaking new ground, and it seems to me that radar has as much to offer entomology now, as it did when as a young man, I looked at our radar screen in Africa, for the first time, and saw, in the famous words of Howard Carter, "*Wonderful things*".

Acknowledgements

I have had the unusual privilege of working closely with two very able colleagues for over a quarter of a century: firstly Alan Smith, the Unit Engineer, who personally designed, built and operated all our radars, and who did so so skilfully that we never had to curtail or abandon an expedition as a result of technical failure, however arduous the conditions. Secondly Don Reynolds, the Unit Entomologist, whose enthusiasm, determination and high academic standards kept us focused on questions of real entomological significance, and ensured that all our results found a place in the scientific literature. Without their dedication and unfailing support, and in more recent years, that of our tireless Scientific Assistant Mrs Ann Edwards, I would not be making this presentation now. Thanks are also due to many other colleagues in NRI who over the years have made major contributions to our work, especially Drs Mike Farmery, Nick Jago, David Pedgley, Mark Ritchie, Derek Rose and Mike Tucker.

I am particularly appreciative of the irrepressible enthusiasm for harmonic radar of Dr Glyn Vale of RTTCP, Zimbabwe, without which we would probably never have had the nerve to attempt its development. Dr Phil Symmons and Professor Reg Chapman of COPR championed the Radar Unit in its early days, when the utility of radar in entomology had yet to be demonstrated, and of course, acknowledgement is due to Dr Reg Rainey whose early advocacy of radar started it all off, and to Professor Glen Schaefer, who showed that it could be done.

Finally, I should like to dedicate this lecture to my wife, Maureen. Her stoic endurance of my long absences overseas, and her unfailing encouragement over 27 years, have made it all possible.

References

Aldous, A. C. (1990) *Insect radar scattering cross-sections*. Ph.D. Thesis. Cranfield, UK: Cranfield Institute of Technology.

Atlas, D., Harris, F. I. & Richter, J. H. (1971) The measurement of point target speeds with incoherent non-tracking radar in atmospheric waves. In: *Proceedings of the 14th Radar Meteorology Conference, Tucson, Arizona, 17-20 November 1970*, 73–8. Boston: American Meteorological Society.

Beerwinkle, K. R., Lopez, J. D., Schleider, P. G. & Lingren, P. D. (1995) Annual patterns of aerial insect densities at altitudes from 500 to 2400 meters in east central Texas indicated by continuously-operating vertically-oriented radar. *Southwestern Entomologist*, supplement **18**, 63–79.

Beerwinkle, K. R., Witz, J. A. & Schleider, P. G. (1993) An automated, vertical-looking, X-band radar system for continuously monitoring aerial insect activity. *Transactions of the A.S.A.E.* **36**, 965–70.

Bent, G. A. (1984) Developments in detection of airborne aphids with radar. In: *1984 British Crop Protection Conference–Pests and Diseases*, 665–74. Croydon: British Crop Protection Council.

Carreck, N. L. (1996) The use of harmonic radar to track flying bees. *Bee Craft* **78** (4), 105–9.

Chen, R.-L., Bao, X.-Z., Drake, V. A., Farrow, R. A., Wang, S.-Y., Sun, Y.-J. & Zhai, B.-P. (1989) Radar observations of the spring migration into northeastern China of the oriental armyworm moth, *Mythimna separata* and other insects. *Ecological Entomology* **14**, 149–62.

Chen, R.-L., Bao, X.-Z., Wang, S.-Y., Sun, Y.-J., Li, L.-Q. & Lu, J.-R. (1992) An observation on the migration of meadow moth by radar. *Acta Phytophylacica Sinica* **19**, 171–4. (In Chinese, English summary.)

Chen, R.-L., Sun,Y.-J., Wang, S.-Y., Zhai, B.-P. & Bao, X.-Y. (1995) Migration of the Oriental Armyworm *Mythimna separata* in East Asia in relation to weather and climate. I.

Northeastern China. In: *Insect migration: tracking resources through space and time*, V. A. Drake & A. G. Gatehouse, (eds), 93–104. Cambridge: Cambridge University Press.

Crawford, A. B. (1949) Radar reflections in the lower atmosphere. *Proceedings of Institute of Radio Engineers* **37**, 404–5.

Dickison, R. B. B., Haggis, M. J., Rainey, R. C. & Burns, L. M. D. (1986) Spruce budworm moth flight and storms: further studies using aircraft and radar. *Journal of Climate and Applied Meteorology* **25**, 1600–8.

Dingle, H. (1996) *Migration: the biology of life on the move*. New York: Oxford University Press.

Drake, V. A. (1981a) *Quantitative observation and analysis procedures for a manually operated entomological radar. Division of Entomology Technical Paper* No. 19. Melbourne: CSIRO.

Drake, V. A. (1981b) Target density estimation in radar biology. *Journal of Theoretical Biology* **90**, 545–71.

Drake, V. A. (1982) Insects in the sea-breeze front at Canberra: a radar study. *Weather* **37**, 134–43.

Drake, V. A. (1985) Radar observations of moths migrating in a nocturnal low-level jet. *Ecological Entomology* **10**, 259–65.

Drake, V. A. (1993) Insect-monitoring radar: a new source of information for migration research and operational pest forecasting. In: *Pest control and sustainable agriculture*, S. A. Corey, D. J. Dall & W. M. Milne, (eds), 452–5. Melbourne: CSIRO.

Drake, V. A. & Farrow, R. A. (1983) The nocturnal migration of the Australian plague locust *Chortoicetes terminifera* (Walker) (Orthoptera: Acrididae): quantitative radar observations of a series of northward flights. *Bulletin of Entomological Research* **73**, 567–85.

Drake, V. A. & Farrow, R. A. (1985) A radar and aerial-trapping study of an early spring migration of moths (Lepidoptera) in inland New South Wales. *Australian Journal of Ecology* **10**, 223–35.

Drake, V. A. & Farrow, R. A. (1988) The influence of atmospheric structure and motions on insect migration. *Annual Review of Entomology* **33**, 183–210.

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*, 444–7. Boston: American Meteorological Society.

Eastwood, E. (1967) *Radar ornithology*. London: Methuen.

Edwards, J. & Houghton, E. W. (1959) Radar echoing area polar diagrams of birds. *Nature* **184**, 1059.

Freeman, J. A. (1945) Studies in the distribution of insects by aerial currents. The insect population of the air from ground level to 300 feet. *Journal of Animal Ecology* **14**, 128–54.

Glover, K. M., Hardy, K. R., Konrad, T. G., Sullivan, W. N. and Michaels, A. S. (1966) Radar observations of insects in free flight. *Science* **154**, 967–72.

Greenbank, D. O., Schaefer, G. W. & Rainey, R. C. (1980) Spruce budworm (Lepidoptera: Tortricidae) moth flight and dispersal: new understanding from canopy observations, radar, and aircraft. *Memoirs of the Entomological Society of Canada* **110**, 1–49.

Greenwalt, C. H. (1962) Dimensional relationships for flying animals. *Smithsonian Miscellaneous Collections*, **144**, No. 2. Washington: Smithsonian Institution.

Hardy, A. C. & Cheng, L. (1986) Studies in the distribution of insects by aerial currents. III. Insect drift over the sea. *Ecological Entomology* **11**, 283–90.

Hardy, A. C. & Milne, P. S. (1937) Insect drift over the north sea, 1936. *Nature* **139**, 510–1.

Hardy, A. C. & Milne, P. S. (1938) Studies in the distribution of insects by aerial currents. Experiments in aerial tow-netting from kites. *Journal of Animal Ecology* **7**, 199–229.

Hardy, K. H., Atlas, D. & Glover, K. M. (1966) Multiwavelength backscatter from the clear atmosphere. *Journal of Geophysical Research* **71**, 1537–52.

Hendrie, L. K., Irwin, M. E., Liquido, N. J., Ruesin, W. G., Mueller, W. M., Voegtlin, D. J., Achtemeier, G. L., Steiner, W. M. & Scott, R. W. (1985) Conceptual approach to modeling aphid migration. In: *The movement and dispersal of agriculturally important biotic agents*, D. R. MacKenzie, C. S. Barfield, G. C. Kennedy, R. D. Berger & D. J. Taranto, (eds), 541–82. Baton Rouge: Claitor's Publishing Division.

Hobbs, S. E. & Wolf, W. W. (1996) Developments in airborne entomological radar. *Journal of Atmospheric and Oceanic Technology* **13**, 58–61.

Johnson, C. G. (1969) *Migration and dispersal of insects by flight*. London: Methuen.

Kennedy, J. S. (1985) Migration, behavioural and ecological. In: *Migration: mechanisms and adaptive significance*, M. A. Rankin, (ed.). *Contributions in Marine Science* **27** (supplement), 5–26.

Kennedy, P. J. (1994) The distribution and movement of ground beetles in relation to set-aside arable land. In: *Carabid beetles: ecology and evolution*, K. Desender, M. Dufrêne, M. Loreau, M.L. Luff & J.-P. Maelfait, (eds), 439–44. Dordrecht: Kluwer Academic Publishers.

Lack, D. & Varley, D. G. (1945) Detection of birds by radar. *Nature* **156**, 446.

Larkin, R. P. (1991) Flight speeds observed with radar, a correction: slow 'birds' are insects. *Behavioural Ecology and Sociobiology* **29**, 221–4.

Larkin, R. P., Griffin, D. R., Torre-Bueno, J. R. & Teal, J. (1979) Radar observations of bird migration over the western north Atlantic. *Behavioural Ecology and Sociobiology* **4**, 225–64.

Larkin, R.P. & Thompson, D. (1980) Flight speeds of birds observed with radar: evidence for two phases of migratory flight. *Behavioural Ecology and Sociobiology* **7**, 301–17.

Mascanzoni, D. & Wallin, H. (1986) The harmonic radar: a new method of tracing insects in the field. *Ecological Entomology* **11**, 387–90.

Meinhertzagen, R. (1955) The speed and altitude of bird flight. *Ibis* **97**, 81–117.

Oertli, J. J. (1991) Interspecific scaling (relative size change) of wing beat frequency and morphometrics in flying beetles (Coleoptera). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **64**, 139–54.

Osborne, J. L., Clark, S. J., Morris, R. J., Williams, I. H., Riley, J. R., Smith. A. D., Reynolds, D. R. & Edwards, A. S. (in press) A landscape scale investigation of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology*.

Pedgley, D. E. (ed.) (1981) *Desert locust forecasting manual*. Vol. 1 and 2. London: Centre for Overseas Pest Research.

Pedgley, D. E., Reynolds, D. R., Riley, J. R. & Tucker, M. R. (1982) Flying insects reveal small-scale wind systems. *Weather* **37**, 295–306.

Pye, J. D. (1978) Some preliminary observations on flexible echolocation systems. In: *Proceedings of the 4th International Bat Research Conference, 1975*, R. J. Olembo, J. B. Castelino & F. A. Mutere, (eds). Nairobi: Kenyan Literature Bureau for Kenya National Academy of Advancement of Arts and Sciences.

Rainey, R. C. (1951) Weather and the movements of locust swarms: a new hypothesis. *Nature* **168**, 1057–60.

Rainey, R. C. (1955) Observation of desert locust swarms by radar. *Nature* **175**, 77.

Rainey, R. C. (1986) Glen Willard Schaefer (1930–1986). *Antenna* **10**, 163–5.

Reid, D. G., Wardhaugh, K. G. & Roffey, J. (1979) *Radar studies of insect flight at Benalla, Victoria, in February 1974. Division of Entomology Technical Paper* No. 16. Melbourne: CSIRO.

Reynolds, D. R. (1988) Twenty years of radar entomology. *Antenna* **12**, 44–9.

Reynolds, D. R. & Riley, J. R. (1988) A migration of grasshoppers, particularly *Diabolocatantops axillaris* (Thunberg) (Orthoptera: Acrididae), in the West African Sahel. *Bulletin of Entomological Research* **78**, 251–71.

Reynolds, D. R. & Riley, J. R. (1997) *The flight behaviour and migration of insect pests: radar studies in developing countries. NRI Bulletin* No. 71. Chatham: Natural Resources Institute.

Richter, J. H., Jensen, D. R., Noonkester, V. R., Kreasky, J. B., Stimmann, M. W. & Wolf, W. W. (1973) Remote radar sensing: atmospheric structure and insects. *Science* **180**, 1176–8.

Riley, J. R. (1973) Angular and temporal variations in the radar cross-sections of insects. *Proceedings of the Institution of Electrical Engineers* **120**, 1229–32.

Riley, J. R. (1974) Radar observations of individual desert locusts (*Schistocerca gregaria*) (Forsk.). *Bulletin of Entomological Research* **64**, 19–32.

Riley, J. R. (1975) Collective orientation in night-flying insects. *Nature* **253**, 113–4.

Riley, J. R. (1979) Quantitative analysis of radar returns from insects. In: *Radar, insect population ecology, and pest management*, C. R. Vaughn, W. Wolf & W. Klassen, (eds), 131–58. *NASA Conference Publication* 2070, Wallops Island, Virginia: NASA.

Riley, J. R. (1980) Radar as an aid to the study of insect flight. In: *A handbook on biotelemetry and radio tracking*, C. J. Amlaner & D. W. MacDonald, (eds), 131–40. Oxford: Pergamon Press.

Riley, J. R. (1985) Radar cross-sections of insects. *Proceedings of the Institute of Electrical and Electronic Engineers* **73**, 228–32.

Riley, J. R. (1989a) Recent developments in the application of radar to biology: millimetric and 3-cm systems for studies of insect flight. In: *Biotelemetry X: Proceedings of the Tenth International Symposium on Biotelemetry*, C. J. Amlaner, (ed.), 210–14. Fayetteville, Arkansas: University of Arkansas Press.

Riley, J. R. (1989b) Remote sensing in entomology. *Annual Review of Entomology* **34**, 247–71.

Riley, J. R. (1989c) Orientation by high-flying insects at night: observations and theories. In: *Orientation and navigation – birds, humans and other animals*. Papers presented at the Conference of the Royal Institute of Navigation, Cardiff, 6–8 April 1989. London: Royal Institute of Navigation.

Riley, J. R. (1992) A millimetric radar to study the flight of small insects. *Electronics and Communication Engineering Journal* **4**, 43–8.

Riley, J. R. (1993) Long-term monitoring of insect aerial migration. In: *Alliance for Aerobiology Workshop Report, Kalamazoo, 10–13 October 1992*, S. A. Isard, (ed.), 28–32. Champaign, Illinois: Alliance for Aerobiology Workshop Writing Committee.

Riley, J. R., Cheng X. N., Zhang, X. X., Reynolds, D. R., Xu, G. M., Smith, A. D., Cheng, J. Y., Bao, A. D. & Zhai, B. P. (1991) The long distance migration of *Nilaparvata lugens* (Stål) (Delphacidae) in China: radar observations of mass return flight in the autumn. *Ecological Entomology* **16**, 471–89.

Riley, J. R., Downham, M. C. A. & Cooter, R. J. (1997) Comparison of the performance of *Cicadulina* leafhoppers on flight mills with that to be expected in free flight. *Entomologia Experimentalis et Applicata* **83**, 317–22.

Riley, J. R. & Reynolds, D. R. (1979) Radar-based studies of the migratory flight of grasshoppers in the middle Niger area of Mali. *Proceedings of the Royal Society*, B **204**, 67–82.

Riley, J. R. & Reynolds, D. R. (1983) A long-range migration of grasshoppers observed in the Sahelian zone of Mali by two radars. *Journal of Animal Ecology* **52**, 167–183.

Riley, J. R. & Reynolds, D. R. (1986) Orientation at night by high-flying insects. *Insect flight: dispersal and migration*, W. Danthanarayana, (ed.), 71–87. Berlin: Springer-Verlag.

Riley, J. R. & Reynolds D. R. (1990) Nocturnal grasshopper migration in West Africa: transport and concentration by the wind, and the implications for air-to-air control. *Philosophical Transactions of the Royal Society of London*, B, **328**, 655–72.

Riley, J. R. & Reynolds, D. R. (1993) Radar monitoring of locusts and other migratory insects. In: *World agriculture 1993*, A. Cartwright, (ed.), 51–3. London: Sterling Publications.

Riley, J. R., Reynolds, D. R. & Farmery, M. J. (1981) Radar observations of *Spodoptera exempta*. Kenya, March–April 1979. *Centre for Overseas Pest Research Miscellaneous Report* No. 54. London: Centre for Overseas Pest Research.

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. *Ecological Entomology* **8**, 395–418.

Riley, J. R., Reynolds, D. R. & Farrow, R. A. (1987) The migration of *Nilaparvata lugens* (Stål) (Delphacidae) and other Hemiptera associated with rice during the dry season in the Philippines: a study using radar, visual observations, aerial netting and ground trapping. *Bulletin of Entomological Research* **77**, 145–69.

Riley, J. R., Reynolds, D. R., Smith, A. D., Cheng, X. N., Xu, G. M., Cheng, J.Y., Bao, A. D. & Zhai, B. P. (1990) Using radar to observe brown planthopper (BPH) migration in China, *International Rice Research Newsletter* **15** (2), 29–30.

Riley, J. R., Reynolds, D. R., Smith, A. D., Edwards, A. S., Zhang, X.-X., Cheng, X.-N., Wang, H.-K., Cheng, J.-Y. & Zhai, B.-P. (1995) Observations of the autumn migration of the rice leaf roller *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae) and other moths in eastern China. *Bulletin of Entomological Research* **85**, 397–414.

Riley, J. R., Reynolds, D. R., Smith, A. D., Edwards, A. S., Osborne, J. L & McCartney, H. A. (in press) Compensation for the wind by foraging bumble bees.

Riley, J. R., Reynolds, D. R., Smith, A. D., Rosenberg, L. J., Cheng, X.-N., Zhang, X.-X., Xu, G.-M., Cheng, J.-Y., Bao, A.-D., Zhai, B.-P. & Wang, H.-K. (1994) Observations on the autumn migration of *Nilaparvata lugens* (Homoptera: Delphacidae) and other pests in east central China. *Bulletin of Entomological Research* **84**, 389–402.

Riley, J. R., Smith, A. D. & Gregory, R. D. (1993) A radar technique for automatically monitoring insect migration and bio-diversity. In: *Proceedings of the 12th International Symposium on Biotelemetry, Ancona, 31 August–5 September 1992*, P. Mancini, S. Fioretti, C. Cristalli & R. Bedini, (eds), 310–7. Pisa: Litografia Felici.

Riley, J. R., Smith, A. D., Reynolds, D. R., Edwards, A. S., Osborne, J. L., Williams, I. H., Carreck, N. L. & Poppy, G. M. (1996) Tracking bees with harmonic radar. *Nature* **379**, 29–30.

Riley, J. R., Valeur, P., Smith, A. D., Reynolds, D. R., Poppy, G. M. & Löfstedt, C. (1998) Harmonic radar as a means of tracking the pheromone-finding and pheromone-following flight of male moths. *Journal of Insect Behavior* **11**, 287–96.

Ritchie, M. & Pedgley, D. (1989) Desert locusts cross the Atlantic. *Antenna* **13**, 10–2.

Roffey, J. (1969) Report on radar studies on the desert locust, *Schistocerca gregaria* (Forskal), the Niger Republic, September–October 1968. *Occasional Report* No. 17. London: Anti-locust Research Centre.

Roffey, J. (1972) Radar studies of insects. *PANS* **18**, 303–9.

Roland, J., McKinnon, G., Backhouse, C. & Taylor, P. D. (1996) Even smaller radar tags on insects. *Nature* **381**, 120.

Schaefer, G. W. (1969) Radar studies of locust, moth and butterfly migration in the Sahara. *Proceedings of the Royal Entomological Society of London*, Series C **34**, 33, 39–40.

Schaefer, G. W. (1972) Radar detection of individual locusts and swarms. In: *Proceedings of the International Study Conference on the Current and Future Problems of Acridology, London 1970*, C. F. Hemming & T. H. C. Taylor, (eds), 379–80. London: Centre for Overseas Pest Research.

Schaefer, G. W. (1976) Radar observations of insect flight. In: *Insect flight*, R. C. Rainey, (ed.), 157–97. *Symposia of the Royal Entomological Society*, No. 7. Oxford: Blackwell.

Skolnik, M. I. (1990) *Radar handbook*. 2nd edn. New York: McGraw-Hill.

Smith, A. D. & Riley, J. R. (1996) Signal processing in a novel radar system for monitoring insect migration. *Computers and Electronics in Agriculture* **15**, 267–78.

Smith, A. D., Riley, J. R. & Gregory, R. D. (1993) A method for routine monitoring of the aerial migration of insects by using a vertical-looking radar. *Philosophical Transactions of the Royal Society*, B **340**, 393–404.

Taylor, L. R. (1985) An international standard for the synoptic monitoring and dynamic mapping of migrant pest aphid populations. In: *The movement and dispersal of agriculturally important biotic agents*, D. R. MacKenzie, C. S. Barfield, G. C. Kennedy, R. D. Berger & D. J. Taranto, (eds), 337–80. Baton Rouge: Claitor's Publishing Division.

Thomas, A. A. G., Ludlow, A. R. & Kennedy, J. S. (1977) Sinking speeds of falling and flying *Aphis fabae* Scopoli. *Ecological Entomology* **2**, 315–26.

Tucker, M. R. (1997) Satellite-derived rainstorm distribution an aid to forecasting African armyworm outbreaks. *Weather* **52**, 204–12.

Urquhart, F.A. (1960) *The Monarch Butterfly*. Toronto: University of Toronto Press.

Urquhart, F. A. (1987) *The Monarch Butterfly: international traveller*. Chicago: Nelson-Hall.

Uvarov, B. P. (1921) A revision of the genus *Locusta*, L. (=*Pachytylus*, Fieb.), with a new theory as to the periodicity and migrations of locusts. *Bulletin of Entomological Research* **12**, 135–63.

Vaughn, C. R. (1985) Birds and insects as radar targets: a review. *Proceedings of the Institute of Electrical and Electronic Engineers* **73**, 205–27.

Vogler, J. G., Maguire, D. J. and Steinhauer, A. E. (1967) DINADE – a new interrogation, navigation and detection system. *Microwave Journal* **10** (6), 1–6.

Wallin, H. (1991) Movement patterns and foraging tactics of a caterpillar hunter inhabiting alfalfa fields. *Functional Ecology* **5**, 740–9.

Wallin, H. & Ekbom, B. S. (1988) Movements of carabid beetles (Coleoptera: Carabidae) inhabiting cereal fields: a field tracing study. *Oecologia* **77**, 39–43.

Westbrook, J. K., Eyster, R. S., Wolf, W. W., Lingren, P. D. & Raulston, J. R. (1995) Migration pathways of corn earworm (Lepidoptera: Noctuidae) indicated by tetroon trajectories. *Agricultural and Forest Meteorology* **73**, 67–87.

Williams, C.B. (1930) *The Migration of Butterflies*. Edinburgh, Oliver & Boyd.

Williams, C.B. (1965) *Insect migration*. 2nd edn. London: Collins.

Woiwod, I. P. & Harrington, R. (1994) Flying in the face of change – the Rothamsted Insect Survey. In: *Long-term experiments in agricultural and ecological sciences*, R. A. Leigh & A. E. Johnson, (eds), 321–42. Wallingford, UK: CAB International.

Wolf, W. W. (1979) Entomological radar studies in the United States. In: *Movement of highly mobile insects: concepts and methodology in research*, R. L. Rabb & G. G. Kennedy, (eds), 263–6. Raleigh: North Carolina State University.

Wolf, W. W., Westbrook, J. K., Raulston, J., Pair, S. D. & Hobbs, S. E. (1990) Recent airborne radar observations of migrant pests in the United States. *Philosophical Transactions of the Royal Society*, B **328**, 619–30.

Medway Campus
Central Avenue
Chatham Maritime
Kent
ME4 4TB

ISBN: 1 86166 129 0