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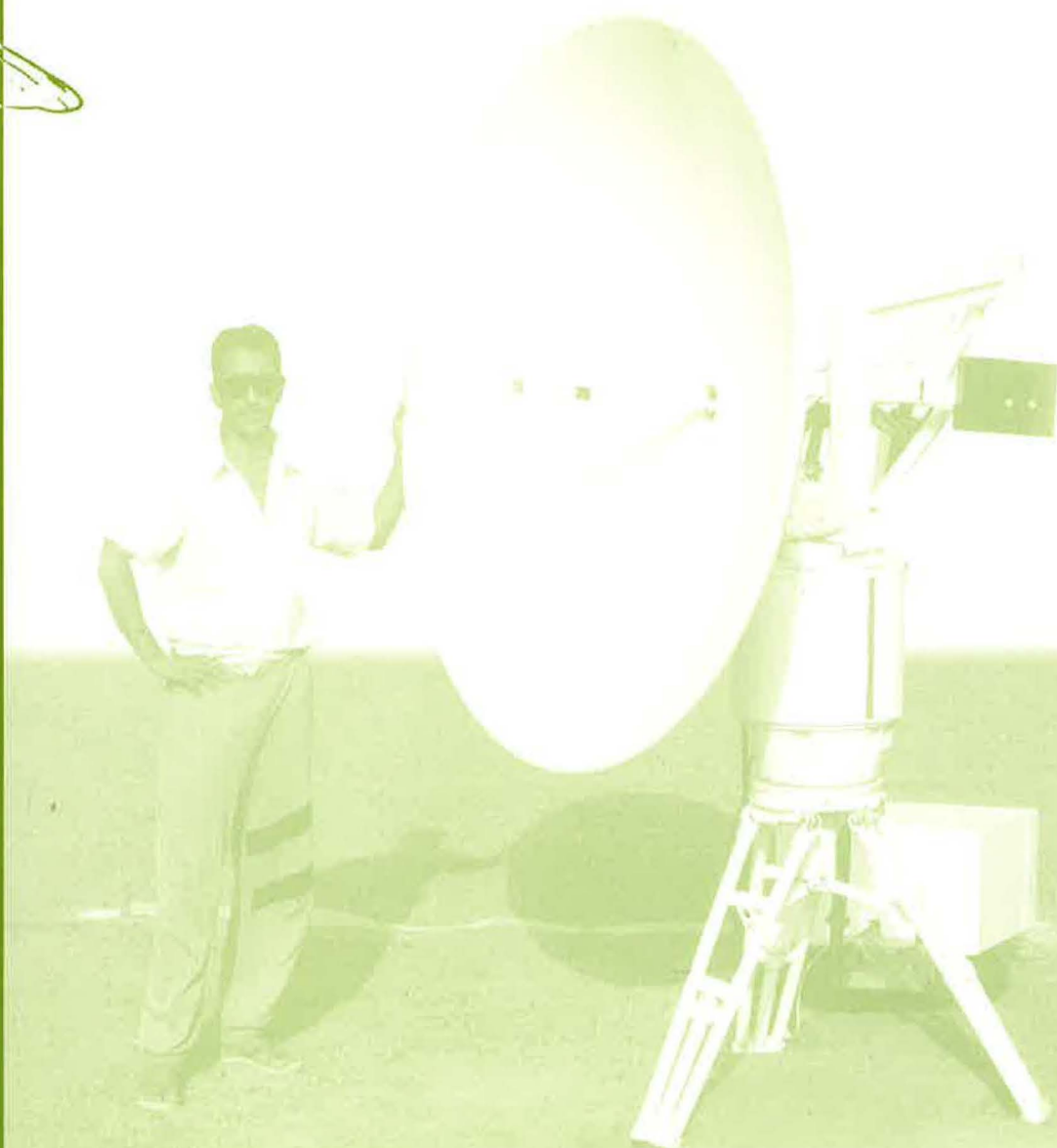
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Bulletin 71

FLIGHT BEHAVIOUR AND MIGRATION OF INSECT PESTS

Radar Studies in Developing Countries



NATURAL RESOURCES INSTITUTE
The University of Greenwich

ODA

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Radar Studies in Developing Countries

D.R. Reynolds and J.R. Riley

Bulletin 71



NATURAL RESOURCES INSTITUTE
The University of Greenwich

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The Natural Resources Institute (NRI) is a scientific institute within the University of Greenwich, and is an internationally recognized centre of expertise in research and consultancy in the environment and natural resources sector. Its principal aim is to increase the productivity of renewable natural resources in developing countries in a sustainable way by promoting development through science.

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Summaries

SUMMARY

The use of radar to make direct observations of insects flying at altitude has provided many new insights into the phenomenon of long-range insect migration. In particular, the technique has produced a wealth of quantitative information on the spatial and temporal distribution of migrants in the air, on the direction, speed and duration of their displacements, and on their orientation behaviour. These data could not have been obtained by any other means, and it is probably fair to claim that our present knowledge of the magnitude and importance of high-altitude insect movement stems very largely from radar observations. The pioneering field studies using the first specially designed entomological radar were undertaken in 1968, with the support of the UK Overseas Development Administration (ODA), and since that time ODA has been responsible for funding almost all of the applications of the technique in developing countries. The motivation for this work was the assumption that it was impossible to design efficient management strategies for migrant pest insects without a good knowledge of their migratory behaviour, and of the role which this played in their population dynamics. The ODA-funded studies thus focused primarily on pest species, and were carried out by the Radar Entomology Unit of the Natural Resources Institute (NRI) and its precursors. In this Bulletin, we give a brief account of the history of radar entomology, with emphasis on studies of insect pests. Next, the different types of entomological radar and some associated analysis methods are outlined, together with descriptions of some ancillary measurement techniques. We then describe in some detail the contributions made by the NRI Radar Unit to current knowledge of the flight patterns of a variety of major insect pests of agriculture and of human health. These pests include: grasshoppers and locusts, the African Armyworm moth, the Rice Brown Planthopper and other rice pests, the Old World Bollworm, and some mosquito vectors of human diseases. Recent developments directed towards long-term monitoring of insect aerial faunas (for environmental impact, biodiversity and conservation purposes), and towards observations of low-altitude flight, are included. The Bulletin concludes with a short overview, in which we speculate how the technique might find application in the future.

RESUME

L'utilisation d'un radar pour effectuer des observations directes sur les insectes volant en altitude a fourni un grand nombre d'idées nouvelles au sujet du phénomène de la migration des insectes sur de grandes distances. Cette technique a, en particulier, généré une mine d'informations quantitatives sur la répartition dans le temps et l'espace des insectes migrants en l'air, sur la direction, la vitesse et la durée de leurs déplacements, et sur leur comportement en matière d'orientation. Comme ces données n'auraient pas pu être obtenues par d'autres moyens, on peut raisonnablement dire que notre connaissance actuelle de l'ampleur et de l'importance des déplacements des insectes à haute altitude découle en grande partie des observations effectuées grâce au radar. Les études de terrain innovatrices, utilisant un radar entomologique spécialement conçu, ont été entreprises en 1968 avec l'appui de l'Overseas Development Administration (ODA) du Royaume-Uni et, depuis, l'ODA a été responsable du financement de presque toutes les applications de la technique dans les pays en développement. La supposition, selon laquelle il était impossible de concevoir des stratégies efficaces de gestion des insectes ravageurs migrants sans une bonne connaissance de leur comportement migratoire et de son rôle dans la dynamique de la population, a motivé les travaux. Les études financées par l'ODA se sont, par conséquent, essentiellement concentrées sur des espèces de ravageurs et ont été menées à bien par l'Unité de Radar entomologique du Natural Resources Institute (NRI) et ses précurseurs. Dans le présent Bulletin, l'histoire de l'entomologie utilisant le radar est résumée, en insistant sur les études des insectes ravageurs. Les différents types de radars entomologiques et certaines des méthodes d'analyses associées sont ensuite esquissées et certaines techniques auxiliaires de mesure sont décrites. La contribution faite par l'Unité de Radar du NRI aux connaissances actuelles sur les types de vol d'une variété d'insectes ravageurs importants dans le domaine de l'agriculture et de la santé humaine est décrite en détail. Ces ravageurs incluent: les sauterelles et les criquets pèlerins, *Spodoptera exempta*, *Nilaparvata lugens* et d'autres ravageurs du riz, *Helicoverpa armigera* et certains moustiques

vecteurs de maladies humaines. Les progrès récents accomplis sur la voie d'une surveillance à long terme des faunes d'insectes aériens (à des fins d'étude de l'impact sur l'environnement, de la biodiversité et de conservation) et de l'observation des vols à basse altitude sont inclus. Le Bulletin conclut par une vue d'ensemble et des spéculations sur la façon dont cette technique pourrait être appliquée dans l'avenir.

RESUMEN

El empleo del radar para realizar observaciones directas del vuelo de los insectos a gran altura nos está proporcionando nuevos conocimientos sobre el fenómeno de su migración a larga distancia. Esta técnica ha servido, de manera particular, para producir un gran acervo de información cuantitativa sobre la distribución espaciotemporal de los insectos en migración, dirección, velocidad y duración de sus desplazamientos y manera como logran orientarse. Dado que no existe ningún otro método para la obtención de esta información, resulta probablemente razonable concluir que nuestros conocimientos actuales sobre la magnitud e importancia de los movimientos de los insectos a gran altura se deben, en gran parte, a las observaciones radáricas. En 1968 y con el apoyo de la Administración para el Desarrollo Ultramarino del Reino Unido (Overseas Development Administration - ODA), se pusieron en marcha los primeros estudios sobre el terreno, utilizando equipo de radar entomológico especialmente diseñado. Desde aquellas fechas, la ODA ha venido financiando la casi totalidad de las aplicaciones de dicha técnica en los países en desarrollo. A la base de esta labor se encontraba el supuesto de que era imposible conseguir estrategias eficientes de gestión para las plagas migratorias de insectos, sin contar con un buen conocimiento de su comportamiento durante la migración y de su papel en la dinámica de la población. Así, pues, los estudios financiados por la ODA –que giraron fundamentalmente en torno a las plagas– estuvieron a cargo de la Unidad de Entomología Radárica del Instituto de Recursos Naturales (Natural Resources Institute - NRI) y de sus precursores. En el presente Boletín presentamos una breve descripción de la historia de la entomología radárica, poniendo un énfasis particular en la realización de estudios sobre plagas de insectos. A continuación, pasamos revista a los distintos tipos de radar entomológico y a algunos de los métodos analíticos asociados y presentamos una descripción de algunas de las técnicas auxiliares de medición. También se proporciona información minuciosa sobre la aportación de la Unidad de Radar del NRI a los conocimientos actuales sobre las características de los vuelos de una gran variedad de importantes plagas de insectos y sobre su impacto para la agricultura y para la salud humana. Valga citar entre las plagas tratadas los saltamontes y la langosta, la polilla combatiente africana, el saltamontes marrón del arroz y otras plagas de los arrozales, la oruga del algodón del Viejo Mundo y determinados mosquitos transmisores de enfermedades a los seres humanos. El Boletín ofrece asimismo una descripción de recientes avances en el sector de la supervisión a largo plazo de la fauna de los insectos voladores, para establecer su impacto ambiental, biodiversidad y conservación y para la realización de observaciones sobre vuelos de baja altitud. Finalmente, el Boletín concluye con una breve panorámica, en la que se apuntan posibles aplicaciones de esta técnica en el futuro.

Section 1

Introduction

The principal objective of this compendium is to draw together in one volume the results of the radar-based research on insect pest migration which has been funded by the UK Overseas Development Administration (ODA) since 1968. Most of the results have been published elsewhere, but as the papers are scattered through the scientific literature and over a period of more than a quarter of a century, it seemed useful to assemble the material into a cohesive whole. It is hoped that this resulting compendium will serve to demonstrate the contribution of ODA-funded radar work to our current knowledge of insect migration, and to the management of migrant pest species in developing countries.

Almost all the ODA-funded work was carried out by a small group based at a Ministry of Defence radar research establishment in Malvern in Worcestershire. This group, now the Radar Entomology Unit of the Natural Resources Institute (NRI) and a part of the University of Greenwich, was originally formed by one of us (JRR) for one of NRI's precursor organisations, the Anti-Locust Research Centre (ALRC). As part of the scientific wing of ODA, the ALRC and its successors were particularly concerned to help the governments of developing countries to evolve efficient forecasting and control strategies against locusts, armyworm moths and other highly mobile insect pests. Populations of these pests often change rapidly in space as well as in time, and it was recognized that the development of optimal management strategies would require a good understanding of the role which migration plays in the population dynamics and general biology of the species concerned. However, long-distance migration by insects usually takes place high in the air, and often at night, and so it is extremely difficult to study by conventional entomological methods. It was for these reasons that ALRC became instrumental in the development of radar entomology from the subject's earliest days, since it was appreciated that radar offered the unique and exciting prospect of making **direct** quantitative observations of the airborne migration of insect pests.

In order to put the contribution of the ODA-funded work in context, we begin this bulletin with a short historical overview of the development of radar entomology. Next we give a brief description of the different methods of using radar to observe insects, and explain how the radar signals are analysed to produce quantitative data on airborne insect fauna. In the next part of the bulletin, we describe examples of studies undertaken by the NRI Radar Unit on migrant insect pests of major economic importance in developing countries. In each case, the state of knowledge of the pest's movement prior to the radar studies is outlined, the main results from the studies are then summarised, and the implications of these findings are discussed. Finally, in

a short discussion section, we review the role of radar entomology in pest management programmes in general, and speculate about its possible uses in the future.

Section 2

An Outline of the Historical Development of Radar Entomology

ODA'S ROLE IN ESTABLISHING RADAR ENTOMOLOGY

From the 1950s onwards, the late R.C. Rainey (of the Desert Locust Control Organization for Eastern Africa (DLCOEA), and then of ODA's Anti-Locust Research Centre (ALRC)) was a consistent advocate of the use of radar for the observation of airborne Desert Locusts (*Schistocerca gregaria*) (Rainey, 1955). As a consequence of his interest, an attempt was made in 1966 by D.G. Smith, on behalf of DLCOEA, to design and build an airborne radar for locust detection, but the programme turned out to be too ambitious for the resources available, and it was eventually abandoned. Rainey's enthusiasm nevertheless remained undimmed, and after hearing a talk by the late G.W. Schaefer, then at Loughborough University, on the detection of bird migration by radar, he persuaded the ALRC to sponsor another attempt to use radar specifically for an entomological experiment. This led to a pioneering radar field study in Niger, under Schaefer's leadership, during September-October 1968. The study was spectacularly successful, producing observations of new and unsuspected features of Desert Locust nocturnal migration (Schaefer, 1969; Roffey, 1969), and it served to establish Radar Entomology as an essential part of insect migration research.

In June 1971, the ALRC broadened its remit, was renamed the Centre for Overseas Pest Research (COPR), and later in the same year engaged one of us (JRR) to set up an in-house Radar Unit to support studies of insect pest migration in the developing world. The Unit quickly demonstrated its competence by mounting a radar field study of locusts in Saudi Arabia in the spring of 1972 (Riley, 1974), and by establishing the radar characteristics of target insects, both in the laboratory and in the field (Riley, 1973). Since then, the Unit has made major contributions to the understanding of the migration of a variety of insect pests in the developing countries in Africa and Asia, and has also been responsible for many of the technical innovations which have increased the power and flexibility of entomological radars. The bulk of this compendium is devoted to documenting these scientific and technical achievements.

Unlike radar entomology units in Australia and the USA (see below) which have worked mainly on insect pests **within** their respective countries, the ODA-funded NRI Unit has directed its efforts almost exclusively to investigations of insect pests in the developing world.

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 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, 1971, 1976).

Between 1973 and 1976, Schaefer (working again with the AARU, and collaborating with, among others, Rainey and M.J. Haggis of COPR) engaged in an ambitious experimental programme for the Canadian Forestry Service to study the movements of Spruce Budworm moth, *Choristoneura fumiferana*. During this large-scale effort, entomological radars specially designed for airborne use were deployed for the first time, in addition to ground-based radar, aircraft-mounted insect sampling nets, and aircraft equipped with Doppler wind-finding equipment (Greenbank, Schaefer and Rainey, 1980).

In 1975, Schaefer set up the Ecological Physics Research Group at Cranfield. He continued his work there on the development of radar and other remote sensing techniques for insect observation, until his death in 1986. Schaefer's contributions to radar entomology are further described in an obituary by Rainey (1986).

Australia

In the meantime, CSIRO had maintained its interest in radar, and established its own capacity to make observations of insect flight, focusing primarily on observations of the Australian Plague Locust, *Chortoicetes terminifera* (Roffey, 1972; Reid *et al.*, 1979), but also mounting studies of insect migration over the Arafura Sea and across the Torres Strait. The CSIRO initiative entered a highly productive phase when Dr V.A. Drake was appointed to a full-time position in 1978 to lead their radar entomology effort. Many papers have been published (including several with Dr R.A. Farrow) describing field observations of grasshoppers, locusts and moths, and of atmospheric phenomena influencing their migration (see, for example, references in Drake and Farrow, 1988).

In 1991, Drake joined the Physics Department of the Australian Defence Force Academy (part of the University of New South Wales) in Canberra, but he continued to play an active role in radar entomology research, particularly in the long-term monitoring of airborne populations using a combination of entomological and meteorological remote-sensing methods (Drake *et al.*, 1994).

The USA

Through the 1960s and 1970s, airborne insects were often 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 and Glover, 1966). Many of these meteorological studies were concerned with investigations of so-called 'dot-angel' echoes, which are now known to be caused mostly by insects (Glover *et al.*, 1966).

The first entomologically oriented radar observations in the USA were those of mosquito swarms made between 1969 and 1972 by E.L. Frost of the Army Electronics Command (e.g. Frost, 1971). Frost used a 1.9 cm wavelength army mortar-locating radar, the scanning pattern of which was not ideal for entomological observations. Radar entomology really established itself in the States when, soon after the experiments in Canada, the United States Department of Agriculture (USDA) entered the field. In 1978, Mr W.W. Wolf, then working at the USDA Western Cotton Research Laboratory, carried out radar observations of insect flight over cotton fields in Arizona (Wolf, 1979). In 1980, Wolf moved to the Insect Biology and Population Management Research Laboratory in Tifton, Georgia, where in close collaboration with the meteorologist, Dr J.K. Westbrook, and entomological colleagues, he engaged in a long-term investigation of the migration of 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 effort to include observations with airborne insect-detecting radar, in collaboration with Dr S. Hobbs of Cranfield University (Wolf *et al.*, 1990; Hobbs and Wolf, 1996). He also configured his ground-based radars into a form which allowed them to be moved and set up quickly, so that observations could be conducted from several sites during a single night.

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 the NRI Unit, of using vertical-looking radar (VLR) with rotating polarization to monitor overflying insects (Beerwinkle, Witz and Schleider, 1993). Using a computerised data logging and processing facility, nocturnal insect flight between 500 and 2400 m above ground was recorded for a whole year in 1990–1991 (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. Apart from the deployment of scanning and vertical-looking radars, and night vision devices, recent innovative field techniques include long-distance tracking of instrumented tetroons (balloons which drift at altitudes of constant air density) as surrogates for migrating moths (Westbrook *et al.*, 1995), and aerial capture of insects using traps attached to tetroons and tethered balloons.

In addition to his work on pest migration, Wolf also collaborated with Dr G.M. Loper of the Carl Hayden Bee Research Center, Tucson, Arizona and Dr O.R. Taylor of the University of Kansas to observe honey bee flight (e.g. Loper, Wolf and Taylor, 1993).

Overall, the USDA radar entomology effort has provided many excellent demonstrations of what could be achieved by combining novel techniques in large-scale field studies, but full accounts of the findings have not always been presented in the scientific literature.

Another large American program was the 1983–1985 Illinois 'Pests and Weather' project which was designed to study the migration of aphids and other insect pests into this State. The project used the Illinois State Weather Survey's 'CHILL' high-power S-band Doppler radar, a tracking X-band radar, as well as a helicopter-borne aerial insect sampler (Hendrie *et al.*, 1985; Irwin and Thresh, 1988).

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 Moth (*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.*, 1985, 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.adfa.oz.au/~vad/trews/>).

Section 3

Radar Techniques

In this section we outline the different radar techniques which have been applied in entomological studies, and we discuss their advantages and limitations. The pulse technique is by far the most commonly used, and the bulk of the section is consequently devoted to the various ways in which pulse radars have been configured and used for observations on insects.

Radar (**RA**dio **D**etection **A**nd **R**anging) is based on the simple concept that radio waves are always reflected to some degree from objects in their path, and that the reflected energy can be used to infer both the presence and location of the reflecting objects. 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 tracking airborne objects, and in the case of biological targets, it offers the great advantage that it does not perturb their behaviour (unless the average energy density of the radio waves is exceptionally high – a condition not approached with entomological radars).

TYPES OF RADAR

Pulse radar

In the case of **pulse** radar, short bursts or pulses of radio waves are transmitted from an antenna designed to focus the bulk of the transmitted energy in a defined direction, i.e., into a beam. If the pulse intercepts an object, a fraction of its energy is reflected or scattered, and some of this is propagated 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) multiplied by half the time elapsing between transmission of the illuminating pulse and reception of the echo. Although the concept is disarmingly simple, its practical realisation in the early 1940s required major resources and exceptional scientific and technical ingenuity. The main difficulty was that of 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 at centimetric wavelengths, because short wavelength meant that highly directional beams could be achieved with small antennas. Technical progress was rapid however, 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 mass

produced, mainly for the marine market. It was the availability of compact and relatively inexpensive equipment of this type that made radar entomology a practicable proposition (Schaefer, 1969, 1972, 1976; Riley, 1974).

FMCW radar

Pulse radars determine target range from the interval between the transmission of a pulse and reception of an echo. In **frequency modulated, continuous wave (FMCW)** radars, the transmitter operates continuously, but its frequency is repeatedly swept at a controlled rate. Reflected signals from a target also show this frequency change, but delayed in time by the interval required for signals to propagate to the target and back. Frequency-sensitive elements in the receiver detect this time delay, and hence determine the target's range. FMCW radars combine exceptional sensitivity with very high range resolution (~2 m), and as a result, they can simultaneously reveal fine-scale details of atmospheric structure, and insects flying within it (Richter *et al.*, 1973; Gossard and Chadwick, 1979; Gossard, Chadwick and Wolfe, 1980; Eaton, McLaughlin and Hines, 1995). Unfortunately, these radars carry the penalty of much greater complexity and expense, and the published FMCW observations of insects have been largely a by-product of research into the structure of the planetary boundary layer.

Doppler radar

If a target has a component of motion directly towards or away from a radar, the Doppler effect causes the frequency of the echo signal to be higher or lower than that transmitted. **Doppler radars** are sensitive to this frequency shift, and so provide a measure of the radial speed of the targets they detect, as well as their position. Large and powerful radars of this type, built for meteorological research, have occasionally been made available for entomological studies; for example, the CHILL 10 cm wavelength Doppler system which was used to study the migration of aphids and other insects in the USA in the mid-1980s (Hendrie *et al.*, 1985; Irwin and Thresh, 1988; Achtemeier, 1992). Reports re-discovering the entomological potential of radars of this type continue to appear in the literature (Russell and Wilson, 1996).

The American network of NEXRAD Doppler meteorological radars (Heiss, McGrew and Sirmans, 1990), in particular, appears to have a unique capacity to monitor the long-range movement and dispersal of insect pests of agriculture in the southern United States, especially if supplemented by measurements of the type made possible by the NRI type of vertical-looking radar (Riley, 1993a). The NEXRAD radars are powerful enough to detect individual insects out to tens of miles, and concentrations at over a hundred miles, but they have very limited capacity to differentiate between the returns from precipitation and those from insects and birds, and they have poor vertical resolution. Both of these shortcomings could be rectified by the use of low-cost nutating VLR equipment (see below), but to date there are no definite plans to exploit this potential.

The well-known microwave Doppler devices used to enforce vehicle speed limits do not measure the range of their targets, but both they, and the commonly used intruder detectors which also work on the Doppler principle, have nevertheless come to be described as radars. Hand-held 'radars' of this sort have been used to estimate the displacement speeds of flying insects

(Wolf, Loper and Grenaker, 1987; Coelho, 1989), but as their effective range is limited to a few metres and they do not measure the position of the target, they cannot be used to observe flight trajectories.

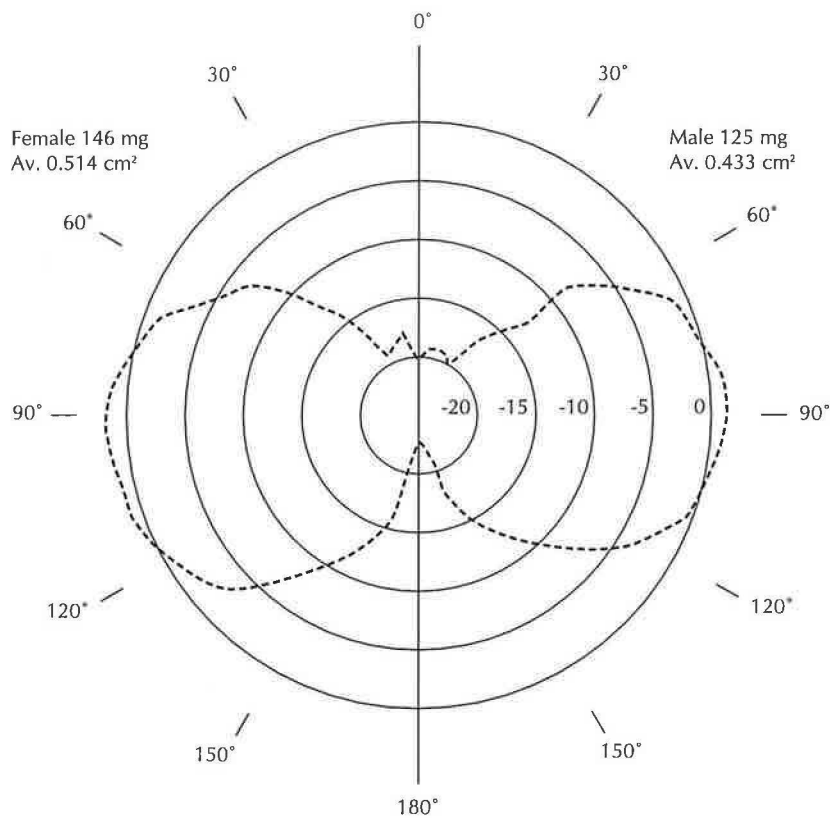
Transponders

The need for radars to be able to identify the aircraft which they detected led to the development of radar **transponders**. These are devices carried by aircraft, which pick up incoming radar signals and reply with a pulse on a slightly shifted frequency. This pulse can carry a code identifying the aircraft and even give its altitude. A secondary advantage of the transponder is that because its signal is at a different frequency to the radar echoes from ground features (clutter), aircraft equipped with them can be tracked even when flying at low altitude in highly cluttered environments. Conventional transponders are far too massive to be used on insects, but **harmonic transponders**, made of a whisker antenna and an electrically non-linear semi-conductor do have potential for entomological use because they need no battery and so can be made very small (Vogler, Maguire and Steinhauer, 1967). How this potential has been realised is described below in the section on **harmonic radar**.

THE RADAR-REFLECTING CHARACTERISTICS OF INSECTS

In order to be able to predict the degree to which an insect will be detectable on radar, it is necessary to know how effective it is at reflecting 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). An example of measurements made by the NRI Radar Unit is shown in Figure 1.

Schaefer discovered that the action of wing beating in flying insects modulated the radar signals they returned (Schaefer, 1969), and he concluded that this was because their RCS was affected by body flexure. The modulation depth of RCS 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 proved 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 passes over individual targets in only $\sim 10^{-2}$ seconds, far too short an interval to determine wing-beat frequency. The procedure to acquire wing-beat modulation is thus to stop rotational scanning, and simply let insects fly through the stationary beam; this gives typical transit times of 1 to 3 seconds. 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 1 The aspect dependence of the radar scattering cross-section of a medium-sized insect

Laboratory measurements show that the radar reflectivity (plotted logarithmically on the radial scale) of a medium-sized insect, typically varies with the aspect which the insect presents to the radar (azimuthal scale). Zero degrees represents the head-on aspect and 180°, tail-on. The body axis of the insect and the electric vector of the 3.2 cm wavelength, linearly-polarized radar wave were maintained in the horizontal plane in which the measurements were made, i.e., the conditions were similar to those experienced by a scanning entomological radar being used at low angles of elevation to observe airborne insects. The data on the diagram are from moths of the African Armyworm, *Spodoptera exempta*: the left half of the diagram shows the results from a female weighing 146 mg and the right half, those from a 125 mg male. It can be seen that insect reflectivity from the side is about 100 times greater than that from the ends. The angular dependence of reflectivity in larger insects usually has a more complicated lobe structure (Riley, 1973; Schaefer, 1976) but the overall pattern of low values from the ends, and high values from near-broadside aspects, is maintained.

The reflectivity is described in terms of radar scattering cross-section and is measured in units of area (here, cm²). The units represent a hypothetical area of an outgoing radar wave which, if its energy were captured and re-radiated isotropically at the target position, would produce the same signal power at the radar as the target does. Although this unit sounds somewhat contrived, it is universally used because it provides a convenient means of calculating the signal power which a target reflects back towards the radar. Measurements of the type shown here need specialized equipment (Riley, 1973, 1985) because the tiny radar returns from insects are easily contaminated by the more powerful echoes from nearby structures or from the insect support platform.

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 ($<10^{-4} \text{ m}^{-3}$) observed at close range ($< 3 \text{ km}$) the spatially discrete returns detectable from individual large- and medium-sized insects are very clearly different from the semi-continuous echoes generated by precipitation and no confusion is therefore likely. Returns from insect concentrations, on the other hand, may be very similar to rain echoes and reliable discrimination between the two may be difficult, especially at long-range when supplementary evidence (i.e., 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 very likely, but no supporting measurements have been reported to date.

Insects and birds

Although the radar cross-sections of birds (Edwards and 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 airspeeds of birds (Meinertzhagen, 1955; Eastwood, 1967) 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 5–6 m/s characteristic of the fastest insects (Larkin *et al.*, 1979; Larkin and 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 $\sim 14 \text{ Hz}$ (Schaefer, 1976), so the range of overlap is effectively reduced to 8–14 Hz.

In summary, aerial targets found to have flying speeds below 6–7 m/s, and generating continuous wing-beat modulation above 14 Hz will almost certainly be insects. In our studies usually only a very 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 polarisation and a small degree of beam nutation (Riley, Smith and Gregory, 1993; Smith, Riley and Gregory, 1993), which is able to make comprehensive estimates of the underside back-scattering properties of overflying insects (see below), and this promises to substantially improve discrimination between insects of different size and shape.

In some situations, radar measurements of wing-beat frequency provide a very 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 and Reynolds, 1979; Reynolds and Riley, 1988) (see also Figure 2). 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 very probable that the abundance of migrant species of very similar sizes, for example in noctuid moths, will 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 and Farmery, 1983) and/or trapping with nets supported by aircraft (Schaefer, 1976; Greenbank, Schaefer and 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 and Farrow, 1983, 1985; Riley *et al.*, 1995b).

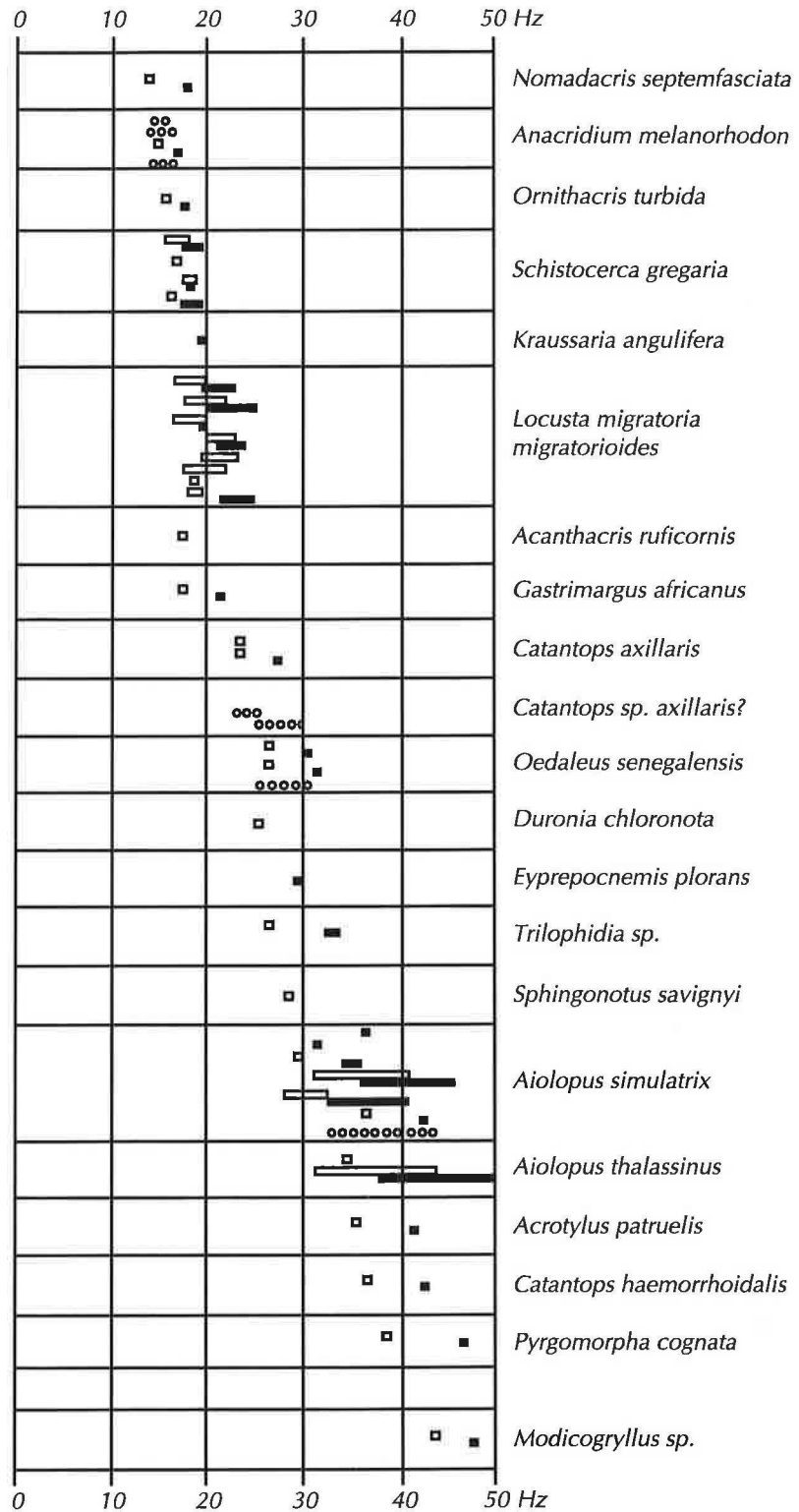


Figure 2 The wing-beat frequencies of grasshoppers found in the Middle Niger area of Mali

The wing-beat frequency data for grasshoppers (and a gryllid) shown on the chart were obtained partly from the literature, and partly by releasing identified insects from a balloon-supported capsule and optically steering the radar beam on to the insects as they flew away (Riley and Reynolds, 1979). The species are arranged in approximate order of size with the largest at the top. Solid bars refer to males, hollow bars to females and circles to unsexed specimens. The accumulated results illustrate how spread within, and overlap between species can make it difficult to identify insects from wing-beat frequencies alone.

Radar returns from small insect species seem not to contain detectable wing-beat modulation (Riley, Reynolds and Farrow, 1987) and in any case, the vast number of species of small insects 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 a very effective and inexpensive means of identification for smaller species. The method works particularly well because radar information about the altitudinal distribution of the insects allows the net to be positioned at altitudes where the insect density is a maximum, and catching rates are often high (Riley, Reynolds and Farrow, 1987; Riley *et al.*, 1990, 1991).

ENTOMOLOGICAL RADARS

When radar entomology began in the 1960s, marine radars which operated at 3.2 cm wavelength (X-band), had peak transmitted powers of 20–25 kW, and pulse lengths down to 0.1 s, were becoming commercially available. It turned out that the transceivers used in this type of equipment were particularly appropriate for an entomological radar, because at 3.2 cm wavelength, the RCS of medium to large-sized insects was large enough (0.5 to 4 cm²) to allow detection of individuals at ranges of up to 1 to 2 km, given a transmitted power of 20 kW, and antenna dimensions of about a metre. 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. The marine equipment also had the great advantages that it was small and compact, relatively rugged, inexpensive, and spares were readily available.

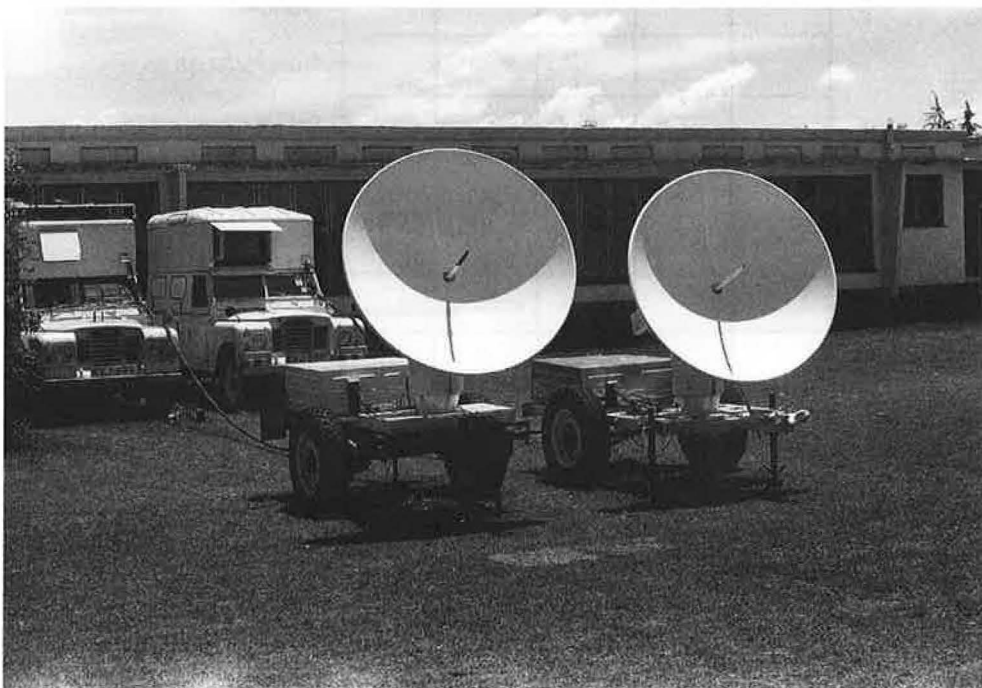


Figure 3 Two scanning entomological radars built by NRI for studying the migration of the African Armyworm moth in Kenya

This photograph shows two NRI radar systems being prepared at the Kenyan Agricultural Research Institute, Muguga, before deployment on an African Armyworm (*Spodoptera exempta*) outbreak site. The system control, display and recording equipment for each radar is housed in the air-conditioned Landrover cabin, and the antenna and radar transceiver are mounted on the two-wheel trailer. Each system is powered by a 5 kVA diesel-electric generator, so that the radars are independent of power supplies and can be deployed in remote areas. During overland travel, the antenna and transceiver are carried by the Landrover and the generator sits on the trailer.

Azimuthally-scanning radars

The design of the marine radar antenna was **not**, however, suited to entomological observations. It produced a 'fan' beam typically 1° or 2° wide in bearing, 30° wide in the vertical plane, and rotating in azimuth, so that all round coverage for surface vessels could be maintained in spite of pitching and rolling by the ship. What was needed in insect flight studies was a means of investigating what was happening at a range of 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 replace the marine antenna with tiltable, parabolic dish and feed, fitted on a rotating mount (Figure 3). This produced a narrow conical beam (pencil beam) which could be adjusted in elevation, and which scanned in azimuth at ~ 20 rpm. The antenna feed was configured so that the transmissions were linearly polarized, with the e-vector horizontal, because the RCS of most insects was a maximum for horizontal polarization. Targets intercepted by the rotating beam were registered on a conventional plan position indicator (PPI) radar display (Eastwood, 1967), which plotted their range and azimuth. The insects' altitude could be calculated by multiplying their range by the sine of the antenna elevation angle (Figure 4). Records of the PPI screen (e.g. Figure 5) were made on 16 mm ciné film, one frame being exposed for every revolution of the antenna.

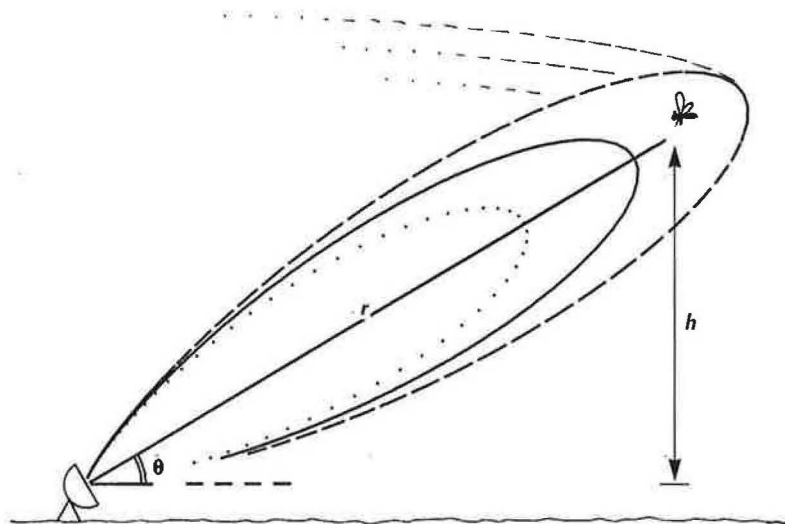


Figure 4 Azimuthal scanning at different elevation angles

The diagram shows how the beam of an entomological radar is scanned in azimuth and how adjusting the elevation angle allows access to insects flying at different heights above the ground. The altitude (h) of a target displayed at a range r on the radar screen, when the beam is at an elevation angle θ , is given by $h \approx r \sin(\theta)$. The beam is represented here by an iso-echoic contour (solid line) in the vertical plane, which defines the locus of those points from which a target presenting a fixed radar cross-section will produce radar echoes of the same amplitude. If the radar threshold of detection is set at this amplitude, targets of the cross-section will be detected anywhere within the contour but not outside it. The volume swept out by the contour when the beam is rotated in azimuth thus determines the aerial volume sensed by the radar for targets of this size. The contour (and hence the sensed volume) is smaller for lower values of cross-section and larger for higher values, so radar sampling is automatically biased in favour of larger targets. In the example shown here, the dotted, solid and dashed contours correspond to targets with radar cross-sections in the ratio 0.4:1.0:2.1. Correction of target size bias requires a knowledge of the distribution of radar cross-sections of the insect population. Fortunately, in cases where insect targets register as individual dots on the radar screen, this information can be acquired by systematically adjusting the threshold of detection and recording the density of dots on the screen at each threshold level (Riley, 1979). The angular width of the beam in this diagram is shown about 10 times larger than it would be in a typical entomological radar so that the differences between the contours can be more clearly seen.

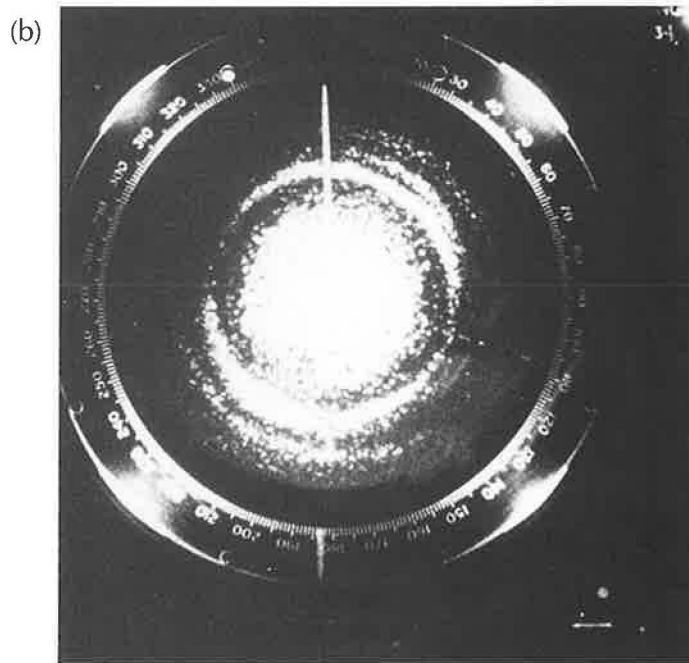
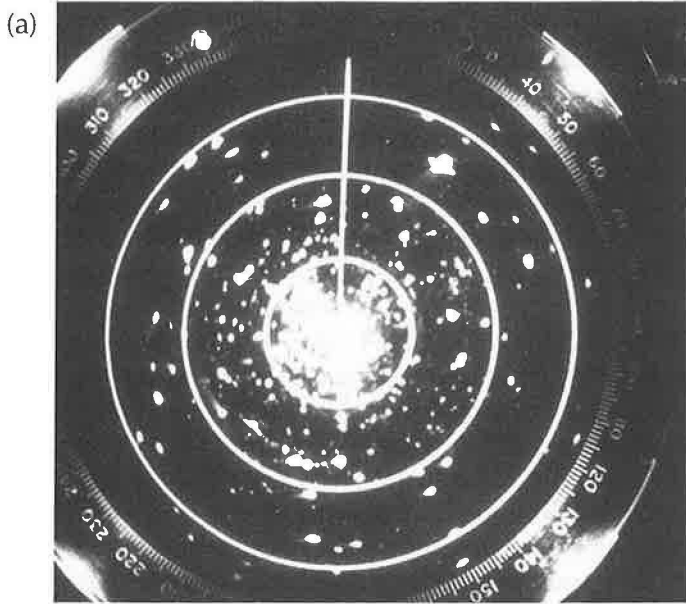


Figure 5

Photographs of the radar PPI screen showing insect echoes

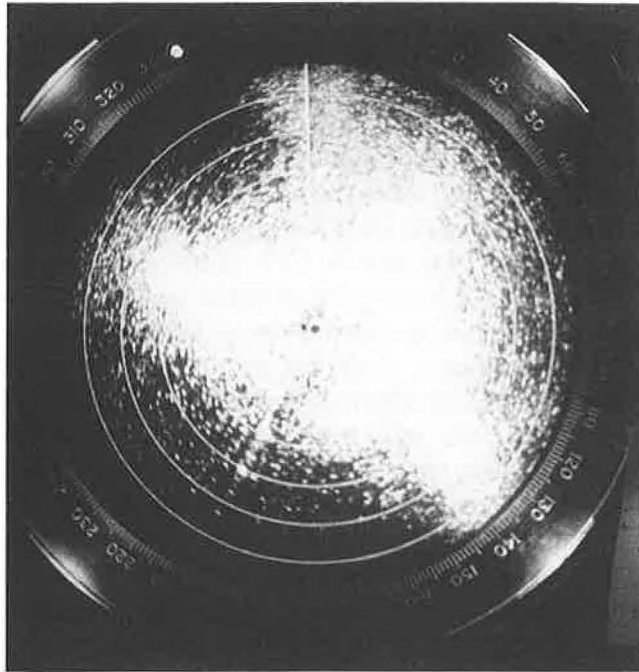
These photographs show how insect echoes can appear on a conventional radar 'plan position indicator' (PPI) display. In all the photographs, the direction of north is indicated by the vertical line.

(a) The insects shown are uniformly distributed and as their aerial density is relatively low ($4-5/10^7 \text{ m}^3$), they appear as individual dots. A large echo from a piece of aluminium foil carried by a freely floating toy balloon filled with helium appears in the northeast quadrant, and its position on sequential frames of the film record shows the wind velocity at the height of the balloon. The rings on the screen represent range intervals of 0.25 nautical miles (463 m).

(b) Here, the majority of the insects are concentrated into horizontal layers and the rotating, elevated radar beam intercepts these layers in a series of circles. However, because the airborne insects have a degree of common orientation along the $110-290^\circ$ axis, those in the north-northeast and south-southwest quadrants are seen predominantly from the side where they present relatively large radar cross-sections. This effectively increases the volume sensed by the radar in these directions and more insects are consequently detected in these two quadrants. The insect layers thus appear as crescents rather than circles.

The observation was made at Kara in the Middle Niger flood plains of Mali on 2 November 1974 at 22.54 h. The radar beam elevation was 20° . The range from the centre to the edge of the screen represents 1.5 nautical miles (2778 m).

(c)



(d)

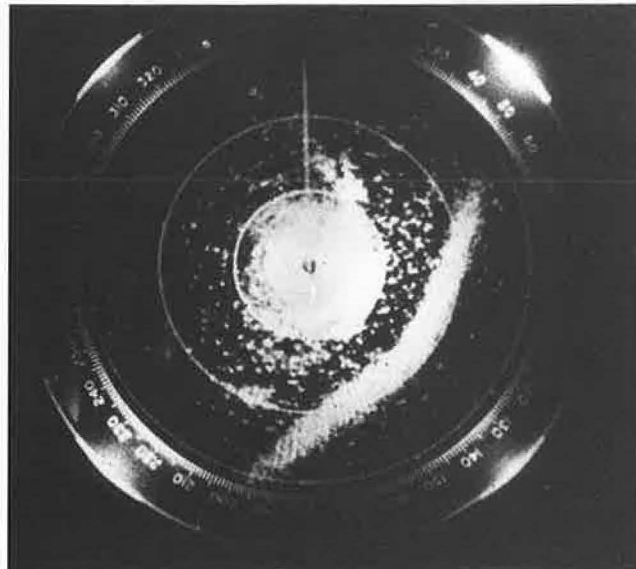


Figure 5 (cont.)

- (c) This is an example of the dramatic concentrating effect which can be produced by wind convergence on insect aerial density. The photograph shows the radar PPI at 19.32 h on 20 October 1978 at Tin Aouker in the Tilemsi Valley in Mali (radar beam elevation = 9° ; range from the centre to the edge of the screen equivalent to 2778 m). Linear zones of horizontal convergence, probably due to outflows from rainstorms, have propagated towards the radar from the east and from the north-northwest. Within the zones, insect aerial density has increased by more than three orders of magnitude. The two line-concentrations are in the process of merging and the combined concentration was seen to move away towards the southwest.
- (d) Linear concentrations of insects detected by radar are not always caused by wind convergence. This photograph of the PPI display at 22.02 h on 14 November 1974 at Kara in Mali shows a dense cloud of insects maintaining themselves above the River Diaka, a distributary of the Niger (radar beam elevation = 6° ; range-rings 463 m apart). These concentrations were detected on many evenings and when very dense, as here, they were mainly attributable to mating swarms of mayflies (Ephemeroptera) (Reynolds and Riley, 1979). The base of the cloud was usually about 30–45 m above the river and the top extended to 90–200 m. Individual insects tended to drift in an approximately downwind direction but consistent with them staying above the river.

Provided that flying insects are separated by distances of 30 m or more, they register as discrete dots on the display of a typical entomological radar operating on its shortest range setting (usually 1.5 or 0.5 nautical miles across the screen). 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 seconds, which provide a measure of its speed and direction of displacement. At low angles of elevation ($< 15^\circ$), speed and direction can be obtained by direct scaling from the screen, but at higher angles, it is necessary to correct for the distortion produced by plotting signals from the elevated beam onto 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, it is usually possible to adjust the beam elevation by trial and error until the echo from the foil is acquired on the radar screen (Figure 5a). (Acquisition is easier if the elevation of the balloon is monitored initially using an optical theodolite, and at night this requires a small lantern to be attached to the balloon.) The balloon's subsequent trajectory on the screen then describes the horizontal velocity of the wind, and the air speed and heading of individual insects flying at the same height as the balloon can be calculated by vector subtraction of this velocity from that of the insects.

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

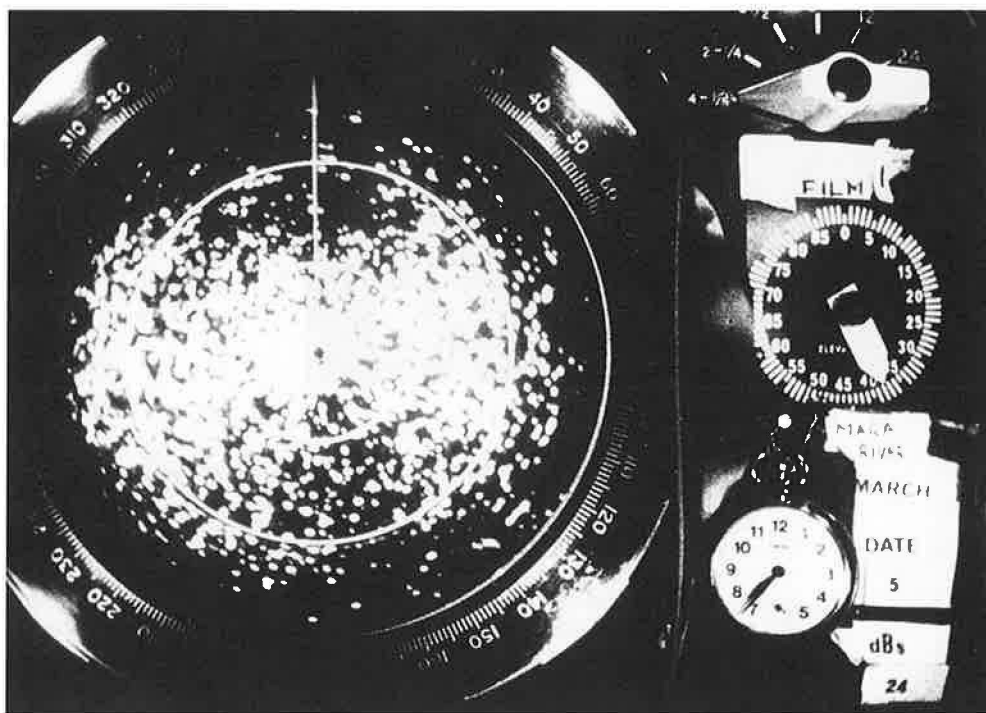


Figure 6 Photograph of a radar PPI screen showing insects with common orientation. This photograph shows another example of the kind of radar display produced by insects flying with a degree of common orientation. In this case their vertical distribution is not stratified and so the echoes form a 'butterfly wing' pattern rather than a crescent. The mean axis of **alignment** of the overflying insects was $350\text{--}170^\circ$, and examination of the time-lapse film showed displacement was towards the northwest at higher altitudes. The observation was made at Mara River in Kenya at 19.37 h on 5 March 1982 (radar beam elevation $\sim 37^\circ$; range-rings are 463 m apart.) The insect echoes were mainly attributable to *S. exempta* moths as large numbers of them were emerging in the vicinity following previous larval infestations.

their echoes merge and can no longer be individually counted; this too, requires information on insect RCS and on radar performance (Drake, 1981b). The importance of information about insect RCS was graphically illustrated during the very 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 (Figure 6). 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 appear 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 led to the discovery of collective orientation in migrating insects.

Further details of quantitative observation and analysis procedures for use with azimuthally-scanning entomological radars can be found in Drake (1981a).

Range-height indicator (RHI) 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 therefore built a 'nodding' antenna which formed a beam which was fan-shaped in the horizontal plane, and which oscillated up and down (Figure 7) to generate a conventional Range Height Indicator (RHI) scan. This system produced dramatic records of ascending layers of insects in Mali in 1978 (Figure 8). We later produced a more unconventional 'toppling' antenna system which provided RHI coverage over 180° in the vertical plane (Figure 9), and used this to record the upward motion of armyworm moths leaving emergence sites in Kenya (Riley, Reynolds and Farmery, 1983). Other examples of insect layers on X-band radar RHI 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} cm² (Riley, 1985), and cannot be individually detected at useful ranges with standard entomological radars. However, in this 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 effective size 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, 1989c, 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 *et al.*, 1990, 1991, 1994) (see also Section 4.4). The maximum range for detection of individual *N. lugens* was in excess of 1 km. This high-frequency Q-band entomological radar is the only one of its type, and has given 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 X-band radars.



Figure 7 Photograph of a Range Height Indicator (RHI) radar

This RHI radar was deployed at Kara in Mali in November 1974. The 'orange peel' antenna produces a fan beam of width 3.9° in the horizontal plane, and 1.5° in the vertical plane, which oscillates or 'nods' at one cycle every 3 seconds over a range of 60° in the vertical. The antenna can be turned to any desired azimuth angle. This arrangement produces a picture of the vertical distribution of insect echoes (see Figure 8) and the climbing or descending trajectories of individuals.

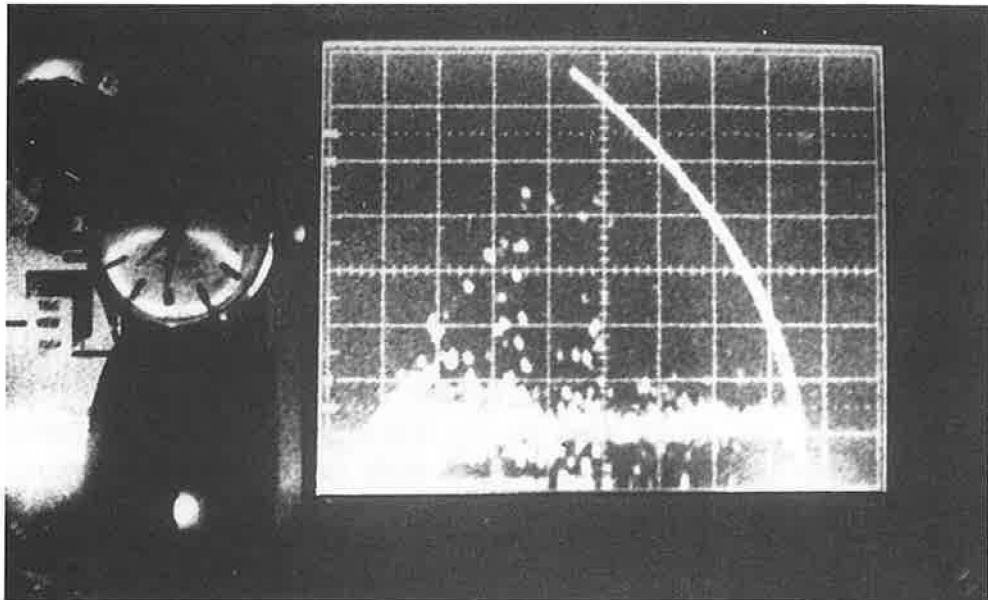


Figure 8 Photograph of the display of the RHI radar
 The display used with the 'nodding' RHI radar illustrated in Figure 7. The squares on the oscilloscope screen represent intervals of 100 m. The display gives a graphic picture of an insect layer at an altitude of about 120 m.

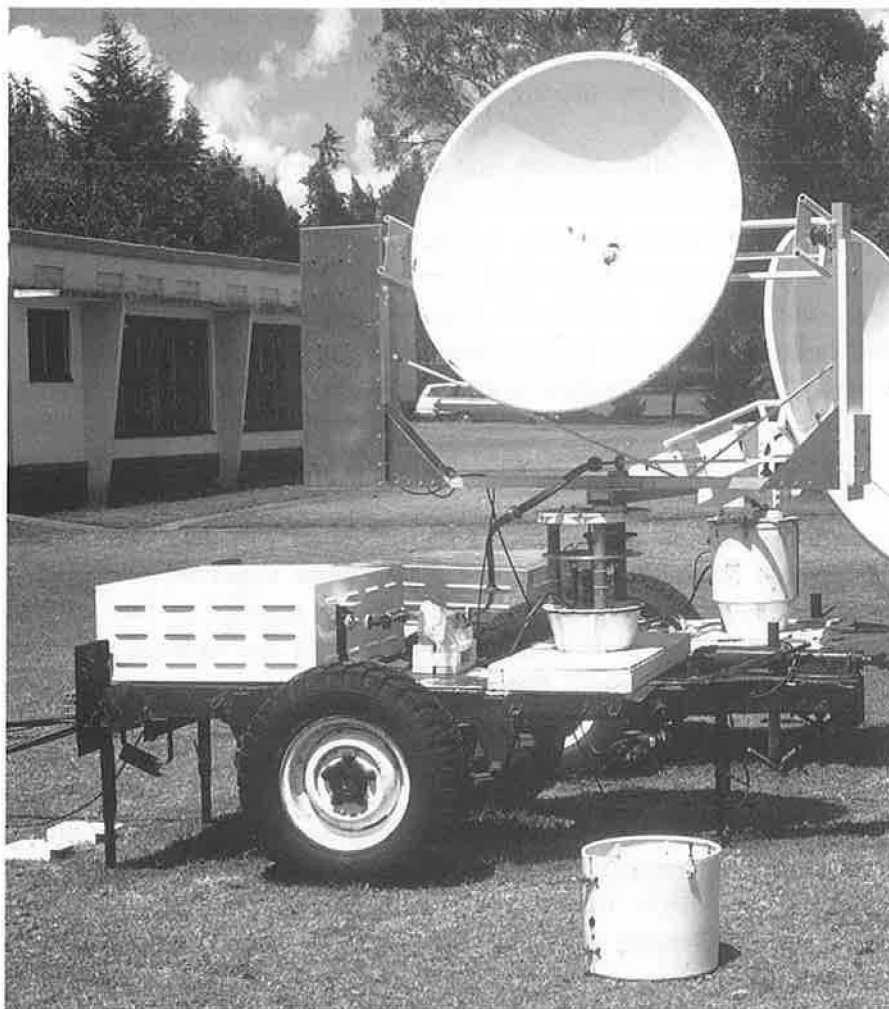


Figure 9 Photograph of a 'toppling' RHI radar being prepared for observations of army-worm moths in Kenya
 This 'toppling' RHI radar (seen here with a conventional azimuthally-scanning radar in the background) uses a parabolic dish rotating continuously about a horizontal axis. The 1.8° wide 'pencil' beam scans through 180° in elevation, so this radar provides three times the coverage of the 'nodding' configuration.

Tracking radars

Tracking radars were developed to follow the motion of one selected airborne target at a time. The original trackers scanned (or nutated) their beams by a fraction of a beamwidth about the antenna boresight, and the variation in signal amplitude provided information used to keep the antenna pointed at the target. Powerful 10.7 cm tracking radars were used to follow insects thrown from aircraft (Glover *et al.*, 1966) in order to prove that individual insects could produce misleading radar echoes or 'angels', but entomological applications of the tracking technique have been limited to observations made by R.P. Larkin (Hendrie *et al.*, 1985; Larkin, 1991), and recent work by the USDA group at College Station (P.G. Schleider, personal communication). Both radars worked at a wavelength of 3.2 cm.

Vertical-looking radar

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

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 and 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 and Richter, 1971).

The radar was deployed in Mali in 1975 and 1978 (Figure 10), and generated signals of the type expected (Figure 11). Analysis of these signals yielded novel measurements of insect heading distributions (Riley and Reynolds, 1979; 1983), 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



Figure 10 Photograph of the original NRI vertical-looking radar (VLR) deployed in Mali in October–November 1975

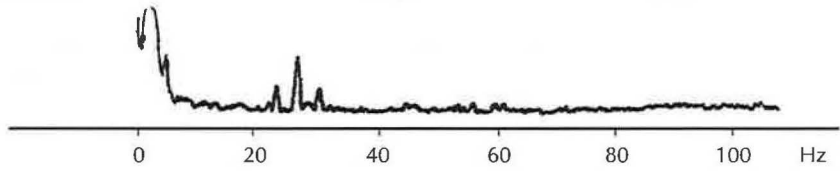
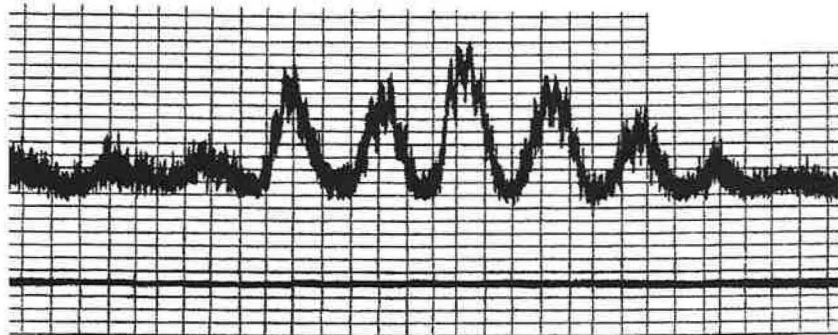
The VLR was set up on top of a building at the OICMA base at Kara in the Middle Niger flood plains. A great practical advantage of VLR is that it can be set up on any flat surface and does not require careful siting in the way that scanning radars do.

ability to resolve fine-scale details of heading distributions (Figure 12), (Riley and Reynolds, 1986). 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.

Some years after rotating polarization VLR was first used, Schaefer introduced an important modification to the VLR concept by adapting the nutating principle used in tracking radars. Bent (1984) later developed Schaefer's idea, and showed that, in principle, this 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. The idea had the great practical convenience that the required nutation could be produced in a conventional VLR by simply offsetting the rotating antenna feed by a small amount. Unfortunately, although the signal analysis procedure developed by Bent worked well 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 analysis (Figure 13), and eventually succeeded in producing a radar system control and analysis algorithm which yielded the target alignment, speed and direction, and three RCS parameters related to insect body size and shape (Smith, Riley and Gregory, 1993; Riley and Reynolds, 1993; Riley, Smith and Gregory, 1993; Riley, 1993a). 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 (see Section 4.9), and we have also operated this radar for extended periods in the UK, including a three-month period of continuous operation during July–September 1995.

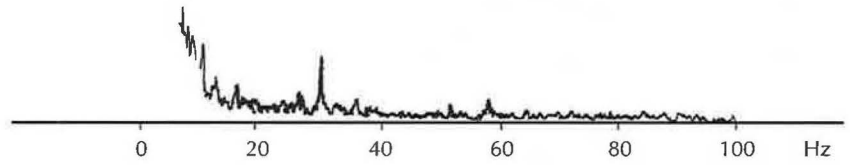
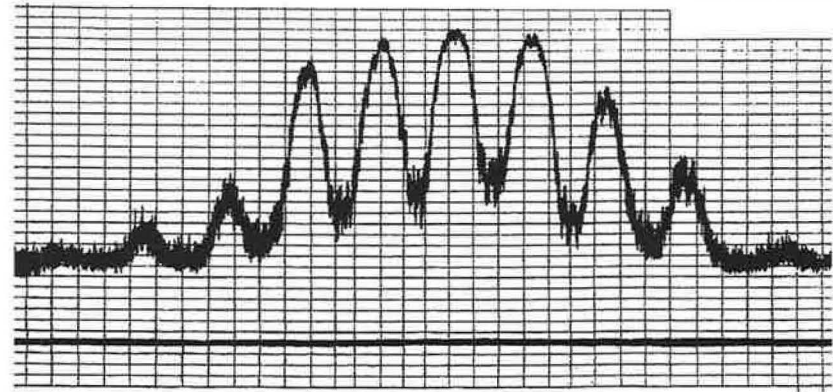
(a)

Mali, 22-Oct-78, 01:03, Gate 4



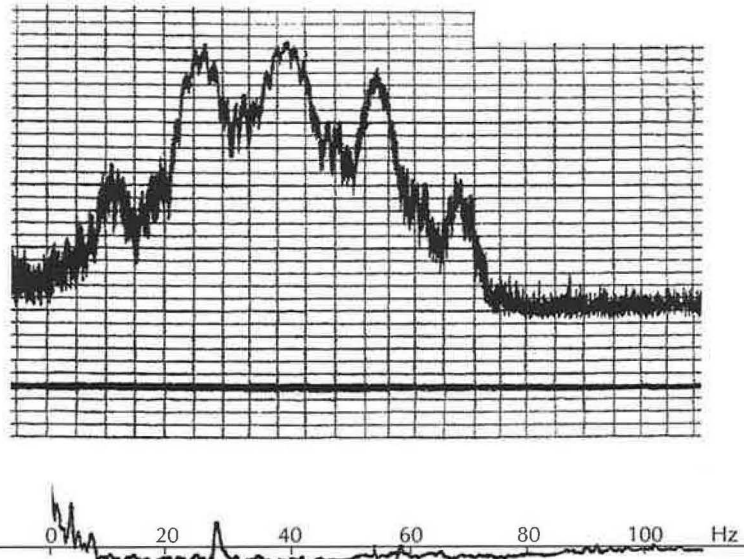
(b)

Mali, 22-Oct-78, 01:05, Gate 4



(c)

Mali, 22-Oct-78, 01:07, Gate 3



(d)

Mali, 21-Oct-78, 22:10, Gate 1

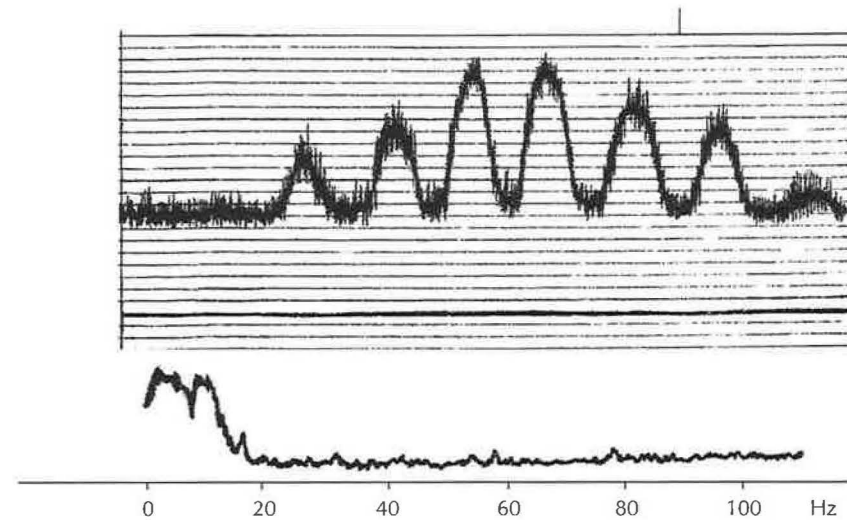


Figure 11

Examples of signals obtained from the vertical-looking radar (VLR) at Daoga, Mali in October 1978

The upper part of each diagram shows the signals received by the VLR as insects fly overhead; vertical deflection is proportional to received power and time is on the horizontal axis (each division represents 0.1 second). The lower part of each diagram shows the result of passing this signal through a spectrum analyser. The distinct, narrow peaks in the spectrum (between 20 and 40 Hz) show the insect **wing-beat frequency**. The smaller peaks flanking the wing-beat frequency in Figure 11a are side-bands thought to be caused by the abdominal respiratory action (Schaefer, 1976). The signals (a-c) show the depth of modulation varies considerably for different targets with very similar wing-beat frequencies. This variation is caused by differences in the shape and size of the insects producing the signals. In signal (d) there is no evidence of a wing-beat frequency peak, and this strongly suggests that the insect from which the signal came was gliding rather than flapping its wings.

The overall envelope of each signal is caused by translation of an insect through the (Gaussian) radar beam, and the deep modulation at 3 Hz results from the rotation of the electric vector in the radiated transmissions; it occurs at twice the frequency of rotation of the antenna feed. Measurement of the position of these peaks in the rotation cycle yields the azimuthal **alignment** of the body axes of the overflying insects (Riley and Reynolds, 1979).

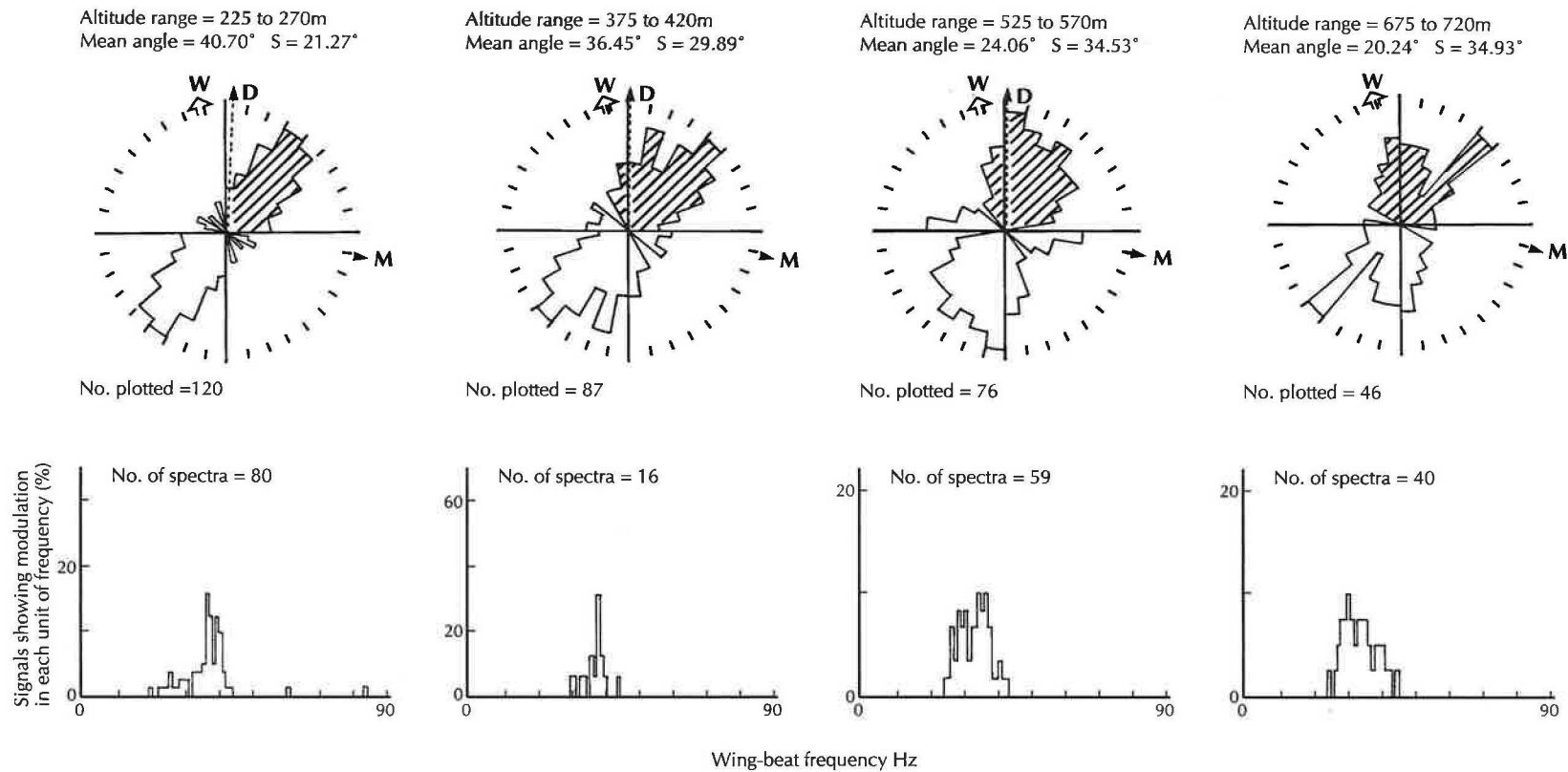


Figure 12

An example of vertical-looking radar (VLR) measurements of the alignment distribution of migrating insects (probably grasshoppers) at Daoga, Mali

As VLR permits the measurement of the body alignment of many individual insects, it is possible to build up a detailed picture of the alignment distribution of an overflying population. These four circular histograms show how insects flying at 225–270 m above ground were aligned about 41° , while those at 675–720 m were mainly aligned towards the north. At intermediate altitudes, these distributions overlap. The overlap is reflected in the bimodality of the wing-beat frequency distribution, and the data strongly suggest that different species in the same aerial environment had different mean headings (Riley and Reynolds, 1986; Riley, 1989b). (*D* = direction of displacement; *W* = direction towards which wind was blowing; *M* = moon's azimuth. *Shaded* section indicates deduced heading distribution.)

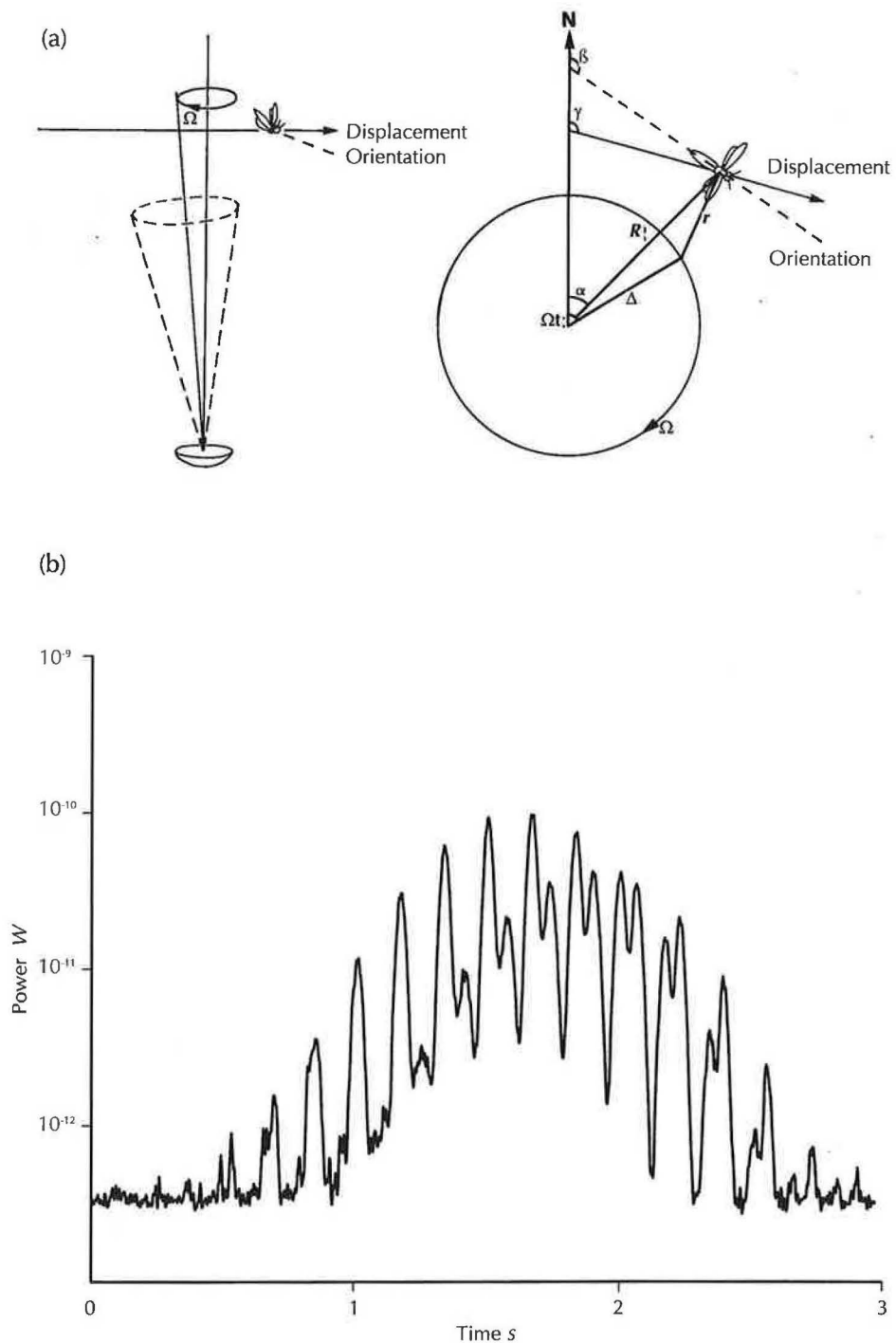


Figure 13

The nutating beam version of the vertical-looking radar (VLR)

The diagram (a) shows how in this VLR the beam nutates by a fraction of a beam-width about a vertical axis. Nutation is produced by off-setting the antenna feed so that the beam wobbles slightly as it rotates about a vertical axis (as often seen in a spinning top). This motion combines with the polarization rotation and translation of the insect through the beam to produce the complex signal shown in (b). By far the most difficult task when implementing the nutating VLR concept was to evolve a means of extracting from this signal the insect's alignment, speed and direction, and three radar scattering terms associated with its size and shape (Smith *et al.*, 1993).



Figure 14 Photograph of the NRI insect monitoring vertical-looking radar (VLR)
A powerful feature of the NRI automated nutating VLR is its capacity to routinely monitor insect migration throughout a season. This photograph shows the antenna and transceiver of the NRI VLR deployed next to the Radar Unit laboratory at Malvern. It is equipped for long-term use and housed in a weathertight enclosure. This radar operated continuously throughout the summer of 1995.

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 computer, it makes long-term, quantitative monitoring of insect migration a practicable and cost-effective option (Figure 14).

Airborne entomological radar

Although the range of radar greatly exceeds that of all other methods of observing insects, it is still very limited when compared to the migratory flight range of many species. To overcome this limitation, Schaefer (1979) designed a downward-looking rotating polarization radar for use in an aircraft, and recent developments of this system on behalf of the USDA are described by Hobbs and Wolf (1989, 1996). Vertical profiles of insect density and average alignment can be measured by the radar over hundreds of kilometres of the aircraft's flight track (Greenbank, Schaefer and Rainey, 1980; Wolf *et al.*, 1990). The measurements revealed correspondingly important information about the dispersal which occurs during long-range migrations, and about the concentrating effect of atmospheric convergence systems. It is unfortunate that the expense of sustaining airborne radar observations has severely limited the application of this very powerful technique. No airborne studies have been carried out by the NRI Radar Unit.

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 (i.e., those concerned with feeding and reproduction) and some migration flights, take place near the ground. In the harmonic technique, the intended radar target is 'tagged' with a small electronic device which absorbs energy from the illuminating radar beam and re-transmits some of it at a harmonic of the incoming signal. The radar receiver is selectively tuned to this new signal, and can detect it even in the presence of vastly stronger 'clutter' at the fundamental frequency (Vogler, Maguire and Steinhauer, 1967; Shefer *et al.*, 1974). A great advantage of this technique for entomological purposes is that the tag needs no battery, so extreme miniaturization is feasible.

This concept was first explored 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* (Klempel, 1977; Barbie, 1978; Shiao, 1978; Boyd, 1979). Unfortunately, this initiative did not produce a working radar, and appears to have been eventually abandoned. The next application of the harmonic principle for entomological studies was by Mascanzoni and Wallin (1986). These authors used commercially available, hand-held equipment which had been developed to locate skiers buried by snow, but they made their own tags from lengths of wire and microwave diodes. The tags were glued to the elytra of several species of ground dwelling, nocturnally active carabid beetles (*Pterostichus melanarius*, *P. niger*, *Harpalus rufipes* and *Carabus granulatus*), and it was found that the beetles could be located from a range of up to 10–12 m. Because the beetles were relatively large (11–23 mm in body length), they were apparently unimpeded by the 2.5 to 5 cm wire aerial, which trailed behind them. The wavelength used by the transmitter 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 equipment was subsequently used in a number of successful studies of pedestrian movements by carabids (Wallin and Ekbohm, 1988; Wallin, 1991; Kennedy, 1994), but it is intrinsically unsuited to tracking the fast translation of insects **in flight**. This was because the very limited range of detection meant that the operator must be able to keep up with the tagged insect by walking after it, and there was no prospect of producing a conventional radar track of target motion. Roland *et al.* (1996) have recently produced a tag which is light enough to be carried by flying insects, but their system is still suitable only for locating resting or very slowly moving individuals from close range. In fact, although called harmonic **radars**, these devices are strictly speaking not radars at all, but direction finders.

The need to be able to track low-flying insects was highlighted by the work of Dr Glyn Vale on tsetse flies, and as a result of his persistent advocacy of the use of radar for this task, NRI undertook a feasibility study to determine if it would be practicable to make a true harmonic radar suitable for insect flight studies. This theoretical study indicated that a detection range of approximately 900 m should be achievable if we based the radar on one of our 3.2 cm, 25 kW transmitters, although it was not at all clear at that stage if it would be possible to produce an harmonic transponder small enough to be carried by tsetse. However, the potential of harmonic radar as a technique for studying low-level insect flight in general was so great that we decided to build a prototype radar to test the theoretical predictions. The development program was jointly supported by ODA and the EEC Regional Tsetse and Trypanosomiasis Control Programme based in Zimbabwe, and it led in 1994 to a field trial of an azimuthally-scanning harmonic radar, the

first of its kind in the world (Figure 15). In 1995, this system was successfully used to track the foraging flights of bumblebees and honey bees (Riley *et al.*, 1996; Carreck, 1996). The transponder tag used in the system weighed approximately 3 mg, and comprised a Schottky diode mounted centrally on a whisker of springy wire which was fixed vertically on the thorax of the bee



Figure 15 Photograph of the NRI harmonic radar
In this prototype harmonic radar, the functions of transmission at the fundamental frequency of 9.4 GHz, and reception at 18.8 GHz, are accomplished using two separate parabolic antennas mounted one above the other and fixed on a platform which rotates in azimuth at 20 rpm. The innovative radar was used at IACR-Rothamsted in 1995 and 1996 to record the low-altitude flight trajectories of bumble bees and honey bees (Riley *et al.*, 1996; Osborne *et al.*, 1997).

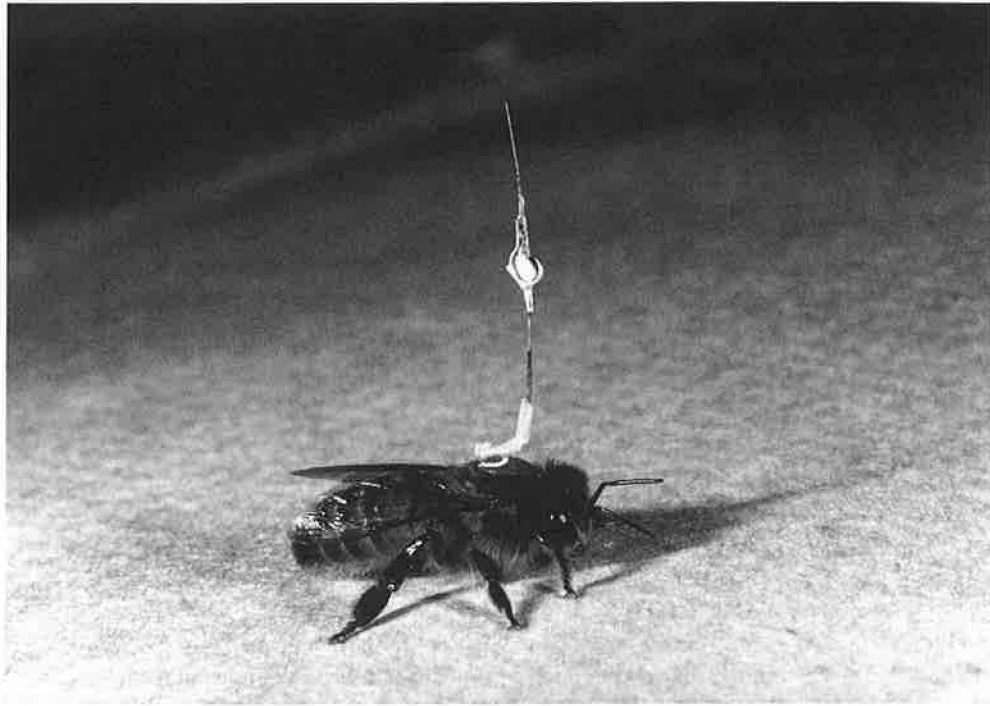


Figure 16

Photograph of a honey bee carrying a harmonic radar tag

The tag carried by the bee receives power at a frequency of 9.4 GHz and re-transmits a portion of the received power at 18.8 GHz. As the energy required to operate the device comes from the illuminating radar, no battery is needed and extreme miniaturization is possible. This tag assembly weighs about 3 mg and its dipole aerial is 16 mm long, but later versions are much lighter.

(Figure 16). It could be detected out to a range of more than 700 m, irrespective of the azimuth orientation of the bee. Further work is in hand to reduce the weight of the tag, and it is expected that the sub-milligram size required for use on tsetse will eventually be achieved. In the meantime, it has become clear that there will be many applications for the harmonic radar system in studies on bees and on a variety of other insects.

ANCILLARY TECHNIQUES

Sensing insects using reflections in the infra-red

In our radar observations of *S. exempta* migration (Section 4.2), we wished to be able to monitor moth flight activity from ground level up to the altitude at which they migrated. Our scanning radar provided coverage at high altitude, but returns from topographic features (clutter) usually meant that heights under 20–30 m were below radar cover. To overcome this constraint, we worked with M.J. Farmery, then a Ph.D. student at the University of York, to develop an optical system which could monitor the passage of low-flying insects, and could also record their wing-beat frequency (Farmery, 1981). The system used an infra-red illuminator so that it would not perturb the insects' behaviour, and the geometry of the components ensured that the field of view of the photomultiplier sensor intersected the illuminator beam at a selected height above ground level. Any insects passing through this intercept volume could be detected, and their wing-beat frequency recorded. The system provided convincing evidence that most of the *S. exempta* moths in low altitude flight subsequently climbed into the airspace monitored by the radar

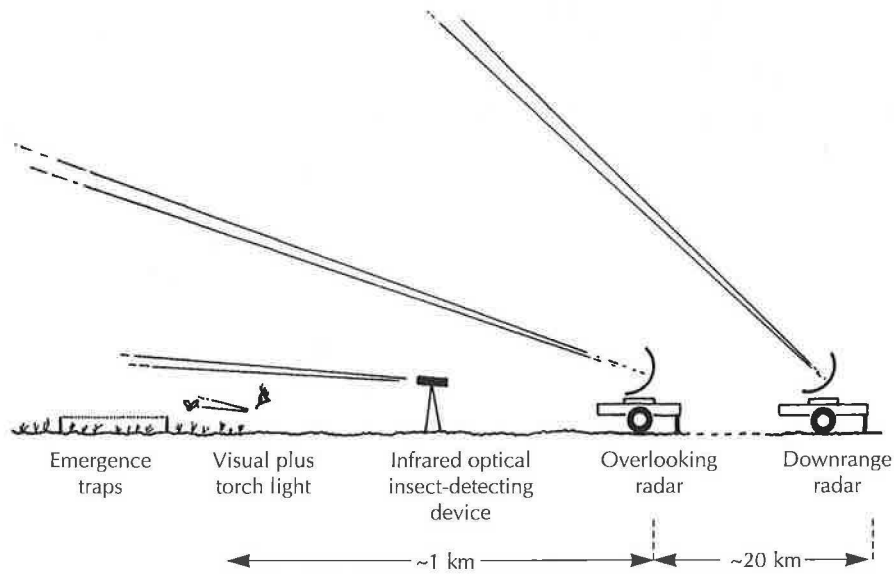


Figure 17 The use of radar and infrared techniques in armyworm migration studies
 This diagram shows how trapping and visual observations at ground level were combined with data from an infrared insect detecting device (Farmery, 1981) and an entomological scanning radar to monitor armyworm moths from their emergence from the soil up to their migration at high altitude (Riley *et al.*, 1981, 1983). A second scanning radar was used to monitor migratory flight at 13 or 19 km downwind from the emergence site.

(Figure 17), and it also showed that the wing-beat frequencies of targets detected by the radar matched those from low-flying *S. exempta* moths (Riley, Reynolds and Farmery, 1981, 1983; Rose *et al.*, 1985). A cautionary result from this work was the discovery that wing-beat frequency of *S. exempta* moths was quite strongly affected by air temperature (Farmery, 1982).

When we discovered in our studies of *Helicoverpa armigera*, that the vast majority of recently emerged moths did not ascend to altitudes covered by the radar (Section 4.3), we again used the Farmery device, but this time supplemented it with a video system, which also worked in the near infra-red. We devised this system so that we could record in three dimensions the low-altitude flight tracks of moths above the crop from which they had emerged (Riley, Smith and Bettany, 1990; Riley, 1993b). The video worked well and produced many tracks which confirmed that the moths were dispersing in low-altitude flight (Riley *et al.*, 1992), but it suffered from the limitation that, like the Farmery device, it became ineffective at dawn and dusk when increased luminance of the sky greatly lowered its sensitivity to insect targets.

Schaefer and Bent (1984) overcome this limitation by using a very bright xenon flash lamp working in the near infra-red, and a video camera equipped with a gated image intensifier which provided high-contrast images of flying insects even in daylight. This sophisticated device has been used for the calibration of light-traps and suction traps in the UK (Schaefer and Bent, 1984; Schaefer, Bent and Allsop, 1985), but it has not been used in studies in developing countries.

THE LOGISTICS OF RADAR ENTOMOLOGY STUDIES IN DEVELOPING COUNTRIES

Unlike radar entomology groups in the USA and Australia, which have the advantage of being able to drive to their field sites from their home bases, the NRI Radar Unit has had to contend since its inception with the problems of operating in remote and sometimes inaccessible areas of the world (Figure 18). This meant that we had to regularly handle the logistics of packing and shipping the vehicles and equipment, and to resolve the non-trivial problems of obtaining permission to operate equipment which was often regarded with suspicion by overseas authorities. There was also a need to be entirely self-reliant in repair facilities and spare parts for the radar and ancillary equipment. It is a matter of some satisfaction that in over twenty years of operations overseas, often with prototype equipment and in harsh environments, we have never had to cancel or terminate an observational programme as a result of a technical failure.



Figure 18 One of the hazards of operating the radar in remote areas
The Radar Unit's Bedford truck being unloaded from a barge at Kara in the Middle Niger flood plains in Mali.

Examples of Radar Entomology Studies in Developing Countries

4.1 *Oedaleus senegalensis* and other Sahelian Grasshoppers

The pest status of *Oedaleus senegalensis* and other grasshoppers in the West African Sahel

The Senegalese Grasshopper, *Oedaleus senegalensis*, is a major pest of millet and other subsistence crops in the Sahelian zone of West Africa, and in some years crop losses can be very severe and the costs of emergency control campaigns high (Cheke, Fishpool and Forrest, 1980; Cheke, 1990; Bernadi, 1986, Coop *et al.*, 1991). *Diabolo-catantops axillaris*, although less serious than *O. senegalensis*, is occasionally of substantial importance as a pest of millet, sorghum and other crops in the Sahel (Centre for Overseas Pest Research, 1982). Of the other grasshopper species commonly encountered during our work, *Aiolopus simulatrix* is a serious pest of grain crops in Sudan, but is of less importance in West Africa, while *Acrotylus* spp. and *Pyrgomorpha* spp. are generally of minor importance in Africa (Centre for Overseas Pest Research, 1982). Serious damage by Sahelian grasshoppers is sporadic, but when it occurs, losses can be considerable: Jago, Kremer and West (1993), from their experience in Mali, estimated that in one in five years, crop loss could be as high as 70–90%.

Uncertainties in knowledge about *O. senegalensis* migration

Prior to the radar studies, there had been many casual observations of *O. senegalensis* and of other Sahelian grasshoppers appearing unexpectedly at artificial lights, and of sudden changes in their ground populations (see references in Riley and Reynolds, 1983). These observations suggested that the species undertook migratory flights at night, but there was little definite information, and many questions remained to be resolved. For example:

- were nocturnal movements a regular occurrence, or did they take place only at high population densities or when the grasshoppers' habitat deteriorated ?
- at what age or physiological stage did migration occur?
- did the emigrating grasshoppers climb to altitudes **above** their 'flight boundary layer' (i.e., the atmospheric layer near the ground where the wind speed is lower than the insect's flight speed) where they would necessarily be displaced downwind?
- did the grasshoppers migrate irrespective of wind direction ?
- how far did the grasshoppers move?

More generally, the relationship between hypothesized seasonal movements of the adults and observed infestations was far from clear. *O. senegalensis*, for example, was known to be able to survive the dry season *in situ* as diapausing eggs, and so sudden infestations in areas apparently free from the species might have resulted from the synchronized hatching of these eggs, rather than from long-range immigration of adults into the area. Most of these uncertainties about *O. senegalensis* movement could be resolved by direct observations of its flight, and radar appeared to offer a unique means by which these could be made.

RADAR FIELD STUDIES IN MALI

In 1973 and 1974, we had undertaken radar studies of the movement of aerial insect fauna at Kara (14° 10'N, 5° 01'W) in the flood plains of the inland delta of the River Niger in Mali (Riley, 1975; Riley and Reynolds, 1979) with logistical support from the Organisation Internationale Contre le Criquet Migrateur Africaine (OICMA) and the UNDP *Locusta* Project. The intention was to focus on the movement of the African Migratory Locust, *Locusta migratoria migratorioides*, but in the event it became clear that this species formed only a small proportion of a very diverse and abundant aerial fauna in the flood plains, and resolution of its aerial movements amongst those of the many other airborne species proved impractical. Nevertheless, these studies provided graphic examples of mass nocturnal migration by grasshoppers and locusts which often concentrated in layers at altitudes of several hundred metres, moving in low-level jet streams at over 60 km per hour. This revelation was particularly dramatic because on many occasions the wind was very light at the surface, and without the radar there would have been no indication that spectacular and rapid migrations were taking place overhead. The results also indicated that grasshopper migrations occasionally covered distances of 300–400 km in a single night's flight. The study also yielded the first detailed description of high-altitude collective orientation by locusts and grasshoppers (Riley, 1975), and quantitative measurements of the phenomenon were made with a novel vertical-looking radar (Riley and Reynolds, 1979). Overall, the flood plain experiments had made it abundantly clear that radar had the capability to make quantitative observations of grasshopper and locust migration, and that if studies were made in a geographical area where the composition of the aerial fauna was much simpler, the results could probably be attributed to particular species. The studies had also served to demonstrate that the Unit could successfully overcome the considerable logistic and technical difficulties of operating an experimental radar in a hostile environment, remote from any sources of technical assistance.

With this experience in mind, we felt confident that it would prove possible to investigate the movement of *O. senegalensis* and other grasshoppers in a more typical Sahelian environment, where the aerial fauna was expected to be much simpler than in the Niger flood plain. Thus, in 1975 some exploratory observations were made near Alfandé (15° 48' N, 3° 04' W) in the seasonally dry lake beds area in the northeast of the Niger delta, and in 1978 we mounted a major field study at two sites, Tin Aouker (16° 48' N, 0° 08' E) and Daoga (15° 53' N, 0° 14' E) in the Gao region of Mali. Both studies focused primarily on *O. senegalensis*.

Take off, ascent and height of flight

The radars at all three sites showed that *O. senegalensis* and other migratory grasshoppers began nocturnal migratory flights just after dusk, with take-off starting at about 20 minutes after sunset and reaching a maximum between 15 and 30 minutes later. This emigration generally caused a spectacular increase in aerial density all around the radar site, but occasionally the take-off of particularly large numbers of grasshoppers from restricted areas appeared as discrete 'plumes' or patches on the radar display (for example, the take-off plumes of *Aiolopus simulatrix* observed at the Tin Aouker site – Figure 19). Time of take-off was almost certainly controlled by light intensity, and it appeared to be triggered when irradiance in the 300–500 nm band fell to 10^{-5} – 10^{-6} Watts/m²/nm. Mass emigration of *O. senegalensis* was detected by the radars on virtually every evening of observations, although its magnitude varied considerably from night to night, probably due to the number of flight-ready grasshoppers in local source areas. Air temperature also appeared to modulate the magnitude of take-off, with larger numbers of grasshoppers taking to the air on warmer nights. Late in the year (November), take-off was inhibited whenever air temperatures at dusk approached or fell below the threshold for flight (approximately 23–24°C). The radars showed that there was no mass take-off by grasshoppers at other times of the night, or at dawn.

After taking off, the grasshoppers appeared to climb steadily, and their ascent rates, which we estimated from their time of appearance at successively higher altitudes, were in the range of 0.4–0.5 m/s (Riley and Reynolds, 1979). Climbing was apparently sustained for 10–30 minutes as the ultimate flight altitudes usually lay in the range 250–900 m. Maximum altitude seemed to be controlled by air temperature, as it was observed to be greater at locations, and during seasons, with generally warmer temperatures. For example, insects were often detected up to 1 km above ground over the Middle Niger flood plains in November, but only up to a maximum of 750 m in the north of the delta where nights were cooler. Generally, after the end of the rainy season in the Sahelian zone of Mali, the majority of grasshopper-sized insects flew below 500–600 m. A striking feature of the insects' altitudinal distribution was that it was often highly stratified, with well-defined dense layers forming at various altitudes. The layers were typically 50–150 m deep, and occasionally there would be two or three of them one above the other (e.g. Figure 5b). Pest grasshoppers, such as *D. axillaris* and *O. senegalensis*, certainly contributed to some of these layers, but in other cases the species forming them were unknown. Sometimes, particularly in the autumn, grasshopper-like targets were seen to be largely restricted to a layer lying somewhere between 150 and 300 m above ground, and corresponding to the top of the surface temperature inversion (Figure 20). In these cases, the insects were simply flying at the level of the warmest air (possibly 5–10°C higher than at ground level), and almost certainly because the temperature at other heights would have been sub-optimal or even below their flight threshold. It seems conceivable that migration may even be prolonged in these circumstances by the disinclination of the insects to descend into the layer of colder air near the ground.

At other times however, layering was not associated with any discernible features in the vertical profiles of air temperature or humidity, and the reasons why the insects selected these particular flight altitudes remains unknown. Possible causes include zones of preferred temperature, or of maximum wind speed. In any event, the phenomenon serves to highlight the

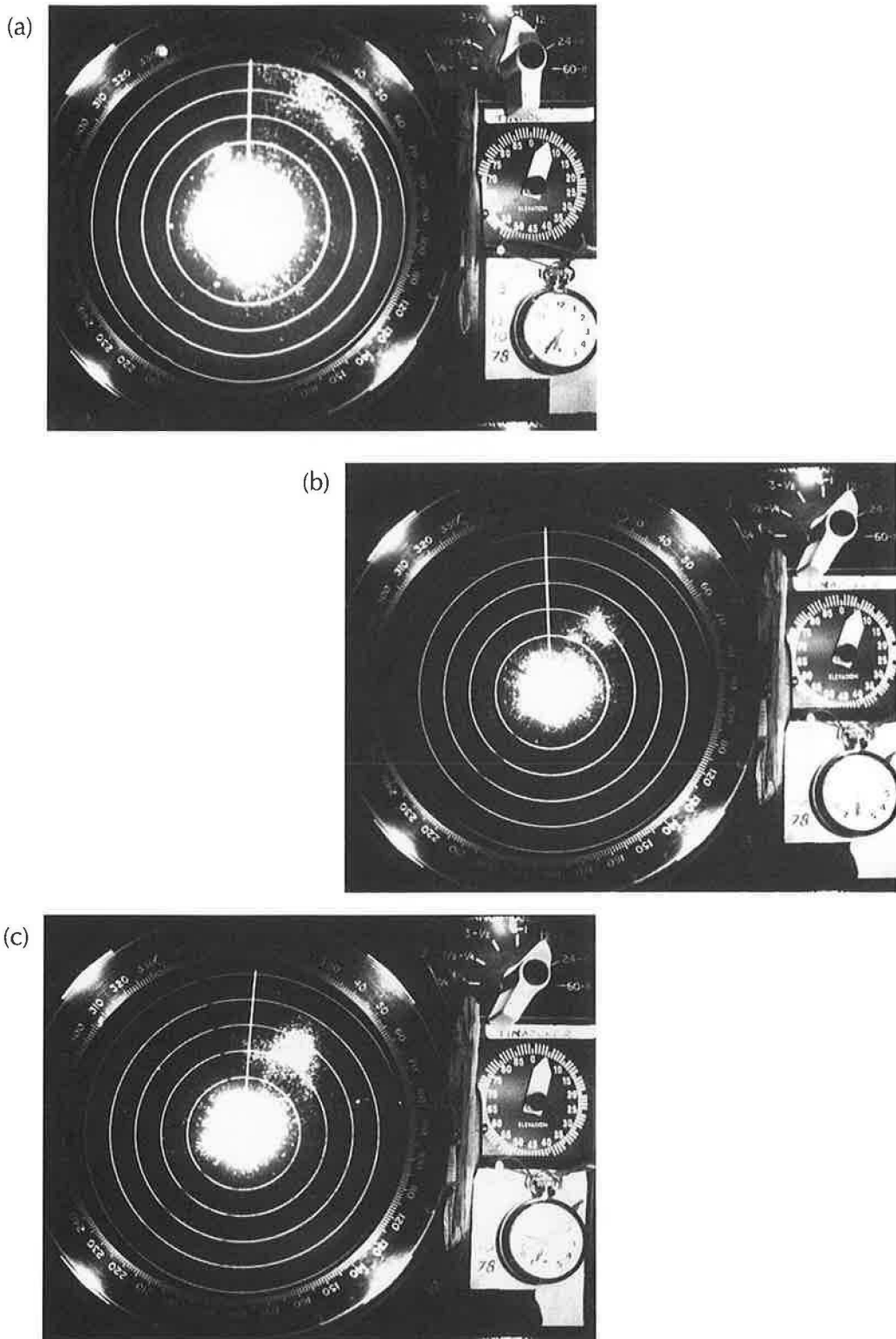


Figure 19 Photographs of the radar PPI display showing long-range detection of dense plumes of *Aiolopus simulatrix* grasshoppers emigrating from areas of clay in the Tilemsi Valley near Tin Aouker, Mali

- The heading marker (vertical line) points to the north in each case.
- (a) 11 October 1978 at 18.35 h. (Radar beam elevation = 5°; distance between range-rings = 1 nautical mile (1852 m).) Plume visible at 5 nautical miles range to the northeast of the radar site. Insects were displacing to the north-west at this time.
 - (b) 18 October 1978 at 18.14 h. (Radar beam elevation = 5°, distance between range-rings = 2 nautical miles (3704 m).) Plume visible at 6 nautical miles range to the northeast. Individual insect displacement was to the north.
 - (c) As (b) but at 18.46 h. During the intervening 32 minutes, the plume has extended to the north and is visible to about 1300 m above ground.

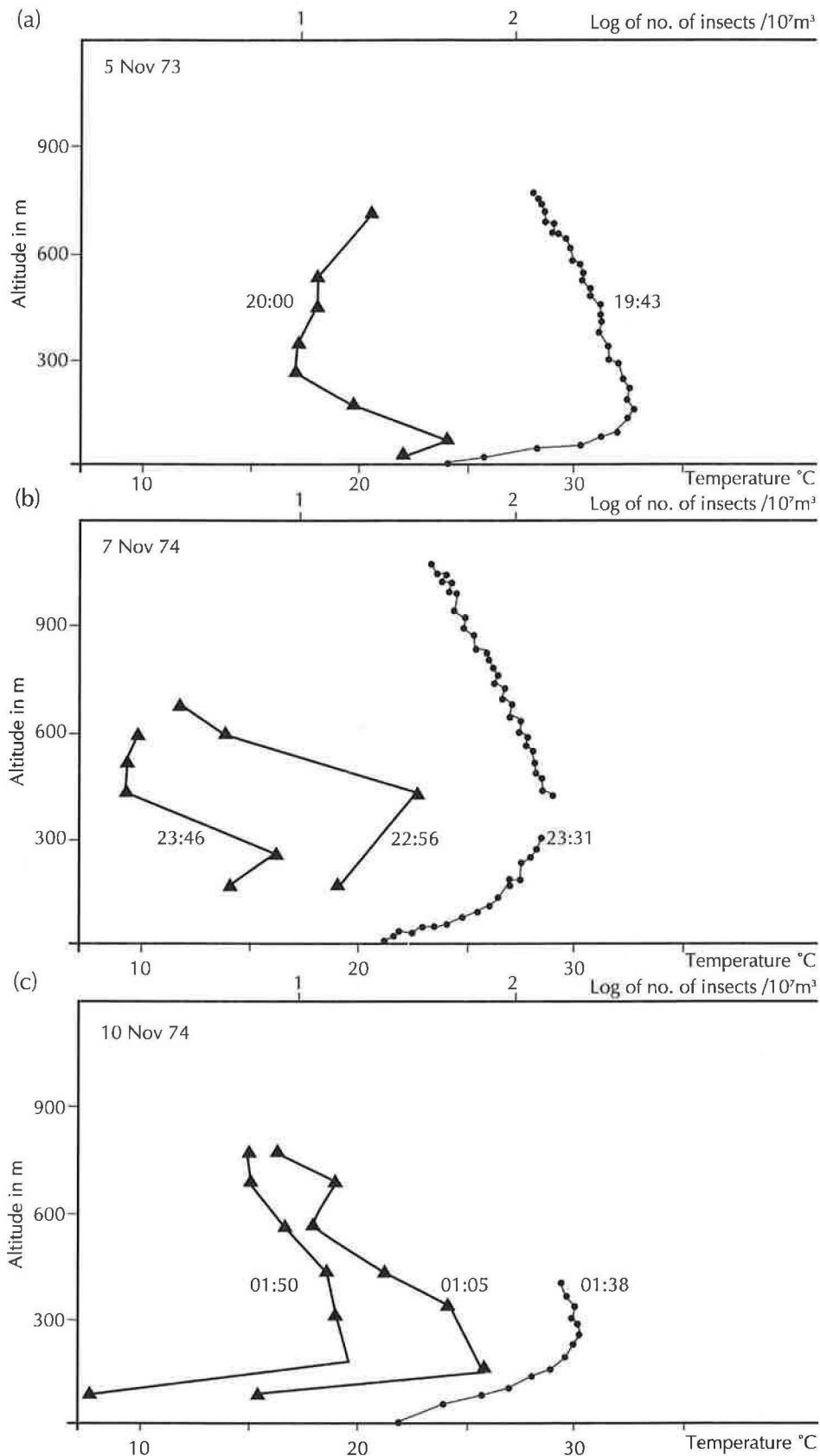


Figure 20 Examples of the vertical distribution of air temperature and insect density in the Middle Niger area of Mali
 ●—● Air temperature from radio-soundings (sonde launch times are shown on the figures); ▲—▲ Aerial density of large insects obtained from X-band radar data (the times of the density measurements are shown). The observations were made at Kara, Mali. Note that a dense layer of insects, including migratory grasshoppers, often occurred near the top of the surface temperature inversion, i.e., at the level of warmest air.

fact that migratory grasshoppers such as *O. senegalensis* actively select and maintain their flight altitudes by sustained and controlled effort, and the often-expressed notion that wind-assisted migrants are transported in a **passive** manner is misleading.

The physiological state of migrating *O. senegalensis*

Studies of ground populations by R.F. Chapman and N.D. Jago (see Riley and Reynolds, 1983) at the 1978 field sites indicated that nocturnal migration in *O. senegalensis* was most likely to occur in young individuals after the cuticle had hardened but before the females started to mature their first egg batch, i.e., between about 3 and 5 days after the final moult. Readiness to fly decreased with the onset of vitellogenesis. However, there was evidence of renewed flight activity after females had laid (or had totally resorbed their eggs) but before they started to develop the next egg batch. The studies thus indicated that, as with many other insects, the main physiological opportunity for migration occurred in the pre-reproductive period in *O. senegalensis*, although females also had a capacity to fly (perhaps over more restricted distances) to different oviposition sites between egg batches.

The magnitude of grasshopper migration

The use of radar to observe grasshoppers in flight allowed nocturnal migration rates to be quantified for the first time, and revealed the magnitude of the populations on the move. In one example, during a 2 hour period around midnight, about 1.9 million grasshoppers, including *D. axillaris* and *O. senegalensis*, crossed **each kilometre** of an imaginary line on the ground lying at right-angles to the general direction of migration. During severe outbreak years the numbers moving after the end of the rains would almost certainly be several times higher.

Duration and range of flight

Our radar technique did not allow us to measure grasshopper flight durations directly. However, likely sources for groups of insects observed overflying the radar could be found by constructing back-trajectories. If the indicated source areas seemed credible, the distance flown by the insects since the dusk take-off could be determined. We found that *O. senegalensis* overflying the radar at the Alfundé site appeared to have covered distances of **at least** 50 km per night, and night flights observed on occasion at Kara appeared to have originated over 300 km away (Figure 21).

Flight durations could also be estimated from the commonly observed rates of decline in the aerial density of populations passing overhead. It appeared that the distribution of flight periods was approximately exponential, with a mean of 2–3 hours, and with some individuals remaining airborne for up to 6 or 8 hours. On one occasion, the **mean** flight duration appeared to be about 6 hours (Riley and Reynolds, 1990). We sometimes observed dense concentrations of grasshoppers, particularly *O. senegalensis* and *D. axillaris*, still airborne at 01.00 h, but it was not clear whether they represented the residue of very much larger concentrations, or whether, on these occasions, the bulk of the population was flying for 6–7 hours. We found no evidence that mass flights by grasshoppers continued all night until dawn.

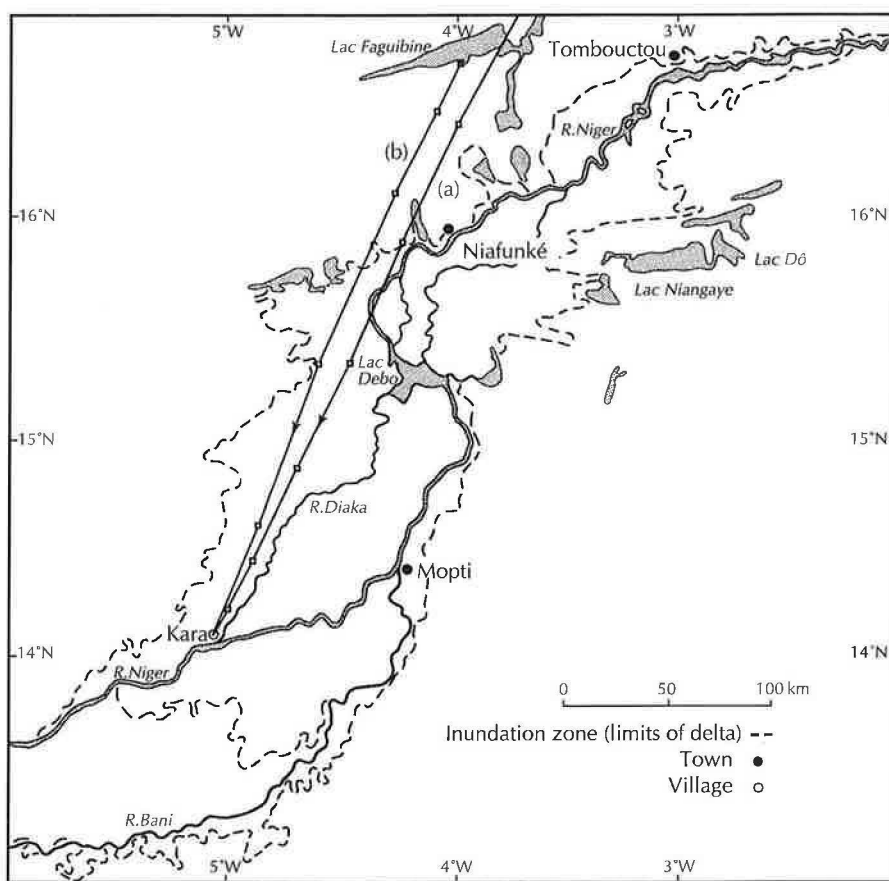


Figure 21 Back-trajectories calculated for layers of insects overflying the radar site at Kara in the Middle Niger flood plains in Mali

Trajectory (a) is for 01.50 h, 10 November 1974, and (b) is for 23.30 h, 10 November 1974. Analysis of radar signatures from insects in the layers suggested that they may well have been grasshoppers; the indicated source areas (in the vicinity of Lac Faguibine) were favourable for grasshopper development at this time.

The back-trajectory calculations were made with the following assumptions: (i) that wind velocity along the trajectory could be obtained by linear spatial and temporal interpolation from pilot-balloon soundings at Tombouctou, Mopti and Kara; (ii) that the orientations observed during the overflight had been maintained since take-off; and (iii) that the take-off period of the insects in the layers was the same as that observed locally.

(Figure from Riley and Reynolds, 1979, with permission from the Royal Society.)

With rare exceptions (e.g. Riley, 1975), the nocturnal migration of grasshoppers took place well above the insects' 'flight boundary layer' (Taylor, 1974), so their speed and direction of travel was largely determined by the wind at their flight altitude, and in this sense their migrations could be described as **windborne**. In the northeasterly 'harmattan' winds prevailing after the end of the rainy season in West Africa, wind speeds of 9–14 m/s were commonly observed at the height of airborne grasshoppers, and for 2 hour flights, these winds would have added displacement distances of about 60–100 km to the 30 km due to the grasshoppers own flight through the air (their orientation often has a large downwind component) at a speed of about 4 m/s. In 6 hour flights, the displacement due to the wind would add 200–300 km to the grasshoppers' 80–90 km.

On one occasion we obtained unequivocal evidence of fast, long-range migration, when the southward passage of a concentration of grasshoppers was recorded sequentially by the radars at Tin Aouker and Daoga (Riley and Reynolds, 1983). The radars were separated by about 100 km, and the interval between appearances of the concentration was 4 hours, indicating a displacement speed of 25 km/h.

The concentrating effect of convergent winds

Differences in the times of take-off and rates of climb between individual grasshoppers, and in their air speeds, headings and flight endurance, all cause migrating populations to become dispersed. Dispersal is accelerated if the insects climb and descend through regions of strong wind shear (where there is a large change of wind velocity with height), and so populations which may have originally been concentrated when on the ground tend to become distributed during migration over a much larger area. This dispersive tendency may, however, be reversed if the insects encounter a zone in which there is net horizontal convergence of the wind (Pedgley, 1990).

We obtained on the radar screen many graphic illustrations of the effect of convergence on the distribution of airborne grasshoppers, particularly during the rainy season (e.g. Figure 5c). These took the form of moving linear concentrations of insects, typically 1.2 to 2 km from front to back (Riley and Reynolds, 1983; 1990; Reynolds and Riley, 1988), but with very much greater lateral extents, probably more than 40–60 km (Schaefer, 1976). Increases in volume density at the leading edge of the line concentrations were typically between 10- and 100-fold, and densities in some of the concentrations could approach those found in sparse locust swarms (~ 1 per 10^3 m³) (Waloff, 1972). These line concentrations were always found to be associated with a windshift line at altitude, and in many cases they were probably caused by a type of atmospheric 'gravity current' (Simpson, 1987) arising from a rain storm, although rainfall was seldom detected within radar range. On the occasions which we examined in detail, there was a net inflow of air at the heights at which most insects were flying, so there was no doubt that the insects were being swept into the line concentration. Once inside, any resistance by the insects to being carried upwards in the updrafts at the leading edge of the gravity current would lead to their accumulation.

The orientation of migrating insects

Our radar observations at all the sites in Mali revealed that larger-sized nocturnal high-flying insects tended not to have randomly distributed headings, but often orientated about some common direction, with standard deviations of typically ± 20 to 30° (Riley, 1975; Riley and Reynolds, 1979). This result was consistent with Schaefer's (1976) report that nocturnally migrating Desert Locusts headed downwind, although in our case, the mean heading was often not directly downwind, but 20 – 40° to the left (in winds blowing towards the southwest). These findings were completely unexpected because it had been generally assumed that no cues to wind direction would be available to high-flying insects at night. The situation was further complicated when we discovered that bimodal heading distributions sometimes occurred in which two insect populations, of different but unknown species, maintained different mean headings when flying in the same aerial environment at the same time (Riley and Reynolds, 1979).

An analysis of the accumulated results from Mali (Riley and Reynolds, 1986; Riley, 1989b) showed that the airborne insects (probably mainly grasshoppers) usually had a non-random heading distribution, and that the mean direction was sometimes downwind, sometimes to the left of the downwind direction (at least in the north-easterlies), and sometimes there was a preferred **compass** direction (viz. towards 25–50°) in light winds from a variety of directions. The compass orientation to the northeast was only observed at the Kara site in the Middle Niger flood plains, and it may represent behaviour which is only adaptive within this particular environment. For example, it may provide a mechanism for the movements of *Locusta migratoria* from southern parts of the delta, against the prevailing winds, towards the northeast in the wake of the retreating floods (Farrow, 1990).

Because winds at the flight altitude of grasshoppers are usually substantially faster than the insects' airspeeds, their orientation in flight has only a secondary effect on their overall direction and range of displacement. Nevertheless, it is energetically efficient for the grasshoppers to maximize the distance flown in a given time by adding their flight speed to the wind speed. Therefore, it is not surprising that in conditions where migrating grasshoppers and other large insects are able (by whatever means) to determine the wind direction, they tend to adopt roughly downwind orientations when flying above their 'boundary layer'. What is more difficult to understand is the frequent observation that insects systematically bias their displacements to one side or another of the downwind direction. It is possible that particular species may have evolved specialized behaviour which aids migration between widely separated, favourable habitats lying in particular geographical directions. For example, *O. senegalensis* and many other species undertake southwards migrations on northeasterly winds at the end of the rainy season, and the headings to the left of downwind, observed by us, may be adaptive because they add a small southerly bias to the wind-induced displacement.

It is, however, quite conceivable that the **function** of common orientation has nothing to do with migration direction at all. For example, it may serve to reduce the dispersal of a population during migration, or it may be an energy-saving strategy, perhaps related to lift available from small-scale Kelvin-Helmholtz waves in layers of wind shear.

Whatever the merits of these hypotheses, it seems unlikely that consideration of common orientation would make much difference to forecasts of the migration paths of *O. senegalensis* on any particular occasion. This is because the errors introduced by uncertainties in wind direction are likely to be much more significant than the effects of common orientation. The phenomenon may have some practical implications, however, in that the adoption of non-random headings will reduce the dispersal of populations compared to random orientation, and thus make it more likely that grasshoppers from high density sources will invade cropping areas in numbers which are still high enough to exceed the economic threshold.

The mechanisms of common orientation

In the case of headings related to wind direction, we have emphasized that (in the absence of an accurate inertial guidance system) the **only** means by which an insect can determine wind direction directly, is by reference to the ground (Riley and Reynolds, 1986). Laboratory studies (Riley *et al.*, 1988) have shown that tethered *Locusta migratoria* flying in wind tunnels are surpassingly sensitive to the movement of dimly lit and slowly moving patterns

and the results implied that *L. migratoria* flying at an altitude of 2000 m and in bright moonlight could visually perceive the drift caused by a cross-wind of 2.4 m/s. This level of sensitivity does not, however, seem to be adequate to explain the perception of wind drift on moonless nights. Another putative directional cue, which may be indirectly related to wind direction, is short-term accelerative motion caused by gusting. Gusting at altitude can be caused by the development of Kelvin-Helmholtz waves in areas of strong vertical shear, but there is as yet no convincing evidence that this is **anisotropic** on scales likely to be perceived by insects, and for the time being it is not clear whether insects use a visual or gust-related mechanism to maintain their wind-related orientation. Similarly, while compass directions might be determined by time-compensated celestial cues or by perception of the earth's magnetic field, no definitive evidence for either was obtained during our studies (Riley and Reynolds, 1986; Riley, 1989b). Thus the mechanism (or hierarchy of mechanisms) by which migratory grasshoppers and other large insects orientate at altitude remains unknown.

The consequences of windborne migration

Our studies established beyond doubt that *O. senegalensis* and other Sahelian grasshoppers routinely embark on nocturnal, high altitude, windborne migration, and that these massive movements must play a critical role in the population dynamics of the species. A consequence of the windborne nature of the grasshopper migrations is that their direction of movement in West Africa is dominated by the wind systems associated with the Inter-Tropical Convergence Zone (ITCZ). Seasonal windborne migrations are generally adaptive because as the ITCZ moves northwards, the prevailing southwest monsoon winds carry grasshoppers to progressively higher latitudes where rain is likely to fall, and where they can take advantage of renewed vegetation growth. Correspondingly, as the ITCZ retreats southwards and northeast winds are re-established, the grasshoppers tend to be transported southwards as their northern breeding sites dry out. In *O. senegalensis*, it is generally the first two generations of adults which move northwards, and a third generation which is carried southwards, but other grasshopper species have different strategies. Superimposed on the seasonal movements of the ITCZ are smaller oscillations over periods of a few days. Thus, not all grasshopper migrations are towards the south or southwest in autumn, as was shown by a case-study in which *D. axillaris* and *O. senegalensis* moved **towards** the northeast and east in October, because the insects happened to be to the south of the ITCZ. The simple pattern of northeasterly harmattan winds to the north of the ITCZ, and southwesterly monsoon winds to the south is frequently disrupted in the rainy season by synoptic and meso-scale disturbances, e.g. squall lines and convective rainstorms. Under these conditions wind fields can be very complex and grasshopper movements may be in a variety of directions.

Nevertheless, as we have observed, conditions early in the harmattan season are often very suitable for the southward 'return' migration with rapid long-distance movements on the strong steady northeasterlies. In addition, the altitude at which nocturnal air temperatures are often most suited to grasshopper flight – the top of the night-time temperature inversion – is usually also where the wind is at maximum speed (up to 20 m/s). Another consequence of windborne migration is that the grasshoppers are subject to aerial concentration in zones of wind convergence on various spatial scales, and the radar studies have showed that aerial densities of flying grasshoppers

may be raised by one or even two orders of magnitude by intense mesoscale convergences due to phenomena such as storm outflows. If the grasshoppers land whilst in or soon after leaving a convergence, these very dense aerial concentrations will produce high ground densities and hence lead to pest outbreaks. Indeed, Joyce (in discussion after Riley and Reynolds, 1990) states that *A. simulatrix* in Sudan is usually a problem **only** when grasshoppers have been concentrated by convergence zones.

The implications for forecasting and control

Information on the long-range, windborne migrations of *O. senegalensis*, obtained by radar-based methods, now forms an essential component of conceptual models (Steedman, 1990; Jago, 1993; Pedgley, Reynolds and Tatchell, 1995) and computer simulation models (Launois, 1979; Holt and Colvin, 1997) of the biology of this species in West Africa. Mass migrations of the type revealed by radar have direct control implications. For example, in years when breeding has been successful in the northern part of the species' range, a rapid southward retreat of the ITCZ in autumn, can be expected to bring vast populations of *O. senegalensis* and other species in its wake. These influxes are difficult to combat because the migrant grasshoppers invade crops suddenly and in numbers sufficient to do serious damage to long-cycle millet and sorghum. Furthermore, windborne movement of *O. senegalensis* at the end of the season will largely determine the specific places where the diapausing eggs are laid. Hoppers hatching from these eggs at the onset of the following rainy season may destroy young millet plants, necessitating a complete re-sowing (Jago, Kremer and West, 1993). Locating dense egg-fields might provide a means of identifying areas liable to early-season attack (N.D. Jago, personal communication), and would give some warning to farmers of impending pest problems.

Although much progress has been made in understanding the biology of pest grasshoppers in the Sahel, it is evident that more work is required to develop models to improve forecasting of outbreaks and to set up an effective framework for farmer-orientated control strategies. Building on conceptual models derived from the radar and other studies in the Sahel, work is now underway to develop a forecasting model for *O. senegalensis* which will incorporate information on the effects of migration and other ecological factors in relation to environmental variables. The new model will include zones connected by migration, based on the timing and movements of the ITCZ, which will be inferred from satellite data. The objective will be to develop a tool for predicting the risk of widespread and major outbreaks of *O. senegalensis* up to one year in advance.

4.2 The African Armyworm (*Spodoptera exempta*)

Outbreaks of caterpillars of the African Armyworm Moth, *Spodoptera exempta*, cause severe damage to cereal crops and pasture, particularly in eastern, central and southern Africa, and in plague years their attacks can be devastating. Because of this, ODA and the EC have supported the regional armyworm forecasting and control organizations over many years, and they have also funded programs of research on the biology of *S. exempta*. The radar studies reported here are one element of a major and multi-disciplinary study of the ecology of the species in East Africa (Rose, Dewhurst and Page, 1995).

Prior to these studies, there was circumstantial evidence for the migration of *S. exempta* moths (e.g. Brown and Swaine, 1966; Brown, Betts and Rainey, 1969), but the significance of the supposed migration was still a matter for debate. The main question was whether outbreaks of caterpillars resulted from sudden, mass immigrations of moths from distant sources, or from an enormous increase in initially small local populations. Brown (1962) presented the arguments for and against these hypotheses, but the question was subsequently complicated when Khasimuddin (1977a) reported the occurrence of a greatly extended duration (diapause) of the pupal stage of *S. exempta*. While this phenomenon was not confirmed by subsequent investigations (Rose, Dewhurst and Page, 1995), it did, at the time, raise the possibility that diapause might allow intrinsically gregarious populations to persist for several generations on the same site, and that outbreaks could result from breeding by these 'resident' populations (Khasimuddin, 1977b). The rationale underlying armyworm forecasting and strategic control hinges critically on the existence of significant long-range movement (Rose, Dewhurst and Page, 1997), and radar offered the prospect of resolving the 'migration question' in a definitive manner.

As a result, radar observations of *S. exempta* moths were carried out in Kenya during the months March to May in three years – 1979, 1980 and 1982 (Table 1) (Riley, Reynolds and Farmery, 1981, 1983; Rose *et al.*, 1985). We worked in close co-operation with members of the DLCO-EA / NRI / EC Armyworm project, in particular with Dr D.J.W. Rose, Mr W.W. Page and Mr C.F. Dewhurst, who supplied most of the (non-radar) entomological data, and provided the biological context in which the radar observations could be interpreted.

Table 1 Locations of radar sites used for observations of African Armyworm (*Spodoptera exempta*) moths in Kenya

| Year | Period of radar observations | Name of main radar site | Location of main radar | Location of downwind radar |
|------|------------------------------|--|-------------------------|--|
| 1979 | 29 March–9 April | Mt Margaret (Maau Mahiu), Rift Valley | 0°59'23"S 36°34' 0"E | 19 km WSW (256°) from main radar |
| 1980 | 25 Feb–2 March | Lukenya Hill Kaputiei Plains | 1°28'10"S 37° 2' 5"E | |
| | 30 March–9 April | Kenplains Estate (Hopcraft's Ranch), Kaputiei Plains | 1°31' 5"S 37° 2'47"E | 13.6 km WNW (291°) from main radar |
| 1982 | 4–10 March | Mau-Mau Farm, Mara River | c. 1°03'S 35°15'E | |
| | 26 April–5 May | Athi River Ranch (Gore's Ranch) | 1°28'54"S 37° 1'24"E | |

The field studies were undertaken at outbreak sites where gregarious *S. exempta* caterpillars were about to (or had already) pupated. The basic plan was to wait for the adult moths to emerge, and then to use entomological radar equipment and other observational methods (Figure 17), to study their subsequent behaviour. A team led by Dr Rose recorded the nightly emergence rate of moths from pupae in the soil, the numbers of moths flying at low altitude through an Aldis lamp beam, and the numbers which congregated in small

trees before embarking on migration (see Rose and Dewhurst, 1979). A specially developed infra-red optical device (see Section 3, and Farmery, 1981) was used to measure insect wing-beat frequencies and aerial densities in the altitude interval between 2 m and ca. 30 m where returns from ground features (clutter) rendered the radar ineffective. As emigrating moths ascended to higher altitudes, they were monitored with an azimuthally-scanning radar, sometimes supplemented with a radar operating in RHI (Range Height Indicator) mode or (in 1982) with a vertical-looking radar. The migratory flight of moths beyond the range of the main radar was observed with another scanning radar deployed ca. 13 or 19 km away in a downwind direction.

Although we were not equipped for aerial netting to confirm the identity of the insects detected by the radars, we were confident that the great majority of the moth-sized radar echoes which we detected were attributable to *S. exempta* for the following reasons:

- the wing-beat frequency distributions from the radar targets were very similar to those recorded by the infra-red detector at the heights where *S. exempta* could be seen visually to be the most abundant airborne moth species (e.g. when they were flying into and out of the trees). These distributions in turn matched those obtained from laboratory measurements for this species;
- the studies took place mostly at the end of the dry season, when radar observations showed that there were relatively few nocturnally-flying insects until the mass emergence of *S. exempta* occurred;
- the dramatic night-on-night increase in aerial density of radar echoes corresponded with a nightly increase in *S. exempta* moths in the emergence traps;
- the plumes and concentrations of *S. exempta*-size targets streaming from outbreak sites were highly characteristic, and were not recorded by radars located away from such sites (e.g. at the 'downwind' radar site).

Daily pattern of emergence and flight activity of *S. exempta* moths on an outbreak site

At an outbreak site, *S. exempta* moths typically emerged from their pupae during the evening, over a period lasting 7 to 12 days, with the bulk of the population appearing during the central, 4–5 day interval. Emergence started at about 19.00 h, i.e., soon after dusk, and continued for about 2–3 hours. After their wings hardened and the moths became able to fly, many moved into nearby trees where large numbers often accumulated, particularly between 23.00 and 03.00 h. As would be expected, little flight activity was seen on the radar during the first part of the emergence and teneral period, but from about 21.00 h onwards, intermittent 'plumes' of radar echoes were detected as groups of moths took off from the trees and were displaced downwind as they ascended (Figure 22). As illumination began to increase just before dawn (but while it still seemed very dark to the human eye), any moths still in the trees left them and climbed to heights of several hundred metres in a mass flight which sometimes produced a spectacular radar display. This 'pre-dawn flight' was short-lived, however, as aerial densities declined very rapidly after about 06.00 h, and the moths had always landed by the time at which middle-distance features became easily visible to the human eye. They then sheltered in refuges during the day, for example, under grass tufts or dried cattle dung. The radar studies showed no evidence that *S. exempta* migrated during the day, and occasional records of short

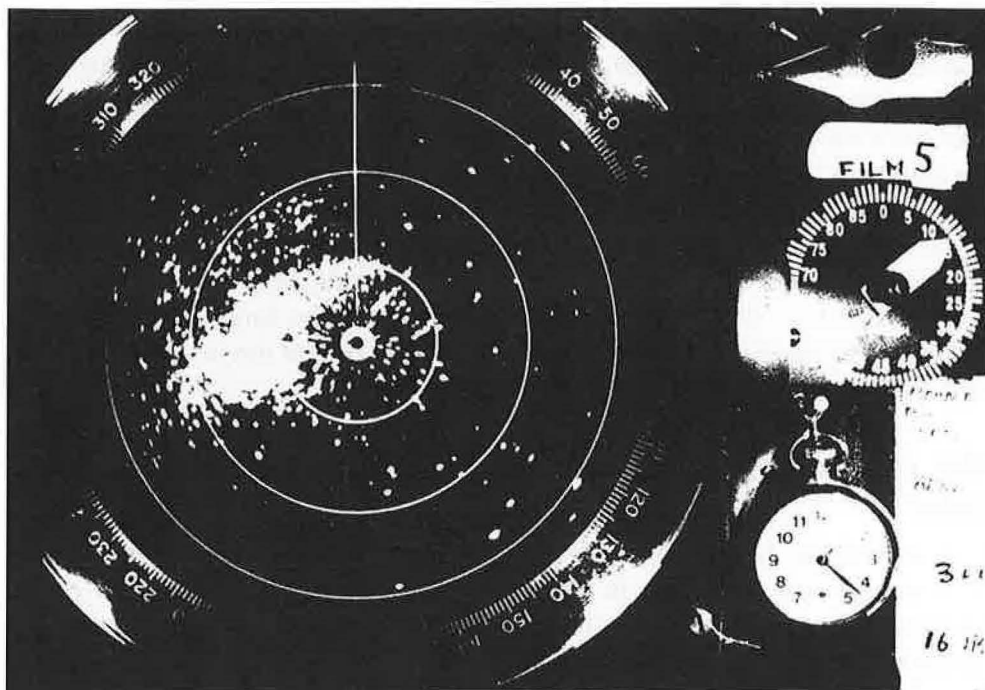


Figure 22 Photograph of radar display showing a plume of *Spodoptera exempta* moths emigrating from an outbreak area in Kenya

PPI display at 01.22 h on 3 April 1979 at a site just northeast of Mount Margaret in the Rift Valley of Kenya (radar beam elevation = 13°; distance between range-rings = 0.25 nautical mile (463 m)). The area was previously infested with gregarious *S. exempta* caterpillars which after pupation in the soil, had given rise to large numbers of adult moths. Apart from mass take-off just after dusk and just before dawn, groups of moths were seen to emigrate at other times of the night, producing localized 'puffs' or plumes on the radar screen. In this display the insects were displacing downwind towards 250°. Wing-beat frequencies recorded from insects engaged in these 'plume flights' were characteristic of *S. exempta* moths.

flights near the ground during daylight were plainly associated with disturbance or 'trivial movements' (Rose, Dewhurst and Page, 1995). The daytime flight of *S. exempta* over the sea, reported by Laird (1962), was almost certainly anomalous behaviour forced on migrating moths by their inability to land safely.

On some of the outbreak sites which we studied, the moths congregating in the trees tended to remain there throughout the night, with a consequent reduction in the 'plume activity' observed on the radar, and a more pronounced pre-dawn flight. The reason for this variability in the time of departure from the trees is still not clear.

At dusk on the evening following their emergence, moths left their daytime refuges and briefly flew into or around nearby trees. They then climbed to altitudes of several hundred metres and embarked on downwind migration. This mass ascent was made evident by the rapid increase (often 2 or 3 orders of magnitude) in the insect aerial density recorded by the radar about 15 minutes after sunset. Aerial densities decreased after about 20 minutes (i.e., ca. 35 minutes after sunset) as the emigrating population moved away downwind, and remained generally low during the early evening until the cohort of moths emerging from pupae that night became flight-ready, and the cycle of flights into trees began again.

The dusk flight, and 'plume' flights early in the night, presented the best opportunities for **long-distance** movements by *S. exempta*, because the emigrant moths would have the maximum period of darkness for migration, and also because strong (~ 9 m/s) easterly winds often occurred in the first half of the night. At least during the periods of our studies, winds regularly became much weaker and more variable from midnight–02.00 h onwards. Long-distance movement during the pre-dawn flights was precluded by their short duration, coupled with the light winds present at this time. It seemed that the primary function of these flights was to distribute the large aggregations of moths in the trees into widely dispersed refuges, before the onset of daylight, and the attendant hazard of predation by birds.

The characteristics of *S. exempta* migration as revealed by radar

Besides helping to elucidate the daily pattern of moth flight activity, radar was particularly valuable in revealing the following information on *S. exempta* migration which would have been impossible to obtain with more conventional entomological techniques.

- (a) The emigrating moth populations climbed with an ascent rate of about 0.5 m/s to heights which were often above the insects' 'flight boundary layer', and thus their displacements were largely determined by the wind.
- (b) The radar estimates of nightly moth emigration were very similar to the accumulated evening emergence rates. This showed that the vast majority of moths left the outbreak sites within 24 hours of emergence, and that *S. exempta* moths developing from gregarious larvae are **obligate** windborne migrants (in contrast to, for example, *Helicoverpa armigera* moths – see Section 4.3). When a further outbreak does occur at the same place, this is very probably due to an influx of immigrants from elsewhere rather than a significant carry-over *in situ* of *S. exempta* from the previous generation.
- (c) Observations of groups of moths which left an emergence site and later overflew another radar situated downwind, demonstrated that mass migration covered **at least** 20 km. This finding served to complement the results of a mark-and-capture study carried out at the Athi River Ranch (Rose *et al.*, 1985) which showed that individual males could move distances of 35–147 km in one night. Further evidence of widespread long-distance migration, particularly following extensive caterpillar infestations, was provided by the observations of continuous overflight of *S. exempta*-like targets for several hours at the radar site near Mara River in March 1982. In summary, it was shown that flights starting at dusk (and also flight in some of the mid-evening plumes) led to **sustained** movement.
- (d) Heights of flight were variable, but away from large topographical features such as the escarpment of the Rift Valley, the average maximum height was observed to be about 420 m above ground. Many moths flew at heights of about 200–300 m, which often corresponded with the height of the strongest mean wind speed in the prevailing easterlies, thus facilitating rapid moth displacement (at least in the first half of the night).

- (e) Radar observations clearly showed that the groups of departing moths dispersed as they were carried downwind, due to the effects of variation in individuals' orientation directions and airspeeds, as well as wind shear and turbulence. There was no indication of interactive behaviour (like that of swarming locusts) which would tend to keep the group together, and in the absence of atmospheric disturbances, the aerial densities of *S. exempta* moths are inversely related to the distance they have moved from the outbreak site.
- (f) The tendency for groups of moths to disperse as they moved downwind drew attention to the need for a mechanism to reconcentrate the populations leading to mass oviposition and larval outbreaks. The radar observed several processes by which this might occur, notably the concentration of migrating moths by wind convergence associated with rainstorm outflows (Figure 23) (which can easily increase the aerial density by an order of magnitude in less than an hour), and the effect of falling rain causing moths to descend from altitude to near ground level.
- (g) Storm outflows are atmospheric gravity currents (Simpson, 1987) and migrating armyworm moths would no doubt be concentrated by other forms of gravity current, e.g. sea-breeze fronts (Simpson, 1994), if these were encountered. Airborne moths can also be concentrated by other atmospheric motions such as topographic vortices (Pedgley,

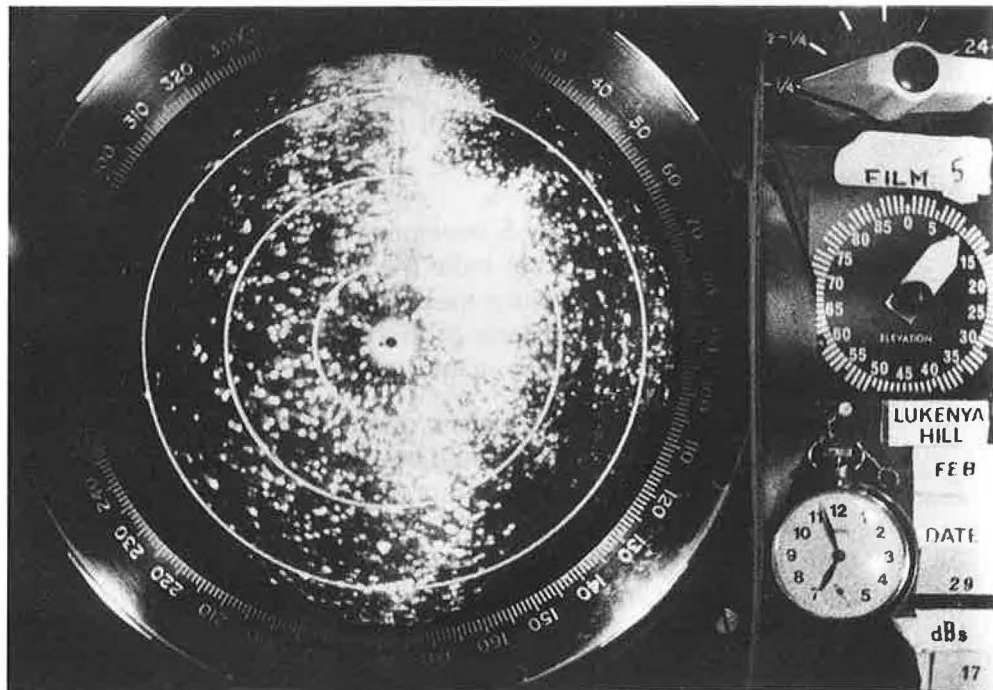


Figure 23 Photograph of radar display showing insects, mainly *Spodoptera exempta* moths, being concentrated in the air by a rainstorm outflow in Kenya

PPI display at 18.57 h on 29 February 1980 at Lukenya Hill, 35 km south-east of Nairobi. (Radar beam elevation = 5°; distance between range-rings = 0.25 nautical mile (463 m).) The dense band of insect echoes is aligned along a wind-shift line and is moving eastwards with it. To the west of the band, the individual insect echoes were being displaced towards the concentration in the cool westerly outflow wind. To the east of the band, insects were displacing towards it from the northeast.

Aerial concentration of armyworm moths by wind convergence leads to mass laying which results in the very dense infestations of gregarious caterpillars characteristic of armyworm outbreaks.

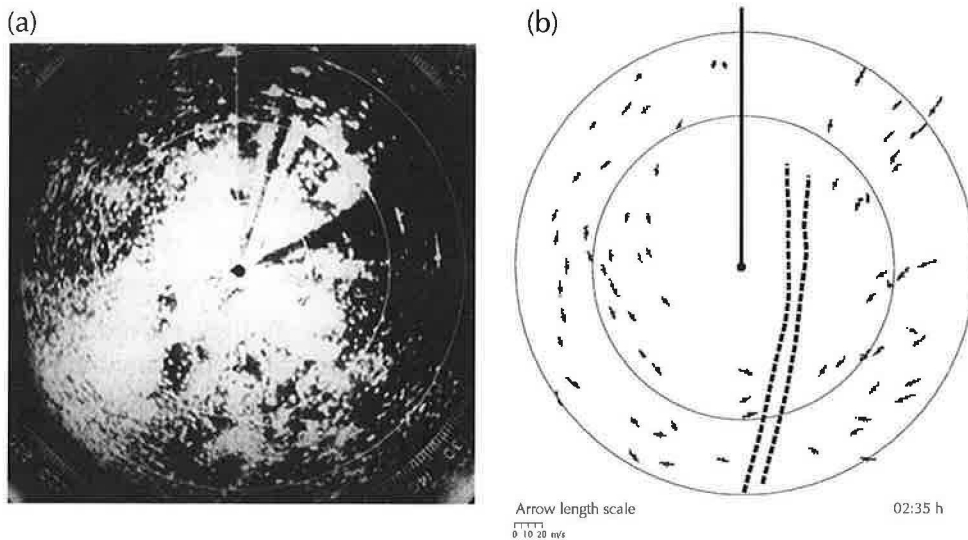


Figure 24 Photograph of radar display showing insects, mainly *Spodoptera exempta* moths, being concentrated by wind convergence probably caused by a rotor

(a) PPI display at 02.32 h on 3 April 1979 at a site just northeast of Mount Margaret in the Rift Valley of Kenya. (Radar beam elevation = 5°; distance between range-rings = 0.25 nautical mile (463 m).) The dense concentration of insects is associated with a zone of convergence probably due to a rotor forming beneath a gravity wave induced by easterly windflow over the Rift Valley escarpment (Pedgley *et al.*, 1982).

(b) The position of the wind convergence is indicated by broken lines. The velocity of individual insect echoes (the arrow length representing the echo speed) is also shown. To the west of the convergence line, insects were being displaced south and east towards it by the northwesterly rotor windflow. To the east of the convergence, insects were being displaced towards the southwest in the general northeasterly flow. Although flying *S. exempta* moths are concentrated in short-lived (~1 h) topographical vortices of this type, landing and mass laying by moths is apparently less likely than after aerial concentration associated with storm outflows.

1990), and in fact, examples of *S. exempta* moths being brought together by a rotor were observed by our radar (Pedgley *et al.*, 1982) (see Figure 24). However, these convergence mechanisms appear to be of less significance than rainstorm outflows in the formation of new outbreaks, perhaps because moths disperse again in the absence of rain.

- (h) The incontrovertible radar evidence of the windborne nature of *S. exempta* migration in East Africa validates the use of techniques such as trajectory analysis and the satellite monitoring of rainstorms in research into armyworm epidemiology (e.g. Tucker, 1993, 1994, 1997). More generally, the observations greatly strengthen the underlying basis of outbreak forecasting and strategic control of the African Armyworm.

Further developments

It is appropriate here to mention briefly two practical developments arising out of the field work on *S. exempta* migration.

Radar observations of aerial concentration of *S. exempta* moths by rainstorm outflows, together with other evidence of an association between rainstorms and armyworm outbreaks (e.g. Tucker and Pedgley, 1983; Pedgley *et al.*, 1989), has eventually led to the use of satellite imagery in East Africa to locate convective rainstorms in order to forecast the likely position of new larval infestations, particularly at the beginning of the armyworm season (Rose, Dewhurst and Page, 1995; Tucker, 1997). Further work is required to properly assess the

value of the technique, but a limited study (Tucker, 1997) found that outbreaks were associated with the **edges** of cold (below -50°C) cloud clusters identified from individual-night cold cloud images. It was concluded that the use of Meteosat images early in the East African 'short rains' season could greatly reduce the areas needing to be surveyed for armyworm infestations.

Despite the value of the radar studies in increasing our understanding of armyworm migration, there has been concern that the data acquired during these studies has not yet been fully exploited to produce 'rule-of-thumb' predictions about moth dispersal/concentration which would be of use in operational forecasting. This will be remedied in the near future by the development of a model to describe the dispersal of moths from outbreak sites, taking into account the effects of wind shear and turbulence, and information on moth behaviour acquired by the earlier radar studies. The model will produce probability 'footprints' of the destinations of armyworm moths under a variety of meteorological conditions, and it will also aim to assess the accuracy of trajectory/dispersal forecasts that can be made with meteorological data derived from synoptic maps or Meteosat data. Findings from the modelling exercise will be incorporated into a system of decision tools, which is being developed at NRI, to aid armyworm surveillance and outbreak prediction.

4.3 The Old World Bollworm (*Helicoverpa armigera*)

Caterpillars of the noctuid moth *Helicoverpa* (= *Heliiothis*) *armigera* are able to thrive on a great range of host plants, and are serious pests of legumes, cotton, maize, sorghum, sunflower, tomatoes and many other crops in the semi-arid tropics of the Old World (Fitt, 1989; King, 1994). Control of the species relies heavily on the use of pesticides, but its increasing tolerance to many formulations is causing concern in India (e.g. Armes *et al.*, 1992; Reynolds and Armes, 1994), and in a number of other countries.

H. armigera moths are strong fliers, and at the time when we started our radar studies there was much evidence that at least some individuals could move hundreds of kilometres (see references in Farrow and Daly, 1987; Riley *et al.*, 1992; King, 1994). Catches of *H. armigera* moths in traps attached to high (40 and 50 m) towers showed that substantial movements can take place well above ground level (Gregg *et al.*, 1993), and because the females in these catches were very largely immature and unmated (Coombs *et al.*, 1993), it appeared that *H. armigera* might be an obligate post-teneral windborne migrant much like the *Spodoptera exempta* moths discussed in the preceding section.

On the other hand, it seemed that in irrigated multiple-cropping areas, and in other places where there was a succession of suitable host plants for *H. armigera*, most moths might actually move only short distances (~ a few hundred metres to a kilometre) (Joyce, 1981; Farrow and Daly, 1987; Fitt, 1989). Some authors maintained that observed fluctuations in the numbers of *H. armigera* adults in an area could be adequately accounted for by local breeding (e.g. Wardhaugh, Room and Greenup, 1980), and that migration was relatively unimportant. A further complication was that *H. armigera* pupae enter diapause under certain conditions, and this would obviously enhance the carry-over *in situ* of populations between seasons, and reduce the importance of immigration. The proportion of the population entering

diapause in central India was unclear, however. The state of the evidence for and against migration, at about the time we carried out our study, is summarised in more detail by Farrow and Daly (1987).

Because of the importance of migration in the population dynamics of the pest, and also because of its possible role in the development and spread of insecticide resistance, NRI decided to attempt to resolve some of the the uncertainties described above. The migration study was a part of a large research programme on the ecology and management of *H. armigera* in central India, and was carried out in collaboration with the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). A multi-disciplinary approach to the flight studies was adopted, including the use of radar and video (Riley, Smith and Bettany, 1990; Riley *et al.*, 1992), mark-and-capture (King, Armes and Pedgley, 1990) and flight mill experiments (Armes and Cooter, 1991).

The radar observations and associated field work were carried out in November–December in the years 1985–1987, during the period of emergence of *H. armigera* moths from plots of pigeon pea on the ICRISAT experimental farm. We employed an array of observational and sampling methods to investigate the temporal and altitudinal partitioning of moth flight behaviour throughout the night:

- detailed visual observations of adult emergence of *H. armigera*;
- records of the numbers and sex of moths emerging into field cages in the pigeon pea plots;
- visual observations of the nocturnal flight activity of 'night 1' moths (i.e., of moths flying on the night **after** the evening on which they emerged) in field cages;
- observation of the dusk take-off of 'night 1' moths from containers, using binoculars or night-vision goggles;
- sampling of moths flying at 1.6–3.5 m above ground with a large, truck-mounted net, and age-grouping of the female *H. armigera* caught;
- stereoscopic recording of moth flight trajectories, in the height range 2–11 m above the crop canopy, using a low-light video system with infra-red illumination;
- recording of wing-beat frequencies from low-flying insects with an infra-red optical device (Section 3) to check that the video targets were largely attributable to *H. armigera*;
- observations with the X-band entomological radar of moth-sized insects flying between about 20 m and 1 km altitude.

Detailed results of the studies are presented in Riley *et al.* (1992): the following is a brief summary. *H. armigera* moths emerged from the soil during the first half of the night usually starting around sunset. They climbed onto the lower part of pigeon pea stems, and remained there while their wings expanded and cuticle hardened. The duration of this period was very variable, and moths sometimes stayed motionless for much of the night, but all fluttered or crawled to shelters in leaf litter or cracks in the soil as dawn approached. Thus there appeared to be little flight activity on the night of emergence.

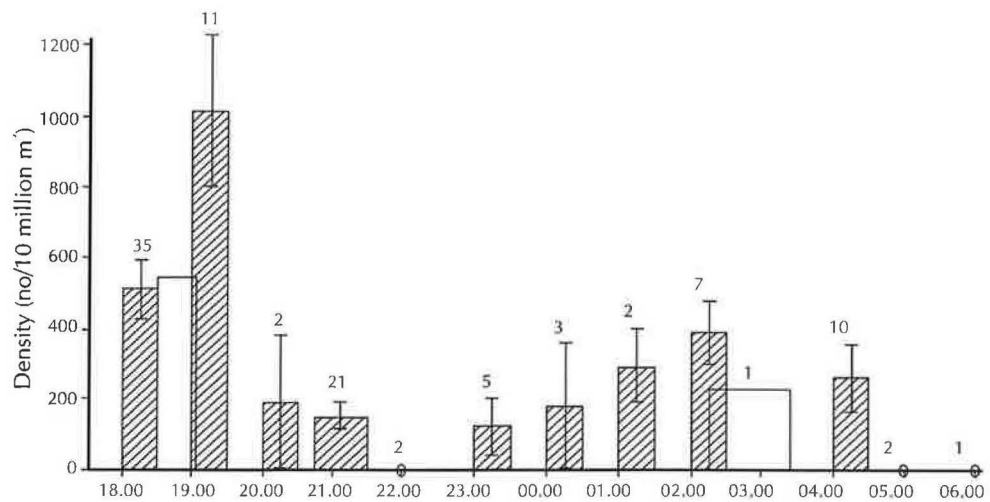


Figure 25 Variation during the night in the aerial density of *Helicoverpa armigera* moths caught in a vehicle-mounted net at ICRISAT, near Hyderabad, India. Hatched columns show the mean density (with bars indicating standard error, and figures indicating number of samples) obtained from pooled data for the 1985, 1986 and 1987 seasons. Open columns show the density for two samples taken at non-standard times. Zeros on the abscissa indicate that samples contained no *H. armigera* (Figure from Riley *et al.*, 1992 with permission from CABI.)

Table 2 Sex ratio of *Helicoverpa armigera* moths caught in vehicle-mounted net samples at various periods of the night at ICRISAT, near Hyderabad, India (Pooled data for the 1985, 1986 and 1987 seasons)

| | Time Periods (h) | | | | | | | | | | | |
|---------------|------------------|----|-------------|----|-------------|----|-------------|---|-------------|---|-------------|---|
| | 18.00–18.30 | | 19.00–19.30 | | 21.00–21.30 | | 23.00–00.30 | | 01.00–03.00 | | 04.00–04.30 | |
| Sex | M | F | M | F | M | F | M | F | M | F | M | F |
| No. caught | 23 | 64 | 2 | 45 | 9 | 11 | 5 | 4 | 12 | 4 | 9 | 5 |
| Sex ratio | 1:2.8 | | 1:22.5 | | 1:1.2 | | 1:0.8 | | 1:0.3 | | 1:0.6 | |
| χ^2 test | P < 0.001 | | P < 0.001 | | N.S. | | N.S. | | P < 0.05 | | N.S. | |

By contrast, the one-day-old moths seen in the field cages showed vigorous flight, starting about 20 minutes after sunset. This activity lasted for an hour at **most**, and can be interpreted as a short migratory phase. Flight then became more fluttering and intermittent for the rest of the night, and was probably associated with foraging for nectar. A small increase in flight activity occurred just before dawn as the moths again sought daytime refuges.

Most of the *H. armigera* females captured by the truck net and flying in the vicinity of the study plots (but generally not originating from them) were found to be 4–6 days old. Feeding and oviposition flights by these mature females caused the peak at about one hour after sunset in the truck-net results (Figure 25 and Table 2). The frequency of these flights declined by about 2 hours after sunset. The slight increase in numbers in the truck-net in the second part of the night (Figure 25) was due to mate-finding flights by males.

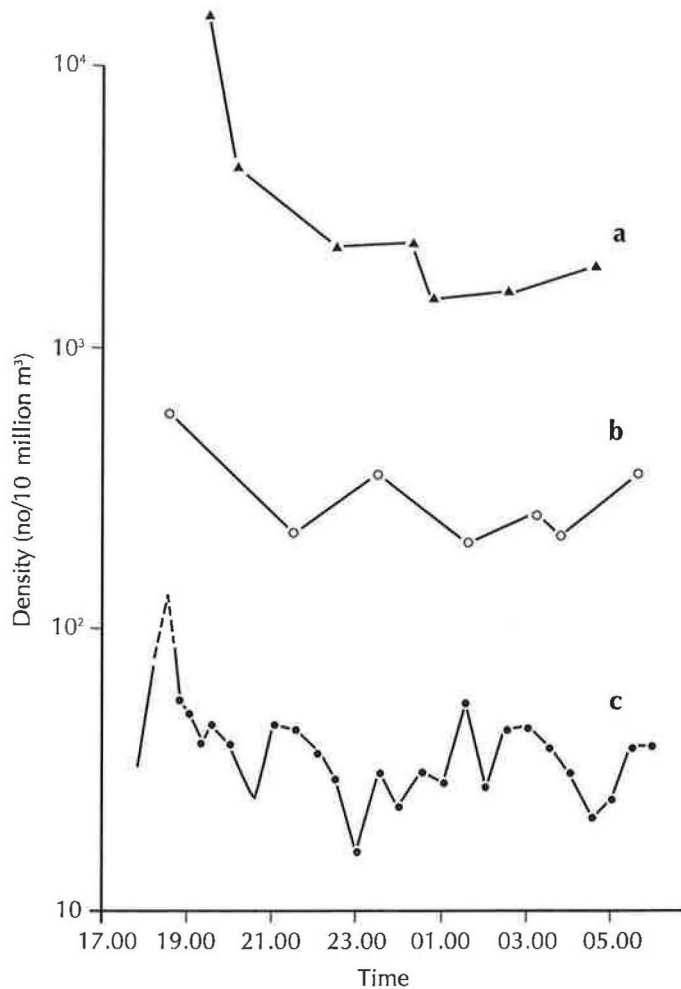


Figure 26 Variation in the aerial density of *Helicoverpa armigera*-sized insects at (a) 4 m (b) 9 m and (c) 26 m above a pigeon pea plot at ICRISAT, near Hyderabad, India. The data are for the night of 3–4 December 1987; (a) and (b) are from video recordings and (c), from radar data. Note the decrease in insect aerial density of approximately two orders of magnitude between the 4 m and the 26 m heights.

It appeared from the results of the truck-net sampling and from casual observations with night-vision goggles, that much of the *H. armigera* flight was at low altitude. This was unambiguously confirmed by the combination of video and radar measurements. We found that:

- aerial densities of *H. armigera*-sized targets decreased greatly between heights of 4 m and 9 m above the experimental plots, and again between the 9 m and 26 m heights (Figure 26);
- most of the three-dimensional flight trajectories reconstructed from the video recording were either level or undulated in the vertical plane, and there was no evidence of mass climbing flight;
- despite the thousands of *H. armigera* emerging each night, there was no indication of dense plumes of insects streaming away from the study plots at the heights (above 20 m) covered by the radar; very weak 'plumes' were occasionally observed, but these could have accounted for only a very small percentage (5% at most) of the emergent moths.

Thus it was clear from our observations that post-teneral *H. armigera* did not automatically climb to high altitude and embark on windborne migration, as gregarious *S. exempta* do. The short dispersal flights undertaken by *H. armigera* at dusk on the night after emergence, would take the moths away from the vicinity of their emergence sites, but most of these flights were at low altitude, within the 'flight boundary layer', and they would probably have taken the moths a few kilometres at most. The capture of a marked individual 3.5 km from our experimental plot (King, Armes and Pedgley, 1990) demonstrated that some moths moved distances of this order. Similar distances might be traversed during the foraging, mate-finding and oviposition flights of the **mature** moths, especially if the sought-after resource (food, a mate etc.) was not encountered quickly. However, it was shown (Armes and Cooter, 1991) that if *H. armigera* females from the ICRISAT area obtain a sugar feed on 'night 1', reproductive maturation is rapid and mating takes place by 'night 2' or 'night 3'. After mating, female flight propensity is considerably reduced and this would preclude long-distance movement.

We conclude that *H. armigera* is a 'facultative' rather than an 'obligate' long-distance migrant, and that if moths emerge into an environment where nectar sources are available, a high proportion of individuals will move relatively short distances. Rather similar conclusions were reached in multidisciplinary studies of *H. armigera* in the Gezira area of Sudan (Joyce, 1982; Topper, 1987) and in Australia (Fitt, 1989; Gregg *et al.*, 1995). On the other hand, long-distance migration appears to predominate if moths emerge when host plants are mature or senescing over a wide area (e.g. Armes and Cooter, 1991 and unpublished). As well as the direct effects of the environment on the migration behaviour in *H. armigera*, it seems likely that there will be interactions through the selection of genes controlling both migratory activity and the length of the pre-reproductive period (in which migratory flight often occurs) (Colvin, 1995).

The ability of *H. armigera* populations to persist within agricultural systems has been increased by irrigation and the consequent extension of multiple-cropping schemes. In these intensive agricultural environments, *H. armigera* would often be subject to strong selection pressure for insecticide resistance, and this is very probably the reason for the large increase in resistant phenotypes which has occurred in many populations (Farrow and Daly, 1987; Fitt, 1989). Our radar observations at ICRISAT, and those made in the Sudan Gezira (Joyce, 1981), indicated that a small percentage (< 5%) of moths climbed to altitude, and these may have engaged in windborne movement over longer distances. There is certainly circumstantial evidence of migration of *H. armigera* **into** the ICRISAT area from distant sources at certain times of the year (Pedgley, Tucker and Pawar, 1987). These long-flying individuals are very probably responsible for the widespread presence of resistant genotypes, even in areas where little insecticide has been used (e.g. Gunning and Easton, 1989).

In addition to the contribution of the radar studies to the understanding of the ecology of *H. armigera* in central India, some of our findings (e.g. height and timing of flight, moth orientation with respect to wind speed and direction, and effect of host plant patches) have been used in a simulation model of *Helicoverpa* moth dispersal (Dillon *et al.*, 1996). This in turn forms part of an Australian regional population model used for forecasting the levels of infestations in crops.

4.4 The Brown Planthopper (*Nilaparvata lugens*) and other Plant- and Leafhopper Rice Pests in the Philippines and China

RADAR STUDIES IN THE PHILIPPINES

In tropical South-East and South Asia, the Green Revolution of the 1960s was characterized by the advent of large mono-cultures of high-yielding rice varieties, shorter inter-crop intervals and larger areas of irrigation. These changes inadvertently increased the frequency and severity of infestations of the Brown Planthopper, *Nilaparvata lugens* (Homoptera: Delphacidae), and the species subsequently became a major pest of irrigated rice throughout much of Asia, where formerly it had been of only minor importance. Losses grew despite the increased use of control measures, since many of the natural enemies of *N. lugens* proved more vulnerable to pesticides than the planthopper itself. In fact, many outbreaks were probably caused by actually inducing *N. lugens* resurgence through the injudicious application of insecticide to control other rice pests. Difficulties of control were further compounded because the resistance to *N. lugens* of each new rice variety proved to be short-lived as a result of the wide genetic variability within planthopper populations. It rapidly became clear that better management techniques were necessary, and that these would have to be based on an improved understanding of the ecology of the species in tropical regions. The International Rice Research Institute (IRRI) therefore initiated an international research programme to investigate the ecology of *N. lugens*, and to develop an integrated management strategy for the species. As a part of this programme, NRI was asked to study planthopper ecology and migration, so that these factors could be incorporated in the design of integrated management methods. The radar observations of *N. lugens* migration in the Philippines formed one component of these studies.

In humid tropical areas, like the Philippines, cultivated, ratoon or wild rice varieties are present throughout the year, so *N. lugens* can generally move between favourable habitats by migrating only short distances. However, it was known that individual *N. lugens* have the capacity to migrate very long distances in the temperate zone, so it seemed possible that outbreaks in the tropics might, in fact, be generated by mass immigration of planthoppers from distant sources. Both strategic and tactical control planning depend on knowledge of how the target pest populations are likely to shift in space and time, so it was important to establish whether long-distance movements were of significance in *N. lugens* population dynamics in the tropics. This information has added importance, because control in tropical areas is based primarily on the use of rice plant varieties which are resistant to *N. lugens*, and migration **range** largely determines the rate at which planthopper genotypes able to overcome this varietal resistance might spread from one part of the region to another. Range is also relevant to the rate of spread of genotypes which harbour resistance to insecticides, and to the epidemiology of the viral diseases of rice which are transmitted by *N. lugens*.

Our radar studies were carried out under the auspices of IRRI and of the South East Asia Regional Centre for Research and Graduate Study in Agriculture (SEARCA). Pilot observations were made on the experimental farm at IRRI, Los Baños, in March 1983, and in March and April of the next

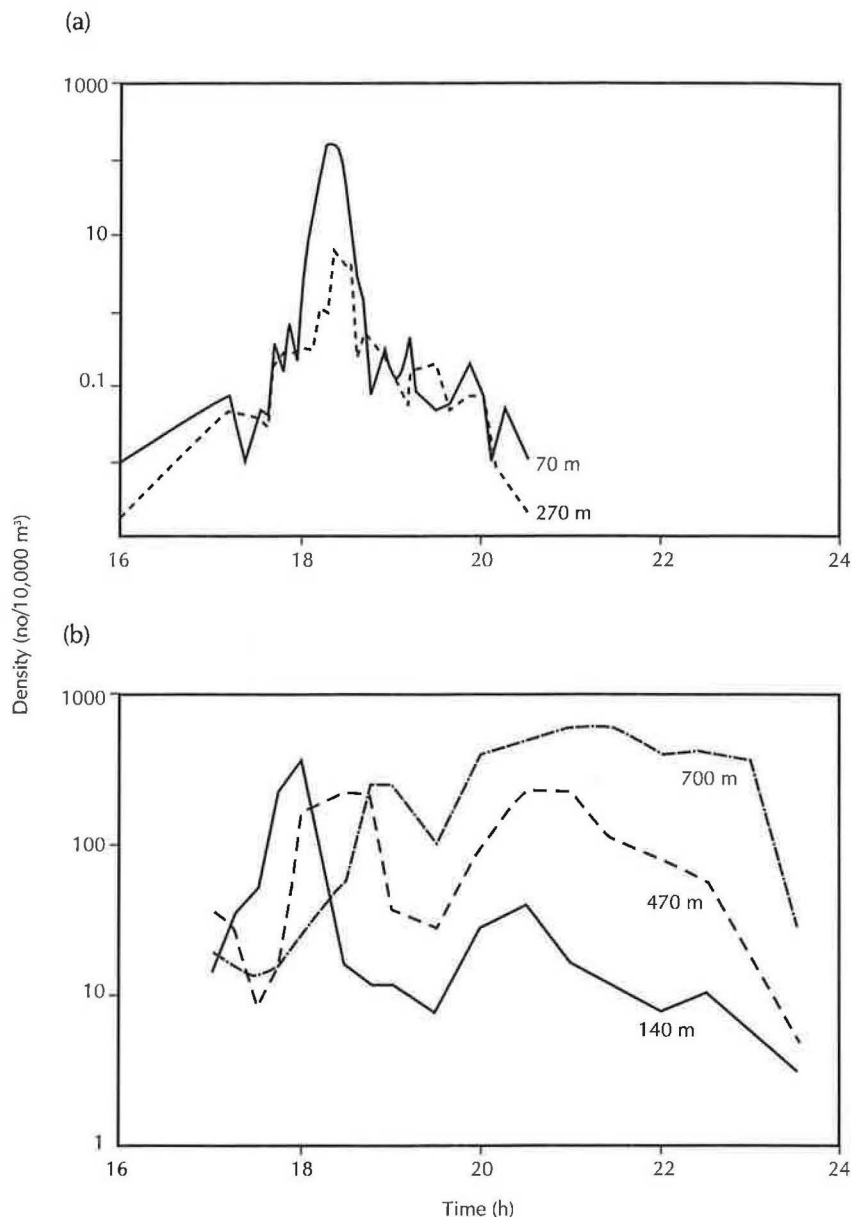


Figure 27 Variation in aerial density of insects at different heights during the late afternoon and evening, as recorded by the Q-band radar in the Philippines and China. Data are from (a) Marsiit, Laguna Province, Philippines (average for 9 observational evenings in March 1984) and (b) Jiangpu, near Nanjing, China on 28 September 1988. The brief dusk flight of rice insects in the Philippines contrasts markedly with the mass overflight of Brown Planthopper, continuing for several hours, observed in China.

year these were followed by a programme of radar and aerial netting studies at the nearby experimental station of Hoechst Philippines Inc., in Marsiit. Both experimental sites were within extensive areas of irrigated rice south of Laguna (lake) de Bay. Earlier data from suction trapping had shown that the aerial density of *N. lugens* reached a maximum at the end of the dry season crop in this part of the Philippines, and we timed our observations to coincide with this period. Dr V.A. Drake and Dr R.A. Farrow of CSIRO, Canberra, Australia, collaborated in the 1984 experiments, with support from the Australian Centre for International Agricultural Research.

Our 1984 study was directed at the migration of *N. lugens* and other rice-associated Hemiptera (Riley, Reynolds and Farrow, 1987), and employed the following methods:

- (a) visual counting of planthoppers taking off and ascending, just after sunset, from infestations on susceptible rice varieties;

- (b) canopy traps to measure the emigration of insects from the rice plots at dusk;
- (c) a suction trap mounted on a scaffold tower to sample insects flying at 11 m above the ground;
- (d) an aerodynamically-shaped balloon or 'kytoon' (or sometimes a parafoil kite), to suspend a net which allowed us to sample insects flying at about 75 m above ground level (see Farrow and Dowse, 1984);
- (e) X-band (3.2 cm wavelength) and Q-band (8 mm) radars to observe insect flight up to an altitude of about 700 m.

Our 3.2 cm radar was of the type normally used in radar entomology studies, and could detect individual *N. lugens* out to a range of only 300 m, although concentrations of the insects were sometimes visible to greater ranges and appeared as areas of collective echo on the radar screen. We had designed and built the Q-band radar specifically for the studies of *N. lugens*, and this radar was able to detect individuals of this species out to a maximum range of 1 km (see Section 3). It provided NRI with a unique facility for the observation of the migratory flight of planthoppers and of other small pest insects (Riley, 1989b, 1992).

We found that *N. lugens* did not dominate the aerial fauna as it did during some later radar studies in China (see below), probably because most of the rice in the area in which we were working was resistant to this species, and populations were correspondingly low. The most common insect at altitude turned out to be an important predator of rice plant- and leafhoppers, the mirid bug *Cyrtorhinus lividipennis*, and this insect accounted for a large proportion (56%) of the total catch from the aerial net. Green leafhoppers (*Nephotettix* spp.) comprised 8.6 %, and *N. lugens* 5.9 %.

The radars showed a very consistent pattern of flight activity from night to night (Riley, Reynolds and Farrow, 1987), with periods of synchronized mass take-off by small insects (including *N. lugens*) occurring around dusk and dawn (Figure 27a), probably stimulated by changing illumination levels. The flight ceiling recorded by the radar varied from night to night, but on average it was 400 m \pm 120 m (s.d). While the dusk flight was at its most intense, we found a linear negative relationship between log aerial density and log height, but afterwards densities quickly fell back to low values at all heights (Figure 28), and we saw no evidence of layers of insects at altitude. We deduced from this that the vast majority of the dusk migrants remained airborne for only 30 minutes or less, and during this time they would have travelled no more than about 30 km. Distances covered in the lighter winds prevailing during the dawn migration would be even shorter. These results were consistent with those acquired in the course of other studies in the Philippines, based on trapping methods, which also suggested that *N. lugens* normally had a short migration range (Perfect and Cook, 1987; Loevinsohn, 1991). Although we found that small numbers of rice cicadellids and delphacids, including *N. lugens*, occasionally extended their migration beyond the dusk flight period, even these individuals probably travelled distances of not much further than 50 km.

Overall, our results demonstrated that short-range movements are the norm in the Philippines, at least during the dry season. Long-distance migration may well be unadaptive in the Philippines, and, perhaps, in other parts of the humid tropics (Perfect and Cook, 1994), because some rice plants are usually available all year round within distances of a few kilometres. Furthermore, long-flying genotypes may be particularly uncommon on tropical islands (such as the

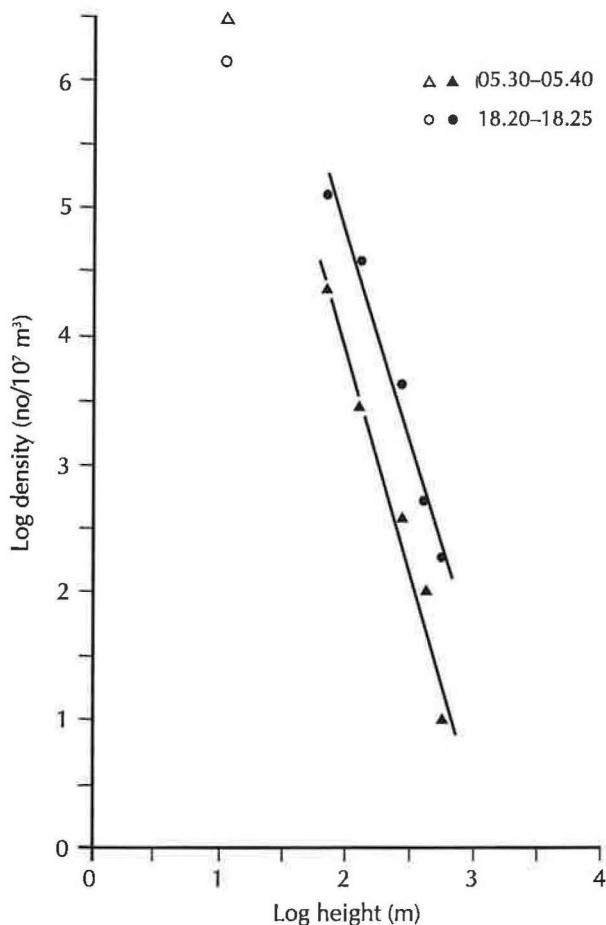


Figure 28 Relationship between the aerial density of small insects and height above ground during the dusk and the dawn flight periods in the Philippines
 Data are from Marsiit, Laguna Province in late March–early April 1984. The open symbols represent densities calculated from suction trap samples at 11 m above ground; the solid symbols are derived from Q-band radar returns. The linear negative relationship shown here between log aerial density and log height occurred only when the dusk and dawn flights were at their most intense; after this, densities quickly declined at all altitudes (see Figure 27a).

Philippines) far from continents, because emigrants leaving the islands are unlikely to be replaced to any significant degree by long-flying immigrants from remote overseas sources. Problems due to *N. lugens* migration can nevertheless still occur in the tropics, but only on a small geographical scale; for example, where massive immigration (from, say, a previous outbreak a few fields away) may overwhelm local populations of the planthoppers' natural enemies (Riley, Holt and Reynolds, 1990; Holt *et al.*, 1996).

RADAR STUDIES IN CHINA

In eastern Asia, destructive outbreaks of *N. lugens* have been recorded intermittently for centuries, but in recent years they have occurred with increasing frequency in many areas, and this despite the use of modern control measures. For example, although great efforts were made to control planthoppers, rice losses in China caused by these species during 1991 were estimated at more than 2 million tonnes (Zhou, Wang and Cheng, 1995). In particular, infestations in northern China threaten the increased production of high quality, high value rice in this area.

The success of the radar work in the Philippines prompted the Chinese Government to ask that similar observations of planthopper migration be made in temperate rice-growing areas of China. The resulting project, which started in 1988, was undertaken under the auspices of a Memorandum of Understanding between the UK and Chinese Ministries of Agriculture, and was carried out in close collaboration with the Department of Plant Protection, Nanjing Agricultural University (NAU). The studies were designed to obtain data on the timing, altitude, density and probable range of *N. lugens* migration in east central China, so that this information could be incorporated into forecasting models being developed at NAU and NRI. The ultimate objective of the studies was to contribute to the improvement of the national planthopper forecast and control procedures which were already in place in mainland China.

Observations at Jiangpu in Jiangsu Province

Observations were made between 11 and 29 September 1988, and between 23 August and 19 September 1990, at the NAU Agriculture Experimental Station at Jiangpu (32° 03' N, 118° 37' E), about 15 km west of Nanjing in Jiangsu Province. The NAU scientists monitored the ground populations of rice planthoppers through field counts and by measuring local emigration with canopy traps. Both our X-band and high frequency Q-band radars were used for the studies, and the identity of insects detected by radars was confirmed by aerial sampling up to an altitude of 450 m above ground, with a net (of aperture of 0.64 m²) attached to the tethering line of a kytoon (Riley *et al.*, 1991). The combination of radar and aerial netting was particularly successful as we were able to use information from the radars to make sure that the net was positioned at altitudes at which insect density was highest. The air-flow through the net was estimated by a wind-run meter hung below the kytoon. At the end of each sampling period, the net was closed by radio-control, the kytoon winched down to ground level, and the detachable bag containing the catch was removed from the net. Aerial densities for the various taxa caught in the net were calculated thus:

$$\begin{aligned} \text{Aerial density} &= \text{catch/volume of air sampled} \\ &= \text{catch/area of net aperture (i.e., } 0.64 \text{ m}^2) \times \text{wind run (m)}. \end{aligned}$$

Values of density found in this way were in good agreement with estimates made from the radar data (Riley, 1992). We determined wind velocity aloft by using the X-band radar to track small, helium-filled balloons carrying a strip of aluminium foil, and we investigated altitudinal profiles of air temperature and humidity by releasing conventional meteorological radiosondes.

In order to identify the likely source areas of insect concentrations which were detected overflying the radar site, we adopted the procedure of constructing **backward** flight trajectories from the site, in the upwind direction (see Reynolds *et al.*, 1997). To do this, we used streamline-isotach maps of the windfield at whichever of the available 'standard' meteorological levels was closest to the height of the concentration, and we assumed that the insects had taken off at the same time that local take-off was observed (~18.00 h). Their elapsed flight time was then taken to be the interval between 18.00 h, and their time of appearance over the radar. Implicit in this construction was the assumption that the insect concentrations moved at the same speed and in the same direction as the wind. In order to estimate the downwind displacement of planthoppers seen emigrating from near the radar site, we assumed that they would fly for about 12 hours, and we used streamline-isotach maps to plot **forward** trajectories, starting at the site at 18.00 h.

Table 3 Mean aerial densities of the Brown Planthopper, *Nilaparvata lugens*, as determined by aerial netting at different times of the day or night, during the 1988 and 1990 observational periods at Jiangpu, near Nanjing, China (Total number of netting hours = 144 in 1988 and 176 in 1990)

| 13–29 September 1988 | | | | 22 August–20 September 1990 | | | | |
|---|--|--------|-----------|--|--|--------|------------|--|
| Sample timing | Aerial density (nos/10 ⁴ m ³) | | | Total volume sampled (m ³) | Aerial density (nos/10 ⁴ m ³) | | | Total volume sampled (m ³) |
| | Mean | Median | Range | | Mean | Median | Range | |
| Dusk (ca. 17.00–19.30 h) | 63.8 | 61.1 | 8.7–190 | 279 448 | 3.89 | 1.62 | 0–13.34 | 705 924 |
| First part of night (ca. 19.30–00.00 h) | 35.6* | 5.8 | 0.1–274.2 | 649 088 | 0.83 | 0.36 | 0–2.99 | 696 256 |
| Second part of night (ca. 00.00–04.00 h) | 2.3* | 2.2 | 1.0–3.6 | 177 280 | 0.35 | 0.50 | 0–0.53 | 111 936 |
| Dawn (ca. 04.00–07.00 h) | 24.7 | 18.5 | 0.0–61.8 | 161 792 | 3.32 | 1.81 | 0.55–10.76 | 250 432 |
| Day (ca. 07.00–17.00 h) | 6.9 | 2.9 | 0.8–51.4 | 734 848 | 0.62 | 0.18 | 0–2.26 | 374 070 |

* Because of marked layering, and depending on whether the net was sampling within a layer, these aerial densities may not be representative of the overall density.

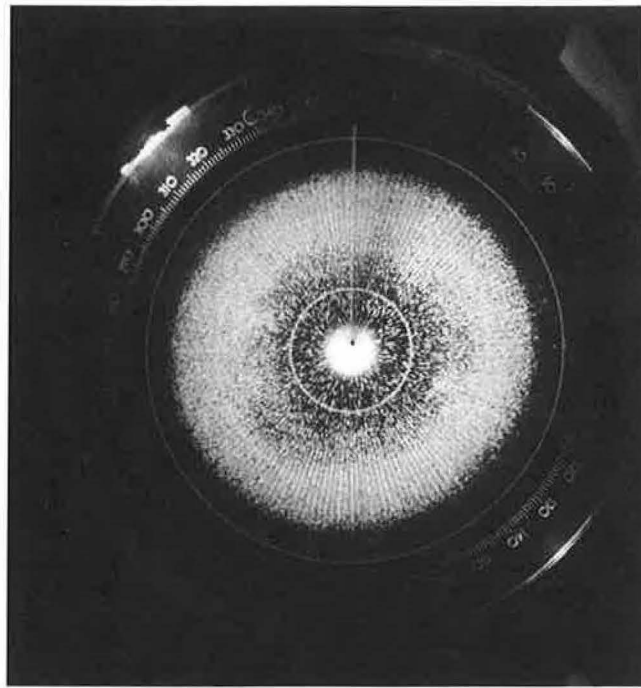
In the 1988 study, we found that *N. lugens* dominated the night-flying aerial fauna, with this species accounting for 58% of all the insects caught in the aerial net samples (Riley *et al.*, 1991). The main emigration occurred during the late afternoon–dusk period, when there was a large increase in both the number of *N. lugens* caught in the aerial net (Table 3), and in the aerial density of planthopper-sized insects recorded by the radar (Figure 27b). The migrating planthoppers then flew for several hours during the evening, often forming a dense layer at heights between about 400 and 1000 m above ground (Figure 29a) (Riley *et al.*, 1990, 1991). These layers often had a well-defined ceiling, which we found corresponded to an air temperature of about 16°C, close to the minimum for sustained flight in *N. lugens*. The mean migration height was **above** the top of the surface temperature inversion, so most of the planthoppers did not fly at the height where the air was warmest. Layers usually lasted until about midnight, but sometimes persisted until dawn, showing that some individuals remained in continuous flight for about 12 hours. We calculated that most of the planthoppers forming the dense layer concentrations overflying the radar in September 1988 had probably emigrated from outbreaks in central Jiangsu Province, up to 200 km away to the northeast. In fact, the presence of these outbreaks upwind of the study site was very probably responsible for the high aerial densities of *N. lugens* detected by the radar. A second period of mass take-off was usually observed at dawn (Table 3), and although insect layers sometimes formed at altitude (Figure 29b) they did not last longer than about 1–1.5 hours. Little flight occurred on some mornings, perhaps because low temperature inhibited take-off.

Overall, the 1988 study demonstrated that mass, long-range windborne movements of *N. lugens* regularly occur in late September, and that the direction of movement is predominantly towards the southwest. These intense, long-range migrations contrasted strikingly with the short mass movements which we observed in the Philippines, where flights at altitude were largely confined to periods of about 30 minutes at dawn and dusk (Figure 27) (Holt *et al.*, 1996).

Our 1990 observations in China were made earlier in the season, so that we could study migration under the wider range of wind directions occurring at this time of the year, and could determine whether significant displacements of *N. lugens* occurred in directions other than to the southwest. We found (Riley *et al.*, 1994; Cheng *et al.*, 1994) that the densities of *N. lugens* both taking off locally and overflying the radar site were considerably lower than in 1988 (Table 3). Nevertheless, the daily pattern of flight activity of *N. lugens* which we had found two years earlier was confirmed, with most migratory flight being initiated in the late afternoon or at dusk. Emigration tended to begin earlier in the afternoon as autumn progressed, and this seemed to be an adaptation to allow flight to start before the air temperature at ground level in the late afternoon fell below the threshold for take-off.

The combined results from both studies clearly showed that migrations of macropterous *N. lugens* adults regularly occur in east central China, and that their density increases from late August until late September as the main rice crop matures and is harvested (Riley *et al.*, 1991, 1994; Cheng *et al.*, 1994). In early and mid September, the resulting windborne migration frequently produces displacements towards the west, although the migration directions range (within the western sector) from south to north. By **late** September, however, displacements are predominantly to the southwest on the then prevailing northeast monsoon winds (Figure 30): migration is particularly rapid when the northeasterlies are reinforced by typhoons over the Pacific or the South China Sea. Planthoppers which emigrate from the vicinity of Jiangpu,

(a)



(b)

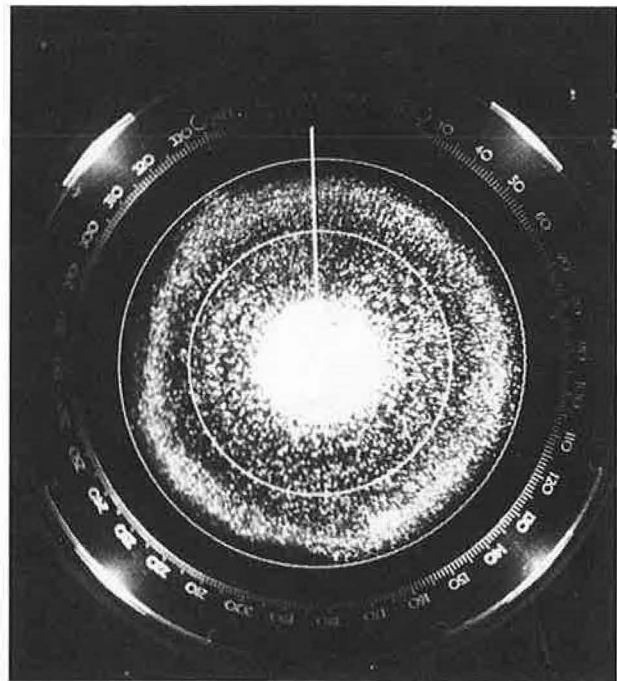


Figure 29

Photographs of the Q-band radar display showing dense layers of small insects, mainly *Nilaparvata lugens*, at Jiangpu, near Nanjing, China

- (a) PPI display at 22.04 h on the evening of 28 September 1988 showing a dense layer overflying the radar 380–825 m above ground level. *N. lugens* comprised 90% of the radar-detectable insects in an aerial netting sample taken from the bottom of this layer. (Radar beam elevation = 44°; distance to outer range-ring = 0.75 nautical miles (1390 m); the heading marker points north.)
- (b) PPI display at 06.46 h on 14 September 1990 showing a layer from about 700–950 m above ground, apparently formed from small insects emigrating around dawn. Aerial netting indicated that 54% of the radar-detectable insects caught at this time were *N. lugens*. The well-defined top of the layer was being disturbed by the passage of an atmospheric wave; the peak is noticeable at 170° and 330° bearing. (Radar beam elevation = 45°; distance to outer range-ring = 0.75 nautical miles (1390 m), the heading marker points north.)

and which are carried towards the southwest, would reach areas in south Anhui Province or north Jiangxi Province if they flew all night. We suspect that these migrations may frequently be channelled through the Changjiang (Yangtse River) valley into the Poyang Hu area of northern Jiangxi, as this valley is aligned along the direction of the wind prevailing in late September. The progeny of the migrants probably augment the infestations which occur on 'late' rice in October and early November.

Oviposition by migrants at the latitude of Jiangpu in early September would probably result in some of their progeny reaching the adult stage before the harvest of the late rice crop. However, oviposition at this latitude, or further north, in **late** September would appear to be unadaptive, as the nymphs would not have time to complete their development in the low temperatures (<18°C) before the cropping season ended and their food source disappeared. At this time, movements to more southerly latitudes thus seem essential for the survival of the planthoppers' progeny, but we found no convincing evidence for preferential emigration on winds blowing towards the south. There were, however, indications that when winds towards the north occurred, the *duration* of migratory flight was curtailed. Irrespective of any possible preference for migration on northerlies, a large proportion of the *N. lugens* population at Jiangpu would in any case be carried in the adaptive, southwards direction (towards the autumn infestation and overwintering areas of the species), simply because the northeast monsoon arrives at a time when the number of flight-ready planthoppers approaches its peak.

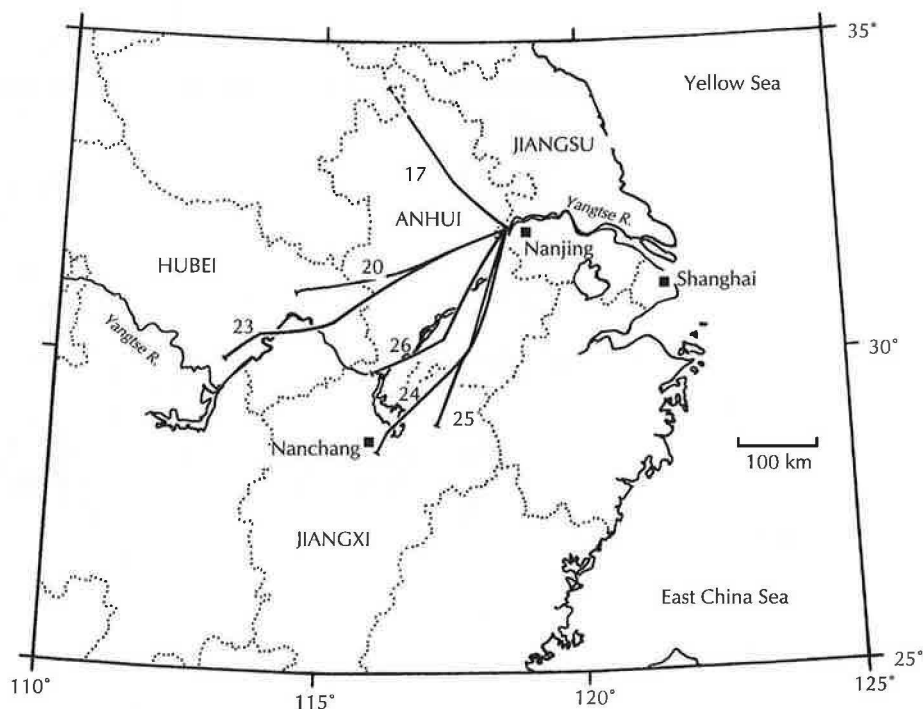


Figure 30 Examples of 12 h forward-trajectories for *Nilaparvata lugens* leaving Jiangpu, Jiangsu Province, China on nights in the second half of September 1988. The trajectories are for 18.00 h departures on 17, 20, 23, 24 and 25 September 1988 (at 900 m altitude) and 26 September (at 600 m). The names of Provinces are in capitals. It can be seen that all-night flights in late September can take migrant planthoppers from southern Jiangsu as far as southern Hubei or northern Jiangxi Provinces.

Observations at Dongxiang in northern Jiangxi Province

The radar studies in 1988 and 1990 had shown that vast numbers of *N. lugens* migrated southwards in autumn from the single cropping area in Jiangsu Province, and it seemed likely that these migrants were the cause of outbreaks on late rice in double cropping areas in southern Anhui and northern Jiangxi Provinces. Thus, in 1991, we extended our study to the south, by setting up our radars in northern Jiangxi. The aims of this study were:

- firstly, to observe insect migration in northern Jiangxi, and to confirm that *N. lugens* infestations which occur on late rice up to early November, are caused, at least in part, by the progeny of immigrants from the north;
- secondly to observe any emigration of the next generation of *N. lugens* from the late rice in early November, and to determine whether it would carry the insects further to the south, towards the extreme south of China and to Indochina where they could overwinter.

The radar equipment was deployed to a site near the Dongxiang County Plant Protection Department (28°14'N, 121°25'E) in northern Jiangxi Province, 470 km south-southwest of Jiangpu, and observations were made there from 29 September to 27 October 1991. In the event, comparatively high densities of the Rice Leaf Roller moth, *Cnaphalocrocis medinalis*, were detected on the radars during this period, and this species was thus made the subject of a special study (see Section 4.5). However, the forward and back-trajectories from Dongxiang which we calculated for this species are also applicable to the movement of *N. lugens*, which was seen to take off from the rice crop during our experiments, and many of which were caught in the aerial net. These trajectories confirmed the suspected southward movement of *N. lugens* from southern Jiangsu Province into northern Jiangxi, and also indicated that the planthoppers could reach the rice-growing areas near the coast of Guangdong Province, where they could overwinter.

Conclusions

Our three collaborative radar studies in China produced much new information on the movement of *N. lugens*, particularly on the magnitude and the altitude of migration, which could not have been obtained by conventional means. They thus contributed substantially to the large, on-going research programme on the life-cycle and migration of this rice pest in China (e.g. Cheng *et al.*, 1979; Zhou, Wang and Cheng, 1995). In particular, the radar data provided incontrovertible evidence that massive windborne southward migrations of *N. lugens* occur in late summer and autumn. Previously, the evidence for migration (derived from ground studies), had been ambiguous because it was difficult to separate putative immigrants from the north, from locally bred populations of the planthoppers (Zhou, Wang and Cheng, 1995). Importantly, the forward trajectories for the concentrations of *N. lugens* overflying the radar showed that it was highly probable that migrants from Jiangsu Province reached southern Anhui and northern Jiangxi, and contributed to outbreaks which occur there on late rice.

The importance of the intensity and the timing of *immigration* in causing rice planthopper outbreaks has led to considerable effort being vested in monitoring and forecasting systems throughout the rice-growing areas of China (Tang, Cheng and Norton, 1994; Zhou, Wang and Cheng, 1995), with warnings being disseminated at a number of institutional levels (national, provincial, county, village and farmer) and over several time scales (ranging

from about two months down to about two weeks before control would have to be implemented). Data on the planthopper population size in distant source areas and on the suitability of weather for the atmospheric transport of the pests are needed to make medium-term predictions about immigrant arrival in an area (Tang, Cheng and Norton, 1994), but it is also necessary to know about the typical migratory flight behaviour of the planthoppers. Knowledge of mean flight altitude, in particular, is a major factor in determining the accuracy of trajectory calculations, because wind speed and direction often vary greatly with height within the planetary boundary layer. Current information on the altitudinal distribution of *N. lugens* during migration, which has been almost exclusively derived from our radar studies, will lead to higher accuracy in modelling the airborne transport of the pests and this will, in turn, lead to improvements in the forecasting of the timing and intensity of inter-regional movements (Dr Zhai Baoping, personal communication).

In order to further apply the knowledge gained from the radar studies, the Chinese Ministry of Agriculture has sponsored proposals to establish several observation stations (which would use automatic vertical-looking radar (VLR)) for the routine monitoring of rice pest migration into northern China. After some delays this project is again making headway, with NRI Radar Unit members advising NAU on the construction, commissioning and operation of a VLR system.

OVERVIEW OF THE DIFFERENCES IN *NILAPARVATA LUGENS* MIGRATION IN TEMPERATE AND TROPICAL REGIONS

Our findings in the Philippines and in China might suggest that short-distance *N. lugens* migration predominates in the tropics and long-distance migration in temperate regions. However, this is not the whole story, because aerial netting studies in India (see below), have shown that long-distance movements by *N. lugens* occur in tropical areas in India (Reynolds and Wilson, 1989; Riley *et al.*, 1995a). Moreover, the extreme south of China and adjoining areas of Indochina, which are tropical, must harbour some long-flying individuals otherwise repeated re-colonization of temperate China would simply not occur. Given these facts, it seems reasonable to conclude that long-distance migration of *N. lugens* is most adaptive in temperate continental areas, moderately adaptive in tropical **continental** areas (especially those with a more pronounced dry season) and least adaptive in archipelagos (e.g. Philippines) or peninsulas (e.g. Malaysia) in the humid tropics.

4.5 The Rice Leaf Roller (*Cnaphalocrocis medinalis*) and other Moths in China

MIGRATION OF THE RICE LEAF ROLLER MOTH

In the course of our radar studies in China, the opportunity was taken to study the Rice Leaf Roller moth, *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae) – the first time that the high-altitude migration of this species had been observed. The insect is widely distributed from Australasia, across Southeast, East and South Asia to Madagascar (though not in continental

Africa). Its caterpillars eat the leaves of a range of grasses and graminaceous crops, but the most economically significant losses are to rice (see references in Khan *et al.*, 1988). In China, *C. medinalis* became a serious pest with the intensification of rice production in the mid 1960s.

Chinese workers have shown that *C. medinalis* cannot survive the winter in regions north of the 4°C isotherm of mean temperature in January (i.e., north of about 30°N latitude), but south of the 16°C January isotherm (i.e., south of about 22°N) it can breed all year round (Zhang *et al.*, 1981; National Co-ordinated Research Team, 1981). Between these areas, some overwintering is possible, but numbers are too low to be the main source of the populations which annually re-infest temperate regions. It was thus postulated that *C. medinalis* moths migrate from the tropics towards the northeast in a series of waves (about five) from March to August each year (Chang *et al.*, 1980, Zhang *et al.*, 1981). This supposition is supported by evidence from mark and recapture studies which showed that at least some *C. medinalis* moths are able to migrate very long distances in a north eastwards direction in China (Zhang *et al.*, 1981). Catches of *C. medinalis* on ships on the Yellow, East China and South China Seas also demonstrate the considerable flight endurance of this species, and there is evidence for windborne migrations of moths from China to Japan every year in the **Bai-u** season (June-July) (see references in Riley *et al.*, 1995 b) – movements analogous to those of the rice planthoppers *Sogatella furcifera* and *Nilaparvata lugens*.

Autumn migrations in China are less easy to document than those of spring and early summer, because any migrants would be moving south into areas which already harbour *C. medinalis*. Nevertheless, it appears that between late August and November, the autumn generations generally move towards the south or southwest which would bring them towards tropical regions (Chang *et al.*, 1980, Zhang *et al.*, 1981). Not all migrants are transported in an adaptive southwards direction, however, because *C. medinalis* can be transported eastwards out to sea in autumn (e.g. Geng *et al.*, 1990), and Wada, Ogawa and Nakasuga (1988) present evidence that some *C. medinalis* arrive in southwest Japan in September and October when they and their progeny will not survive.

Although it was known before we began our experiments that the changing seasonal distribution of *C. medinalis* moths in China is due to long-distance migration, there was a need for more precise information on how these migratory flights were achieved. In particular, characteristics such as the altitude, timing and duration of migratory flight, and their relationship to atmospheric factors, needed to be determined. This information was required for the forecasting and decision-making models being developed in China as part of an integrated management strategy against *C. medinalis* and other rice pests.

Results from the *Cnaphalocrocis medinalis* studies

C. medinalis moths were caught in the aerial net at both the Jiangpu and Dongxiang sites, but the radar observations of this species were made largely by the Q-band radar at Dongxiang in October 1991.

The moths were caught in the aerial net only during the period from dusk up until midnight, indicating that mass emigration occurred at dusk and was followed by a few hours of windborne movement. This agreed with the radar observations which showed that densities of *C. medinalis*-sized targets were greatest at about 18.30–19.00 h and then tended to decline through the evening. Insect densities generally were usually sparse after midnight and mainly comprised moths larger than *C. medinalis*, but it is quite likely that some Rice Leaf Roller migration continued at densities too low to be

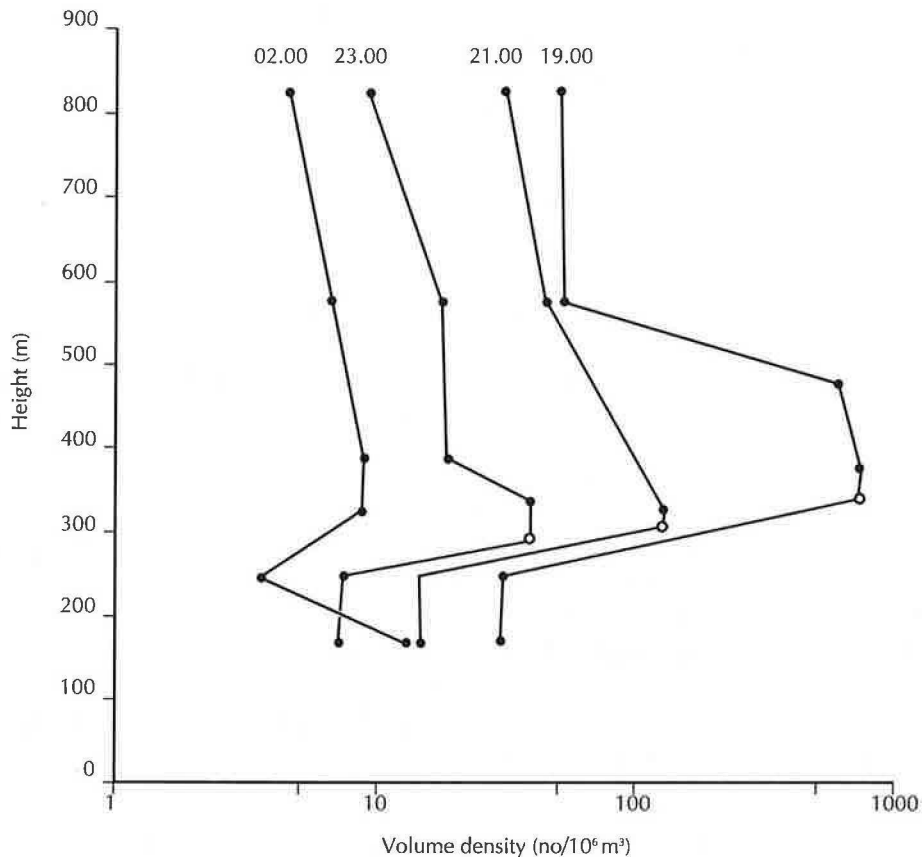


Figure 31 The vertical distribution of moth density on the night of 17–18 October 1991 at Dongxiang in Jiangxi Province, China
 A dense layer, with a distinct lower boundary (open circles) at about 300 metres, was present in the first half of the night. The Rice Leaf Roller, *Cnaphalocrocis medinalis*, accounted for 23 of the 26 moths caught between 19.16 and 23.53 h by aerial netting within this layer.

detected by our aerial netting regime. (Similar netting studies carried out in northeast India showed that *C. medinalis* were flying at altitude after midnight (S. Mukhopadhyay *et al.*, unpublished).)

The radar showed that maximum densities typically occurred between about 250 and 550 m above ground, and a well-defined layer containing many *C. medinalis* formed on some nights (Figure 31), particularly those with strong northerly or north-easterly winds at flight altitude. Above the dense layer, sparser and less well-defined layers sometimes occurred up to ca. 800 m or more, and these appeared from the radar data to be composed mainly of larger moths (e.g. *Agrotis ipsilon* and *Spodoptera litura*). In contrast to our findings for the Brown Planthopper, there was no clear evidence that the upper boundary of the *C. medinalis* layers corresponded to the species' low temperature threshold for sustained flight. The majority of migrating moths flew at an altitude where the wind speed was highest, and this sometimes corresponded to the height of a pronounced low-level wind jet. This is clearly an adaptive strategy for the moths in view of the large distances which they have to traverse to their overwintering areas. The cues used by the migrants to maintain themselves at these altitudes were not clear.

Females of *C. medinalis* taken by aerial netting from the dense, migrating layers were found to have immature ovaries, a result consistent with the reproductive status of the local (emigratory) ground population which also had a high proportion of immature unmated females. This provides good evidence for post-teneral, pre-reproductive migration in this species.

We found that in early September, migrant *C. medinalis* from southern Jiangsu Province were carried on the prevailing winds in an approximately westwards direction. However, the winds prevailing in **late** September and in October took migrants from both southern Jiangsu and northern Jiangxi Provinces towards the southwest or south. Southerly movement is highly adaptive at this time because moths are transported towards subtropical and tropical areas, where overwintering is possible.

More specifically, the back-trajectories indicated that the sources of *C. medinalis* overflying the Dongxiang radar extended to the northeast, and were mainly within the rice-growing area to the east of the Poyang lake, but south of the Huang Shan mountains (Figure 32). On some occasions, however, the insects may have come from north of the mountains (Figure 32), from the lowland area where eastern Anhui Province meets southern Jiangsu and northern Zhejiang Provinces.

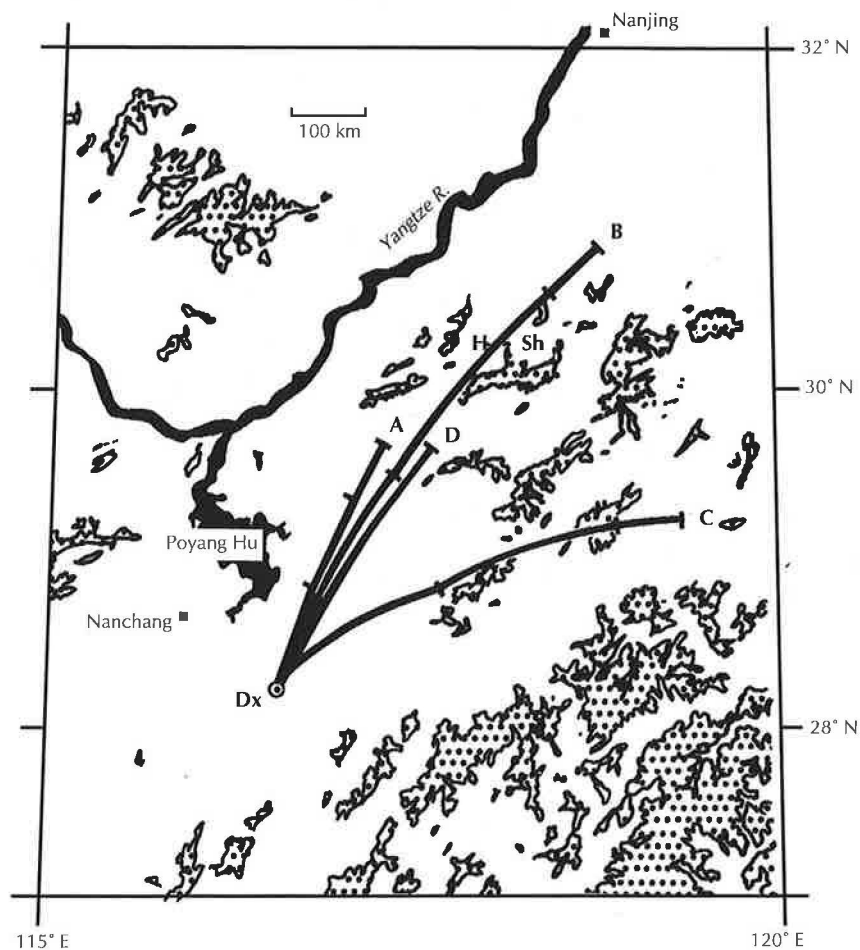


Figure 32 Examples of back-trajectories for insects crossing the radar site at Dongxiang in Jiangxi Province, China, in late October 1991

Trajectory **A** is for 01.00 h on 19 October; **B**, 03.00 h on 20 October; **C**, 01.15 h on 21 October and **D**, 22.00 h on 26 October. Take-off time 18.00 h. Stippled areas = land over 610 m (2000 feet). Dx = Dongxiang; H-Sh = Huang Shan (mountains). Most of the migrating rice insects overflying the radar appeared to have come from rice cultivations south of the Huang Shan but sometimes (e.g. Trajectory B) insects flying late in the night might have originated to the north of these mountains in cultivations near the southern edge of Jiangsu Province (c.f. Figure 30).

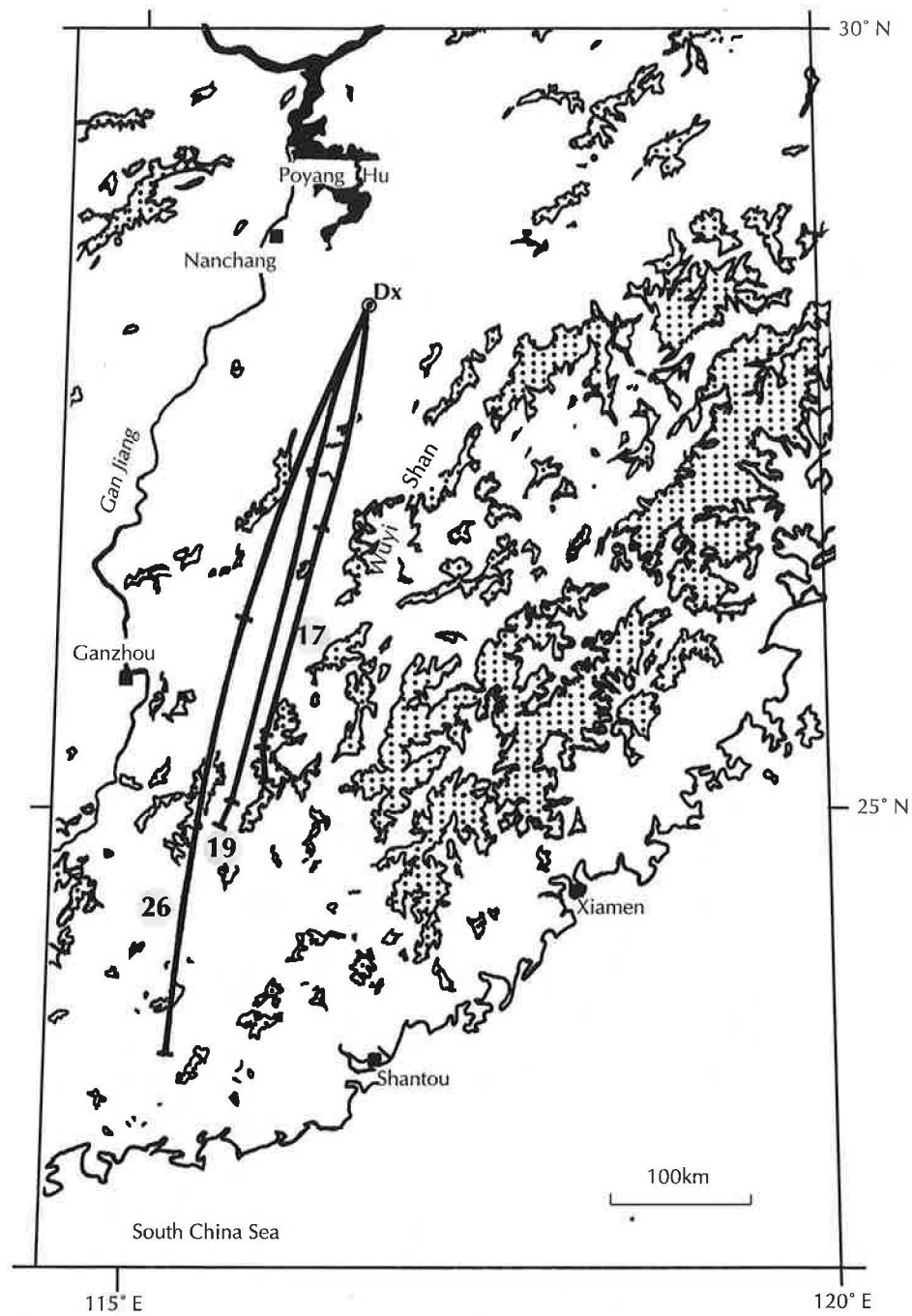


Figure 33 Examples of 11 h forward-trajectories for insects (including Rice Leaf Roller moths) emigrating from Dongxiang in late October 1991
 The trajectories are for 18.00 h departures on 17, 19, and 26 October 1991 at altitudes of 500 m, 500 m and 600 m, respectively. (Stippled areas = land over 610 m (2000 feet). Dx = Dongxiang.) Migration on the strong northerly winds on these occasions would allow the Rice Leaf Roller, *Cnaphalocrocis medinalis*, to reach areas near the south China coast where year-round breeding is possible.

A question of interest was whether moths which took off from the vicinity of the Dongxiang site, could have crossed the intervening mountainous areas and reached the rice-growing areas near the south China coast (where year-round breeding is possible). The flight paths of insects crossing the highlands of southern Jiangxi Province are less predictable than those over extensive lowland plains such as Jiangsu Province, where the low altitude wind fields are well ordered. Nonetheless, it seemed likely that the strong north or north-northeasterly winds occurring in October would tend to carry migrants to coastal Guangdong via the somewhat lower upland areas (e.g. Gan Jiang valley) (Figure 33). We calculated 11-hour, forward flight trajectories for *C. medinalis* and other insects taking off at dusk from the vicinity of Dongxiang during October, and the results indicated that the moths may have been able to cross the mountainous areas to the south of the site, and to reach the rice-growing areas near the south China coast where winter breeding can occur. In fact on some occasions, migrants could have penetrated almost to coastal Guangdong after only one night's flight. Thus it would appear that the migration pattern of *C. medinalis* in East Asia is, to a certain degree, a **circuit migration** and not merely a one-way movement from which the migrants' progeny never return to the overwintering areas.

The radar studies at Dongxiang in late October 1991 allowed direct observations of nocturnal mass migration of *C. medinalis* to be made for the first time, and the flight behaviour of the migrants to be characterized. As in the case of the rice planthoppers outlined above, the timing of immigration and the numbers of immigrant *C. medinalis* are crucial factors in the initiation of outbreaks in China. The data from the radar studies thus was thus of immediate value in the trajectory models developed by NAU to predict the arrival of potential damaging populations of *C. medinalis* and other lepidoteran pests (Zhai, 1993; Zhai, Zhang and Cheng, 1997).

THE MIGRATION OF OTHER PEST MOTHS IN CHINA

During the studies at Jiangpu and Dongxiang, pest moths other than *C. medinalis* were sometimes caught in the aerial net (Riley *et al.*, 1995b). *Omiodes* (= *Lamprosema*) *indicata*, a leaf-rolling pyralid pest of soyabean, was common in the 1990 study at Jiangpu, and other pyralid species taken in the aerial samples were: *Maruca testulalis*, the Legume Pod-borer, a pest of legumes in tropical and subtropical regions throughout the world; *Ostrinia furnaculus*, the Asian Corn Borer, an important pest of maize and cotton which is widespread in Asia and Australasia; *Spoladea* (= *Hymenia*) *recurvalis*, a pest of sugar beet and brassicas; and *Anomis flava*, a cotton pest.

Some noctuid moth pests were also caught, among them *Mythimna separata* (the Oriental Armyworm), *Agrotis ipsilon* (the Black Cutworm), *Spodoptera litura* and *Ctenoplosia agnata*.

Omiodes indicata

During the 1990 study at Jiangpu, the radars detected a dense plume of *Omiodes indicata* moths emigrating from infested soyabean fields at dusk on a succession of evenings from late August to mid September (Figure 34). The moths climbed to altitudes where they were transported on the wind, which



Figure 34 Photograph of the Q-band radar display during the dusk emigration period at Jiangpu, Jiangsu Province, China, on 3 September 1990

PPI display at 18.55 h on 3 September 1990. (Radar beam elevation = 4.9°; distance between range-rings = 0.25 nautical miles (463 m).) Note the dense plume of insect echoes visible to at least 2700 m range (on a bearing of 220° from the radar) streaming downwind towards the west-southwest. Similar plumes were seen just after dusk on several evenings between 29 August and 6 September. They were very probably due to *Omiodes indicata* moths emigrating from soybean fields in the vicinity of the radar site (see Riley *et al.*, 1995b).

was generally towards the western sector, although displacement towards the north or the south occurred on some occasions. It thus seems clear that this species is a windborne migrant, at least under the conditions pertaining in autumn in Jiangsu Province. Migration in *O. indicata* was not restricted to short periods around dusk, however, because the species was caught at heights of 140–250 m during the sampling period from ca. 19.45 h to midnight and, on two occasions, in the period commencing at about midnight. It seems likely that these overflying individuals had taken off at dusk (like the local emigrants detected on our radars), and that the species maintains continuous flights of at least five hours.

Mythimna separata

Outbreaks of the caterpillars of the Oriental Armyworm, *M. separata*, can cause serious damage to cereal crops and pasture grasses in eastern Asia, and Australasia. It is well known that the species is a windborne migrant in the moth stage, and regions of China north of 32–34° N are re-populated each spring and early summer by movements from the south (Li, Wong and Woo, 1964; Chen *et al.*, 1989). In autumn, 'return' movements by later generations towards the south would seem to be advantageous, and there is evi-

dence that they occur (Li, Wong and Woo, 1964). Our observations at Jiangpu in September showed that this species was migrating on winds that would **not** displace individuals significantly further south, and even on winds with a component towards the north. This is consistent with the finding of Chen *et al.* (1989) that *M. separata* migrates in all synoptic situations, and does not show a preference for winds which would carry it in apparently advantageous directions.

Agrotis ipsilon

The economically-important noctuid, *A. ipsilon*, is known (or suspected) to be a long-range migrant in several regions of its almost world-wide distribution (Odiyo, 1975; Showers *et al.*, 1993). The species is unable to overwinter in northern China – none survive north of about latitude 33° N, and the main overwintering area is south of 24–26° N (Nationwide Co-operative Group on Black Cutworm Research, 1990). Moreover, temperatures in the latter area become unsuitably high during summer, so long-range northwards movements in the spring are clearly adaptive for this species in China. It has been suggested that in autumn, *A. ipsilon* moths also move southwards to re-invade their overwintering areas (Nationwide Co-operative Group on Black Cutworm Research, 1990), and our detection of *A. ipsilon* flying on strong northerlies in October provides persuasive evidence that such movements do occur.

Spoladea recurvalis

S. recurvalis is clearly capable of very long migrations because it has been known to invade New Zealand from Australia, together with other Lepidoptera (Fox, 1978). There is also evidence that it migrates to Japan from China in early summer (Miyahara, 1993). The captures of *S. recurvalis* at altitude at both Jiangpu and Dongxiang on nights with strong northerly winds demonstrate that this species undertakes rapid southward movements in China during the autumn, and these could be interpreted as 'return' migrations.

4.6 Insect Pests and Vectors of Plant Viruses in India

Many winged insect pests of agriculture are very small, but in spite of this, they are able to climb to altitudes of several hundred metres and maintain themselves aloft for many hours. Although their flying speeds are low (typically less than 1 m/second), by flying high they benefit from strong winds and can thus achieve rapid, long-distance movements. As well as the aforementioned Brown Planthopper, taxa of importance include other planthoppers, leafhoppers, whiteflies and, particularly, aphids, all of which damage crops, either directly through their feeding activities, or by the transmission of plant viruses. Outbreaks of these pests, or of the pathogens they carry, can be initiated by immigrants from source areas which are tens or even hundreds of kilometres distant from the affected areas. The migratory movements of insect vectors thus play a fundamental role in the epidemiology of the virus diseases they transmit, and some understanding of these movements is necessary for the development of rational disease management strategies.

The migration of a few key vector species in temperate zones has been studied in detail, and it has been possible to devise regional forecasting and warning systems based on monitoring the redistribution of migrant populations (e.g. Tatchell and Woiwod, 1990; Tatchell, 1991). By contrast, little is known of the migration of small insect pests and vectors in the tropics, and this lack of knowledge formed the context for the investigations described below.

Some small migrant insects are sufficiently abundant in the air to be adequately sampled by nets supported by kites or by tethered balloons, and we have frequently made use of such aerial sampling systems to identify the insects detected at altitude by our entomological radars (e.g. Riley, Reynolds and Farrow, 1987; Riley *et al.*, 1991). Thus when we were asked to investigate the atmospheric transport of plant disease vectors in the Indian subcontinent we were well equipped to respond to the request, and carried out aerial netting studies in Andhra Pradesh in central India, and in West Bengal in northeast India. This was the first time that samples had been taken of the insect fauna flying high above the ground over the Indian subcontinent.

AERIAL NETTING STUDIES IN CENTRAL INDIA

This investigation was carried out between 25 November and 14 December 1985 at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, near Hyderabad, in Andhra Pradesh (Reynolds and Wilson, 1989), and was an opportunist expansion of our study on *Helicoverpa armigera* movement in the 'rabi' (post-rainy) season in central India described above (Section 4.3).

Insects flying at about 100 m from the ground were captured in a net of 0.64 m² aperture, equipped with a radio-controlled closing device and a detachable sample bag, and suspended below a 4.18 m² parafoil kite. The equipment and operational procedures were similar to those of Farrow and Dowse (1984), except that our net could be raised and lowered **without** bringing down the kite (see Reynolds and Wilson, 1989), and it carried a wind-run recorder. The insects deposited in the net sample bags were later sorted, and aerial densities were calculated for the various taxa. The height of the net above the ground during sampling runs (typically 100 m) was measured with our X-band entomological scanning radar, or was calculated from the elevation angle subtended by the net (measured by theodolite) and the length of the tethering line paid out. The radar was designed for observations on noctuid moths, and it was not sensitive to **individual** micro-insects: it could, however, detect concentrations of small insects if their densities were high.

Composition of the aerial samples

The taxa caught in the aerial net at the ICRISAT site are listed in Table 4; particular efforts were made to identify species or groups which were likely to be vectors of plant viruses or other crop pests (Reynolds and Wilson, 1989). It was found that insects associated with rice comprised about half of the catch. These included important pests such as *Nilaparvata lugens* (the Brown Planthopper), *Sogatella furcifera* (the White-backed Planthopper), *Recilia dorsalis* (the Zigzag Leafhopper), *Nephotettix virescens* (the Green Leafhopper),

and also predators of rice plant- and leafhoppers such as the mirid bug, *Cyrtorhinus lividipennis*, and the veliid bug, *Microvelia atrolineata*. In fact, there was a distinct similarity between these aerial samples and those taken from above rice paddies during the dry season in the Philippines (Riley, Reynolds and Farrow, 1987), with, for example, *C. lividipennis* being the species most commonly caught in both studies. This similarity was at first sight very surprising because the fields in the ICRISAT district generally contained semi-arid crops such as pigeon pea, chick pea and sorghum, with only small areas of rice. However, our results on the timing and altitude of flight suggested that at least some of the insects caught at ICRISAT had probably migrated from areas far from the site, where there were extensive rice cultivations (see below).

Aphids formed a significantly greater proportion of the Indian samples than of those from the Philippines, and this was presumably a reflection of the greater variety of host crops (other than rice) within migration range of the ICRISAT site. Among the aphid species caught were *Rhopalosiphum rufiabdominalis* (Rice-root Aphid), and the *Aphis craccivora* (Groundnut Aphid) group. The latter transmits about 30 plant virus diseases, and is known to be migratory in other parts of the world (Kranz, Schmutterer and Koch, 1977).

Source areas of micro-insects overflying the ICRISAT site

In the Philippines, high aerial densities of small insects were restricted to short periods around dusk and dawn, but at the ICRISAT site, both the aerial netting and the radar data showed that high densities also occurred at other times of the night. These were indubitably caused by the overflight of migrants from distant sources, and although the numbers of insects were much less than we observed some years later in China (Riley *et al.*, 1991), the events represented substantial migrations. We analysed two of the overflights in detail and used meteorological streamline-isotach maps to construct back-trajectories (Reynolds *et al.*, 1997). The analysis showed that in one case, on the night of 10–11 December, *N. lugens*, *C. lividipennis* and the other overflying, rice-associated insects probably originated from the maturing 'kharif' rice grown along the Krishna River, about 160 km southeast of ICRISAT (Figure 35), or from the area between there and the Andhra Pradesh coast. On this night there was a veering and strengthening of the winds aloft due to the movement of a cyclonic disturbance from Goa to inland Maharashtra State. A rapid movement of *H. armigera* moths into the Hyderabad area from the Krishna Valley or coastal Andhra Pradesh (Pedgley, Tucker and Pawar, 1987) was found to be associated with similar weather. In the second case, on the evening of 25 November, micro-insect densities were the highest recorded during the aerial netting study at ICRISAT (9 per 10⁴ m³), and the migrants included rice pests such as *N. lugens* and *R. dorsalis*, and their natural enemies (*C. lividipennis* and *M. atrolineata*), and aphids (*Aphis* spp). A back-trajectory analysis identified their source areas as being to the east, probably in the region of the Musi and Palleru Rivers (Figure 35).

This short but very informative study established that, at least in the rabi season, semi-arid areas of central India are liable to invasion by a variety of economically important Homoptera. Furthermore, the regularity, intensity and range of the windborne movements is such that pests would almost inevitably be able to colonize even small isolated cropping areas (e.g. small

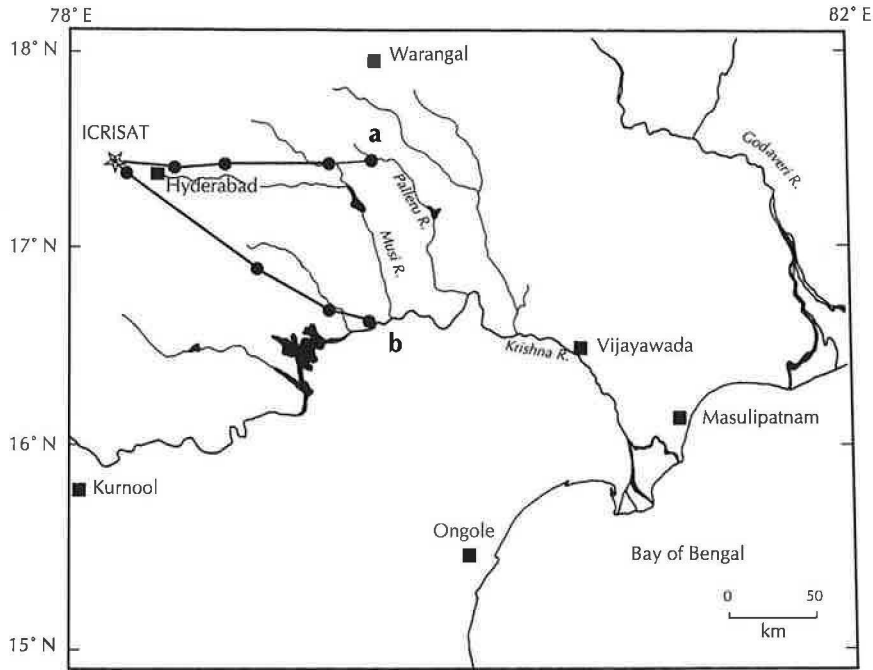


Figure 35 Examples of back-trajectories for small insects migrating over ICRISAT, near Hyderabad, India in late November – early December 1985

The trajectories shown are for small insects overflying the radar/netting site at ICRISAT (a) at 23.45 h on 25 November and (b) at 23.15 h on 10 December assuming take-off at 18.00 h. Species caught included the Brown Planthopper, other planthopper and leafhopper rice pests, aphids, and Heteroptera predators of rice pests. On the first occasion, the migrants appeared to have originated in the region of the Musi and Palleru Rivers and on the second occasion, from cultivations along the Krishna River.

areas of rice paddy surrounded by large areas of rain-fed agriculture). The study also drew attention to the almost ubiquitous presence of certain migratory rice pests, such as *N. lugens*, and it is clear that long-range movement of this species is more common (and presumably more adaptive) in tropical India than it is in the Philippines (see Section 4.4).

Table 4 Composition of aerial net samples taken at a height of 150 m above ground at ICRISAT, near Hyderabad, India, 25 November–14 December 1985

| Order | Family | Species | Total | % of total catch |
|-------------|-------------|--------------------------------------|-----------|------------------|
| Homoptera | Delphacidae | <i>Nilaparvata lugens</i> (Stål) | 52 | 4.1 |
| | | <i>Sogatella furcifera</i> (Horváth) | 12 | 1.0 |
| | | <i>Toya propinqua</i> (Fieber) | 5 | 0.4 |
| | | <i>Toya</i> sp. | 9 | 0.7 |
| | | <i>Sogatodes pusanus</i> (Distant) | 1 | 0.1 |
| | | <i>Sogatella</i> sp. | 1 | 0.1 |
| | | Unidentified | 4 | 0.3 |
| | | Total | 84 | 6.7 |
| Meenoplidae | | <i>Nisia nervosa</i> (Motschulsky) | 1 | 0.1 |
| | | <i>Nisia</i> sp. | 3 | 0.2 |
| | | Total | 4 | 0.3 |

continued

Table 4 continued

| | | | | |
|--------------------------|---|---|-------|-------|
| Cicadellidae | <i>Recilia dorsalis</i> (Motschulsky) | 57 | 4.5 | |
| | <i>Recilia</i> sp. | 4 | 0.3 | |
| | <i>Nephotettix virescens</i> (Distant) | 6 | 0.5 | |
| | <i>Cicadulina bipunctata</i> (Melichar) | 1 | 0.1 | |
| | <i>Cofana spectra</i> (Distant) | 2 | 0.2 | |
| | <i>Inemedara distincta</i> (Motschulsky) | 2 | 0.2 | |
| | <i>Empoascanara</i> sp. | 15 | 1.2 | |
| | <i>Balclutha</i> sp. | 16 | 1.3 | |
| | <i>Empoasca</i> sp. | 6 | 0.5 | |
| | <i>Exitianus</i> sp. | 1 | 0.1 | |
| | <i>Sardia</i> sp. | 2 | 0.2 | |
| | <i>Orosius</i> sp. | 2 | 0.1 | |
| | Unidentified | 2 | 0.2 | |
| | <hr/> | | <hr/> | <hr/> |
| Total | | 115 | 9.1 | |
| Aphididae | <i>Aphis craccivora</i> group + <i>Aphis</i> spp. | 28 | 2.2 | |
| | <i>Aphis</i> spp. | 41 | 3.3 | |
| | <i>Aphis fabae</i> group | 1 | 0.1 | |
| | <i>Rhopalosiphum maidis</i> (Fitch) | 4 | 0.3 | |
| | <i>Rhopalosiphum rufiabdominalis</i> (Sasaki) | 21 | 1.7 | |
| | <i>Saltusaphis scirpus</i> Theobald | 2 | 0.2 | |
| | <i>Hysteroneura setariae</i> (Thomas) | 1 | 0.1 | |
| | <i>Myzus persicae</i> (Sulzer) | 1 | 0.1 | |
| | <hr/> | | <hr/> | <hr/> |
| | Total | | 99 | 7.9 |
| <hr/> | | <hr/> | <hr/> | |
| Homoptera total | | 302 | 24.0 | |
| Heteroptera | Miridae | | | |
| | | <i>Cyrtorhinus lividipennis</i> Reuter | 339 | 27.0 |
| | | Unidentified | 10 | 0.8 |
| | Veliidae | <i>Microvelia atrolineata</i> Bergroth | 121 | 9.6 |
| <hr/> | | <hr/> | <hr/> | |
| Heteroptera total | | 470 | 37.4 | |
| Lepidoptera | Pterophoridae | <i>Sphenarches anisodactylus</i> Walker | 1 | 0.1 |
| | Gelechiidae | <i>Sitotroga cerealella</i> Olivier | 2 | 0.2 |
| | | <i>Timyra</i> sp. | 1 | 0.1 |
| | | Unidentified | 1 | 0.1 |
| | Stathmopodidae | <i>Eretmocera</i> sp. | 1 | 0.1 |
| | Cosmopterigidae | <i>Cosmopterix</i> sp. | 1 | 0.1 |
| | | <i>Pyroderces</i> sp. | 2 | 0.2 |
| | | Unidentified | 2 | 0.2 |
| | Yponomeutidae | <i>Prays</i> sp. | 1 | 0.1 |
| | <hr/> | | <hr/> | <hr/> |
| Lepidoptera total | | 12 | 1.0 | |
| Coleoptera | Curculionidae | <i>Apion benignum</i> Fst. | 8 | 0.6 |
| | | <i>Nanophyes pallipes</i> Roelofs | 1 | 0.1 |
| | | <i>Bagous</i> sp. | 2 | 0.2 |
| | Chrysomelidae | <i>Altica cyanea</i> (Weber) | 1 | 0.1 |
| | <hr/> | | <hr/> | <hr/> |
| Coleoptera total | | 12 | 1.0 | |
| <hr/> | | <hr/> | <hr/> | |
| Other insects (unsorted) | | 461 | 36.7 | |
| <hr/> | | <hr/> | <hr/> | |
| Grand total | | 1257 | 100 | |

AERIAL NETTING STUDIES IN NORTHEAST INDIA

The success of the opportunistic aerial netting work at ICRISAT led several years later to more formal, collaborative work with the Departments of Plant Pathology and Entomology, Bidhan Chandra Krishi Viswavidyalaya (BCKV), Kalyani, West Bengal. Two short aerial netting field studies were undertaken (in November 1992 and March 1994) in northeast India to investigate the

movements of insect pests and vectors, and to train Indian scientists in the use of the aerial trapping techniques. This work was followed by two independent field studies (in May and October 1994) by BCKV staff, with some funding of operational costs from NRI. The collaboration operated under the auspices of a British Council 'Academic Link' scheme, and practical support was also received from the India Meteorology Department (IMD).

We used a kytoon rather than the parafoil kite, because it was a much more convenient and reliable means of suspending the net, particularly in the rather light winds often experienced over India. We had hoped to take a vertical-looking radar sounder so that we could examine the vertical profiles of aerial density with height, and then position the net at the best height for sampling (within any dense layer, for example). In the event, importation constraints ruled this out, but the idea of using a compact and inexpensive radar sounder to support aerial trapping experiments remains very attractive.

All four field studies were carried out in the grounds of the Department of Animal Resources (Government of West Bengal) guest-house at Haringhata, which is adjacent to BCKV campus at Mohanpur, on the outskirts of the town of Kalyani. The aerial netting equipment and procedures were similar to those described in Riley *et al.* (1991) and in Section 4.4 above. We maintained semi-continuous sampling day and night, except during occasional periods of very light winds at altitude (the net will not sample satisfactorily if the wind speed is below about 3 m/second), and the daily sampling regime was mostly divided into six periods: dusk, pre-midnight, post-midnight, dawn, morning and afternoon. The sampling height, which ranged from 130 to 180 m above ground, was calculated from the length of tethering line paid out and the elevation angle (determined using an inclinometer) subtended by the net at the tethering point. The airflow through the net during the sampling interval was estimated from a wind-run meter hung below the kytoon.

Insect pests flying near the ground were monitored using yellow pan traps and a light trap. Synoptic weather data were provided by the IMD at Calcutta airport, and the Department kindly made some additional upper air soundings on our behalf. In 1992, the Department of Electronics and Communications of the Indian Statistical Institute, Calcutta, also participated in the study and deployed a monostatic non-Doppler sodar sounder which allowed us to determine the height of the night-time temperature inversion. We identified likely source areas of the insects caught in the aerial net, by constructing back-trajectories, using the usual streamline-isotach method.

Seasonal changes in the aerial fauna

The total duration of sampling at the Haringhata site was 63.9 hours in the March study, 11.8 hours in May, 112.8 hours in October and 102.6 hours in November. The May study was short because frequent 'Nor'wester' storms with high winds interfered with the sampling programme. The four experiments were timed to represent significant points in the annual cropping cycle:

- March represented end of the winter crop
- May—the beginning of the summer crop
- October—the end of the rainy season crop
- November—the beginning of the winter crop.

The composition of the aerial catches taken in each of the studies is shown in Table 5. Analysis of this data set is continuing (Reynolds *et al.*, in preparation), but it is already clear that seasonal changes in the cropping pattern correlated strongly with the composition of the aerial insect fauna.

Table 5 Composition of aerial netting samples taken about 150 m above ground at Haringhata, near Kalyani, West Bengal

| Order | Family | Species | Sample Period | | | | | | | | | | |
|---------------|--|---|---------------|------|--------------|-------|--------------|------|--------------|-------|-------|-------|--|
| | | | 9-14 March 94 | | 15-17 May 94 | | 21-31 Oct 94 | | 14-23 Nov 92 | | | | |
| | | | No. | % | No. | % | No. | % | No. | % | | | |
| Homoptera | | | | | | | | | | | | | |
| | Delphacidae | <i>Nilaparvata lugens</i> (Stål) | | | 13 | 5.26 | 679 | 6.15 | 136 | 3.17 | | | |
| | | <i>Sogatella furcifera</i> (Horvath) | | | 14 | 5.67 | 323 | 2.92 | | | | | |
| | | <i>Sogatella kolophon</i> (Kirkaldy) | | | | | 11 | 0.10 | | | | | |
| | | <i>Sogatella vibix</i> (Haupt)? | | | | | 1 | 0.01 | | | | | |
| | | <i>Sogatella</i> spp. | 3 | 0.24 | | | 40 | 0.36 | | | | | |
| | | <i>Coronacella sinhalana</i> (Kirkaldy) | | | | | 6 | 0.05 | | | | | |
| | | Unidentified | 12 | 0.98 | 6 | 2.43 | 305 | 2.76 | 126 | 2.94 | | | |
| | Lophopidae | <i>Pyrilla perpusilla</i> (Walker) | | | | | 3 | 0.03 | 2 | 0.05 | | | |
| | Meenoplidae | <i>Nisia nervosa</i> (Motschulsky) | | | | | 29 | 0.26 | 14 | 0.33 | | | |
| | Cicadellidae | <i>Nephotettix virescens</i> (Distant) | | | 2 | 0.81 | 64 | 0.58 | 3 | 0.07 | | | |
| | | <i>Nephotettix nigropictus</i> (Stål) | | | | | 1 | 0.01 | 2 | 0.05 | | | |
| | | <i>Recilia dorsalis</i> (Motschulsky) | | | | | 11 | 4.45 | 77 | 0.70 | 99 | 2.31 | |
| | | <i>Cofana spectra</i> Distant | | | | | | 25 | 0.23 | 12 | 0.28 | | |
| | | <i>Cofana unimaculata</i> (Signoret) | | | | | | 4 | 0.04 | 1 | 0.02 | | |
| | | <i>Macrosteles</i> sp. | 1 | 0.08 | | | | | | | | | |
| | | <i>Empoasca</i> spp. | 2 | 0.16 | | | | | | 6 | 0.14 | | |
| | | Unidentified | 12 | 0.98 | 18 | 7.29 | 461 | 4.17 | 21 | 0.49 | | | |
| | Membracidae | | | | | | 1 | 0.01 | | | | | |
| | Psyllidae | | 1 | 0.08 | | | | | | | | | |
| | Aleyrodidae | <i>Bemisia tabaci</i> (Gennadius) | | | | | | | | 1 | 0.02 | | |
| | Aphididae | Mainly <i>Lipaphis erysimi</i> (Kaltenbach) | | | | | | | | 762 | 17.78 | | |
| | | <i>Myzus persicae</i> (Sulzer) | 1 | 0.08 | | | | | | | | | |
| | | <i>Sitobion</i> sp. | 13 | 1.06 | | | | | | | | | |
| | | <i>Brachycaudus</i> sp. | 1 | 0.08 | | | | | | | | | |
| | | <i>Aphis gossypii</i> Glover | 3 | 0.24 | | | | 1 | 0.01 | 16 | 0.37 | | |
| | | <i>Rhopalosiphum rufiabdominalis</i> (Sasaki) | 3 | 0.24 | | | | 2553 | 23.11 | 13 | 0.30 | | |
| | | <i>Prociphilus</i> sp. | 3 | 0.24 | | | | | | | | | |
| | | <i>Ceratovacuna</i> sp. | 4 | 0.33 | | | | | | | | | |
| | | Unidentified | 5 | 0.41 | | | | | | | | | |
| Heteroptera | | | | | | | | | | | | | |
| | Miridae | <i>Cyrtorhinus lividipennis</i> Reuter | | | | | 11 | 4.45 | 1621 | 14.67 | 864 | 20.16 | |
| | | Unidentified | 3 | 0.24 | 44 | 17.81 | 90 | 0.81 | 27 | 0.63 | | | |
| | Veliidae | <i>Microvelia</i> sp. | | | | | | 29 | 0.26 | | | | |
| | Nabidae | | 2 | 0.16 | | | | | | 6 | 0.14 | | |
| | Hydrometridae | | | | | | | 1 | 0.01 | 2 | 0.05 | | |
| | Pyrrhocoridae | | | | | | | | | 1 | 0.02 | | |
| | Alydidae | <i>Leptocoris acuta</i> (Thunberg) | | | | | | 5 | 0.05 | | | | |
| | Pentatomidae | | | | | | | | | 3 | 0.07 | | |
| | Corixidae | | 1 | 0.08 | | | | | | | | | |
| | Unidentified | | 2 | 0.16 | | | | 89 | 0.81 | 10 | 0.23 | | |
| Ephemeroptera | | | | | | | | | | 1 | 0.02 | | |
| Odonata | | | | | | | | 3 | 0.03 | | | | |
| Orthoptera | | | 2 | 0.16 | | | | 44 | 0.40 | 22 | 0.51 | | |
| Dermoptera | | | | | 2 | 0.81 | | | | | | | |
| Psocoptera | | | 1 | 0.08 | | | | | | | | | |
| Thysanoptera | | | | | | | | | | | | | |
| Thripidae | Unidentified | | | | | | | 2 | 0.02 | 1 | 0.02 | | |
| Neuroptera | | | | | | | | | | | | | |
| Lepidoptera | | | | | | | | | | | | | |
| Yponomeutidae | <i>Plutella xylostella</i> (L.) | | 1 | 0.08 | | | | | | | | | |
| Eucosmidae | <i>Cydia</i> sp. | | | | | | | | | 1 | 0.02 | | |
| Pyralidae | <i>Cnaphalocrocis medinalis</i> Guenée | | | | | | | 26 | 0.24 | 3 | 0.07 | | |
| | <i>Scirpophaga incertulas</i> (Walker) | | | | | | | | | 1 | 0.02 | | |
| | Unidentified | | 1 | 0.08 | 1 | 0.40 | 1 | 0.01 | 2 | 0.05 | | | |
| Noctuidae | <i>Anomis</i> sp. | | | | | | | | | 1 | 0.02 | | |
| | Unidentified | | | | | | | | | 1 | 0.02 | | |
| Nymphalidae | <i>Melanitis</i> sp. | | | | | | | 1 | 0.01 | | | | |
| Unidentified | | | 5 | 0.41 | 3 | 1.21 | 57 | 0.52 | 9 | 0.21 | | | |
| Coleoptera | | | | | | | | | | | | | |
| Carabidae | <i>Casnoidea indica</i> (Thunberg) | | | | | | | 16 | 0.14 | 6 | 0.14 | | |
| | Unidentified | | | | | | | 11 | 0.10 | 9 | 9.21 | | |
| Staphylinidae | <i>Paederus fuscipes</i> Curtis | | | | | | | 132 | 1.19 | | | | |
| | Unidentified | | 2 | 0.16 | 19 | 7.69 | 26 | 0.24 | 114 | 2.66 | | | |
| Lampyridae | | | 1 | 0.08 | | | | | | | | | |
| Coccinellidae | | | 1 | 0.08 | 1 | 0.40 | 28 | 0.25 | 7 | 0.16 | | | |
| Chrysomelidae | | | 1 | 0.08 | | | | 3 | 0.03 | 3 | 0.07 | | |
| Unidentified | | | 4 | 0.33 | 42 | 17.00 | 93 | 0.84 | | | | | |

continued

Table 5 continued

| | | | | | | | | |
|-------------------------|------|--------|-----|--------|-------|--------|------|--------|
| Hymenoptera | 2 | 0.16 | | | 39 | 0.35 | 28 | 0.65 |
| Diptera | | | | | | | | |
| Culicidae (see Table 6) | 42 | 3.42 | | | 76 | 0.69 | 12 | 0.28 |
| Chironomidae | 332 | 27.01 | | | 5 | 0.05 | | |
| Other small Diptera | 87 | 7.08 | | | 309 | 2.80 | | |
| Larger Diptera | 11 | 0.90 | | | 48 | 0.43 | 38 | 0.89 |
| Spiders | 3 | 0.24 | 4 | 1.62 | | | 239 | 5.58 |
| Minute arthropods | 661 | 53.78 | 56 | 22.67 | 3708 | 33.57 | 1654 | 38.60 |
| Total | 1229 | 100.00 | 247 | 100.00 | 11047 | 100.00 | 4285 | 100.00 |

In March, there is little rice under cultivation, and this was reflected in the almost complete absence of rice-associated insects in the aerial samples. A variety of aphid species were caught in this month, among which were pests and virus vectors of winter crops, e.g. rape-seed, mustard, potato and vegetables. Generally, aerial densities were comparatively low, and apart from minute arthropods which were not identified, Diptera (particularly Chironomidae) formed the largest proportion of the March catches. Forty-two mosquitoes also were caught including species which are important vectors of human diseases (see Section 4.7).

The May results were in sharp contrast to those found in March. The early stage of the 'aus' rice crop produced a preponderance of rice-associated insects in the aerial net. These included the planthoppers *N. lugens* and *S. furcifera*, the leafhoppers *R. dorsalis* and *N. virescens*, and predators such as the mirid *C. lividipennis* and the staphylinid beetle *Paederus fuscipes*. No aphids were found in the aerial net during the May study, although species such as *Aphis gossypii* were caught in the pan traps.

The overall aerial density of insects was highest in the October study (over three times higher than in November which had the next highest density) probably because many rice insects were produced from the maturing early-sown kharif rice, and also due to the generally favourable temperature and humidity. There was a greater variety of rice Hemiptera in October than in May: besides large numbers of *N. lugens*, *S. furcifera*, *N. virescens* and *R. dorsalis*, other rice Delphacidae, Lophopidae, Meenoplidae and Cicadellidae were taken in the aerial net. Large numbers of predators, particularly *C. lividipennis*, but also veliid bugs, and staphylinid and carabid beetles, were found to be migrating along with their plant- and leafhopper prey. The presence of high numbers of *N. lugens* in the October netting samples was reflected in the subsequent wide spread incidence of this pest in the kharif crop in 1994. This observation indicates that it may be feasible to use the results of routine aerial trapping to forecast rice pest outbreaks.

Aphids were also very numerous in the October netting samples (2554 specimens caught), but virtually all of them were of one species, *Rhopalosiphum rufiabdominalis*. There was convincing evidence that, on some occasions, populations of this species overflying the site had come from distant sources. In contrast, the yellow pan traps showed that *Aphis gossypii*, *Myzocallis* sp. and *Pentalonia nigronervosa* were flying near the ground.

In November, the rice insect fauna caught in the net was generally similar to that in October. Aerial densities were somewhat lower, which is to be expected because early-sown and short-duration rice had been harvested. Aphids were also common in the aerial net in November, but in contrast to

the previous month, the majority were *Lipaphis erysimi* (a vector of some legume viruses and a pest of rape-seed, mustard and several vegetable crops) with only small numbers of *R. rufiabdominalis* and *A. gossypii*.

Long-range movement in northeast India in November

Data from the November study (the first to be carried out) have been subjected to detailed analysis (Riley *et al.*, 1995a). A notable finding was that substantial densities of aphids, particularly *Lipaphis erysimi*, often migrated at altitude, particularly between midnight and dawn, and the evidence suggested that these flights had started at sometime during the previous day. Continuation of flight into the night by aphids and other small insects is known to occur elsewhere (see references in Riley *et al.*, 1995a), and it may be common on warm nights in continental areas. Nocturnal flight would significantly extend the aphids' range of migration, especially if the insects encounter the fast, low-level wind jets which can develop at night above a temperature inversion.

Our back-trajectories indicated that the *L. erysimi* which overflew the site probably came from 100 to 300 km away to the northeast. As the dominant winds in the post-monsoon 'rabi' season are the northeasterly trades, displacement will frequently be towards the southwest quadrant (as was the case during the present study), unless the weather is affected by disturbances such as cyclonic storms.

In India, *L. erysimi* is virtually absent from the plains during the hot summer, and the species is believed to re-invade lowland cropping areas each autumn from the hills (Kranz, Schmutterer and Koch, 1977). The long-distance movements from the northeast which we detected are clearly consistent with this hypothesis. There are also putative movements of aphids on the **southwesterly** winds in spring, and these would tend to carry the insects from the plains back towards the hills (S. Mukhopadhyay, unpublished). These seasonal migrations may well be adaptive if they allow aphids like *L. erysimi*, which breed parthenogenetically in the tropics, to avoid both the high summer temperatures of the plains and the low winter temperatures of the upland areas. However, even allowing for the seasonal reversal of prevailing winds, aphids are undoubtedly carried in a wide variety of directions and so only a proportion of the migratory population would reach habitats which are, for various reasons (including altitude), seasonally favourable.

The aphids *Rhopalosiphum rufiabdominalis* and *Aphis gossypii* were also found in the post-midnight aerial samples in the November study, and this indicated that, like *L. erysimi*, these species make long-range movements. This was not surprising because captures at sea have shown that both species have at least the **potential** for long flights, and we had already established that *R. rufiabdominalis* engages in nocturnal windborne migration over the Hyderabad area of central India (see above) (Reynolds and Wilson, 1989).

Unlike the aphids, other common species caught in the aerial net in November, such as *C. lividipennis*, *N. lugens*, and *R. dorsalis*, emigrated at dusk. This was reflected in the very low densities (or absence) of these species at altitude during the day, and the massive increase in density around dusk, generally followed by a decline through the night. In some species, like the leafhoppers *R. dorsalis* and *Nephotettix* spp., the decline in density after dusk tended to be fairly rapid, suggesting that **most** individuals flew for only 1.5 hours or less. On the other hand, the netting results showed that substantial numbers of *C. lividipennis* and *N. lugens* remained in flight for many hours during the night, like those in central India, but in contrast to their

behaviour in the Philippines. An overview of the differences in *N. lugens* migration in temperate regions and in various parts of the tropics has been given at the end of Section 4.4.

Technology transfer

During the field studies, BCKV collaborating scientists were given thorough practical training in the use of the aerial sampling system. Further training of junior Indian scientists in the interpretation of synoptic weather data, in trajectory analysis methods and in plant virus detection, was given during their subsequent exchange visits to NRI, which were supported under the NRI-BCKV Academic Link. At the end of the March 1994 study, the complete sampling system was officially handed over to BCKV (along with funds for the purchase of helium for the kytoon). The successful transfer of the aerial sampling technology and expertise to BCKV scientists allowed them to investigate independently the patterns of the airborne migration of insect pests and vectors over northeast India.

Conclusions from the aerial sampling in India

The kytoon-borne netting system was found to be an effective and inexpensive method of investigating the windborne movements of small insects in India. The major drawback of the system was its vulnerability to the sudden onset of strong winds. Our studies provided the first direct demonstration that vector/pest movement occurs at high altitude in northeast India, and we collected convincing evidence for medium- and long-range mass migration by a number of important aphid, leaf- and planthopper vectors of plant viruses, as well as by other insect pests.

Through their participation in the studies, our Indian colleagues came to appreciate the extent of windborne migration of pests and vectors in their region, and of the need to consider the role of invasions from distant source areas in the development of outbreaks. This should lead to improvements in the management of sporadic epidemics of these pests and diseases through improvement of monitoring methods and outbreak warning systems, and through advice on the timing of control measures.

4.7 *Culex tritaeniorhynchus* and other Human Disease-transmitting Mosquitoes

STUDIES OF THE WINDBORNE MIGRATIONS OF *CULEX TRITAENIORHYNCHUS* IN CHINA, AND THE IMPLICATIONS FOR ITS MODE OF OVERWINTERING

Japanese Encephalitis (JE) remains a serious human health problem in east and south Asia (Rosen, 1986). The virus causing the disease is transmitted to humans from pigs and birds by mosquito vectors, principally *Culex tritaeniorhynchus*. In some temperate areas of East Asia (Japan, Korea, northern China) JE reappears in spring or summer, year after year, but it is not known how (or if) the virus survives the winter in these areas. Very few overwintering *Cx. tritaeniorhynchus* adults have ever been found, despite much effort spent in searching for them, and furthermore there is no evidence that the few individuals discovered were carrying the virus through the winter (Rosen, 1986).

These difficulties have led to controversy over the mode of overwintering of *Cx. tritaeniorhynchus*, and about the source of adults of this species which appear suddenly in early spring. Some authors think that local overwintering *in situ* by adult mosquitoes is important, while others maintain that the few individuals which overwinter in this way are not the main source of the next season's mosquito populations, believing that these stem from seasonal invasion by migrants from elsewhere (Ming and Xue, 1997).

Prof. J.-G. Ming of the Shanghai Medical Institute and his co-workers espouse the invasion theory, and had obtained circumstantial evidence that the reappearance of *Cx. tritaeniorhynchus* in the Shanghai area in early spring each year was due to the immigration of insects transported on seasonal south-westerly airflows from tropical or subtropical regions, where the species can breed all year round (Ming *et al.*, 1989). Prof. Ming and his colleagues heard of our radar studies of planthopper migration in China, and saw them as an opportunity to look for direct evidence of windborne migration of *Cx. tritaeniorhynchus*. As a result, they joined us at our experimental site in 1990, and took on the task of sorting and identifying the mosquitoes caught in the aerial net. They also regularly sampled the mosquito population at ground level, using sweep nets.

We caught 15 specimens of *Cx. tritaeniorhynchus* in the aerial net during the September 1990 study at Jiangpu, and consequently thought it worthwhile to make more detailed observations in our next study which was planned for October 1991 in Dongxiang. Forty-four mosquitoes, of which 31 were identified as female *Cx. tritaeniorhynchus*, were caught at Dongxiang, at heights of 80–380 m above ground, and in winds ranging from easterly to north-northwesterly. Most of the female *Cx. tritaeniorhynchus* dissected by Prof. Ming had ovaries with first follicles in the 'N stage' (Ming *et al.*, 1993). Our results thus provided very good evidence for the windborne migration by mosquitoes towards the south in autumn, with the majority of the females in a state of reproductive diapause. Southward migration seems to be adaptive at this time of the year because it takes the mosquitoes towards areas where the breeding season is longer and where winter survival is more likely.

More significantly, our results imply that *Cx. tritaeniorhynchus* also make long-range **northward** migrations into temperate areas of Asia each year in spring, and that this migration is likely to be the vehicle which regularly re-introduces JE into northern latitudes. It would be well worthwhile using aerial netting to find out whether this northward movement actually occurs, and to determine whether any of the migrating females had previously taken a blood meal, and might therefore have acquired the virus.

THE MIGRATION OF MOSQUITO VECTORS OF HUMAN DISEASES IN NORTHEAST INDIA

During the aerial netting studies at Kalyani in West Bengal (see Section 4.6), we caught several medically important species of mosquito (including *Cx. tritaeniorhynchus*) flying at about 150 m above ground (Reynolds *et al.*, 1996). Table 6 gives details of the mosquito catches, and of the human diseases transmitted by these vectors. The fact that the mosquitoes were flying at altitude strongly suggests that these species sometimes engage in long-range windborne movement in this area of the tropics, with consequent implications for the epidemiology of the diseases that they transmit.

Table 6 Mosquitoes in aerial netting samples taken at a height of 150 m above ground at Haringhata, near Kalyani, West Bengal

| Species | Sample Period | | | Human Diseases Transmitted (after White, 1987) |
|---------------------------------------|------------------|-----------------|-----------------|--|
| | 9-14 March 94 | 21-31 Oct 94 | 14-23 Nov 92 | |
| <i>Anopheles vagus</i> Donitz | 16 | | | Bancroftian filariasis |
| <i>Anopheles hyrcanus</i> (Pallas) | | 1 | | Bancroftian filariasis Brugian filariasis |
| <i>Culex fuscocephala</i> Theobald | 4 | | | Japanese encephalitis |
| <i>Culex gelidus</i> Theobald | | 25 | | Bancroftian filariasis Japanese encephalitis |
| <i>Culex quinquefasciatus</i> Say | 20 | 2 | | Bancroftian filariasis*, West Nile virus |
| <i>Culex tritaeniorhynchus</i> Giles | | 19 | | Bancroftian filariasis, Japanese encephalitis*, West Nile virus |
| <i>Culex vishnui</i> Theobald | | 17 | | Bancroftian filariasis, Japanese encephalitis, Ganjam, West Nile virus |
| <i>Culex pseudovishnui</i> Colless | | 4 | | |
| <i>Culex</i> spp. | 2 | | | |
| <i>Mansonia annulifera</i> (Theobald) | | 2 | | Brugian filariasis |
| <i>Mansonia indiana</i> Edwards | | 1 | | Brugian filariasis |
| Unidentified | | 5 | 12 | |
| Total | 42 | 76 | 12 | |

Note: Some aerial samples were also taken between 15–17 May 1994, but no mosquitoes were caught.

4.8 The Desert Locust (*Schistocerca gregaria*)

The Desert Locust (*Schistocerca gregaria*) is the classic outbreak pest. Initially low and innocuous populations of the species can, under favourable conditions, expand enormously and rapidly invade agricultural areas in numbers far above the economic injury level. Large-scale destruction of crops then follows before control measures can be implemented. Thus concentrations of *S. gregaria* occurring virtually anywhere in its distribution area are viewed as a potential threat, and are consequently treated as targets for strategic control. To gain more time in which to plan and initiate control measures, we need the capacity to **forecast** the size and location of potentially damaging concentrations, and, in fact, Desert Locust forecasting has been carried out routinely for more than 50 years (Pedgley, 1981; Magor, 1995).

A characteristic of the Desert Locust which makes forecasting and control particularly difficult, is the great mobility of both the swarms of the gregarious form, and individuals of the solitary form (Pedgley, 1981; summary in Pedgley, Reynolds and Tatchell, 1995). The potential of radar as a means of detecting Desert Locust swarms was realized as early as 1950 (Rainey, 1955; Riley, 1980), and the fortuitous radar observation of a swarm by a ship in the Persian Gulf soon confirmed Rainey's supposition (see below).

In contrast to the day-flying swarms, the migration of *solitarious* Desert Locusts takes place at night and at high altitude, and it is consequently very difficult to study with conventional entomological techniques. Although the seasonal migration pathways of the solitarious form had been broadly defined (largely by analogy with the movements of swarms), and some short-range observations of Desert Locust night flight had been made with searchlights (Roffey, 1963), prior to the advent of radar there was an almost complete absence of information about the migratory flight behaviour of solitarious locusts in the field (e.g. altitude and range of flight, winds used by the migrants, aerial densities, etc.). It was in an attempt to overcome this deficiency, that the Anti-Locust Research Centre sponsored the pioneering radar entomology field trial in Niger in 1968 (as described in Section 2).

EARLY OBSERVATIONS

The first reported radar observation of Desert Locusts was the detection, from a warship of the Royal Navy, of a large swarm over the northern Persian Gulf in March 1954 (Rainey, 1955). The swarm was at least 50 km across, and was composed of mature individuals probably originating from the area of Kuwait about 160 km to the west and northwest. The locusts were airborne after dark, in contrast to the normal behaviour of swarms flying over land, which is to settle around sunset. There has been little direct evidence of nocturnal swarm movement over the sea, although there have been a number of instances where this has been inferred from trajectory calculations (Pedgley, 1981).

Another fortuitous set of radar observations of *S. gregaria* was made when a high-powered 3.2 cm wavelength meteorological radar, operated by the Rain and Cloud Physics Research Centre of the Indian National Physical Laboratory, recorded the passage of some very large swarms over Delhi between 26 and 29 July 1962 (Ramana Murty *et al.*, 1964; Mazumdar, Bhaskara Rao and Gupta, 1965; Rainey, 1967). Assessments were made of the area covered by the swarms, of their aerial density and vertical extent. Rainey (1967) estimated that the number of locusts present within a 100 km of Delhi on 27–28 July was of the order of 10^{11} . The swarms, or parts of the swarms, appeared on the radar in a variety of shapes, particularly long wavy bands, which sometimes coalesced to form larger concentrations: convection cells were also visible in the mass of locusts. Finally, the effects of meso- and synoptic scale winds and zones of convergence on the swarms were studied.

The first **planned** radar observations of Desert Locusts were made during a field study led by G.W. Schaefer in 1968. The vehicle-mounted radar equipment, designed specifically to detect locusts, was deployed in the Tamesna area of Niger in September–October. It turned out most fortunately that this area was traversed by part of the large trans-Saharan migration of *S. gregaria* which occurred at that time (Roffey, 1969; Schaefer, 1969, 1972, 1976). In addition to day-flying locusts in swarms, scattered night-flying locusts overflowed the experimental site, particularly when the wind was from the east or south-east. The radar provided novel measurements of the aerial density, height distribution and ground speed of the locusts, as well as recording events such as synchronized, mass emigration at dusk, concentrations associated with wind-shift lines and common orientation in nocturnal high-flying insects, all phenomena which have subsequently been observed in radar studies of other species. Regarding the unexpected discovery of common orientation, Schaefer found that although the locusts were migrating at low aerial densities, at a mean altitude of about 400 m, and on moonless nights, they nevertheless

somehow managed to 'almost invariably' orientate downwind, and thus maximize their displacement (ground) speed. Other species were subsequently found to have the ability to adopt common orientation (although not always in the downwind direction), but the cues used to achieve and maintain this orientation are still unknown (Riley and Reynolds, 1986; Riley, 1989b). Another discovery, this time not unexpected, was that the returned signal (the radar 'signature') from a flying locust or other large insect was amplitude modulated at the insect's wing-beat frequency – an effect known to occur in radar returns from birds (Eastwood, 1967). Schaefer used the radar-derived wing-beat modulation data to distinguish Desert Locusts from smaller species of acridoids, and even to distinguish male locusts from females.

S. gregaria was also the subject of the first field trial of the newly formed COPR Radar Entomology Unit. The trial was carried out on the northern Tihama of Saudi Arabia in February and March 1972, in collaboration with the Desert Locust Research Centre, Jiddah. Unfortunately, the planned observations on naturally occurring Desert Locusts were frustrated by the extremely low locust populations in the Tihama at the time, which was partly due to a very intensive locust control campaign which had recently been carried out. Nevertheless, the trial was worthwhile in that the observational procedures of the new unit were developed and refined, and useful technical information was acquired from radar observations of released laboratory-bred *S. gregaria* (Riley, 1974). The field study data were complemented by laboratory measurements of the azimuthal dependence of locust radar cross-sections (Riley, 1973).

RADAR OBSERVATIONS OF DESERT LOCUSTS IN MAURITANIA

Despite the great potential of entomological radar demonstrated by the early studies, its use for investigations of Desert Locust migration was not followed-up for many years. This was partly due to the practical difficulties of deploying the radar equipment in a suitable location for observing migrating locusts, particularly during recession (non-plague) periods, but also because of demands to apply the technique to other migratory pest problems.

The next opportunity to make radar observations of Desert Locust flight came during field assessments of the NRI Vertical-Looking Radar (VLR) system in Mauritania in 1993 and 1994. The results from the VLR trial are described in Section 4.9. In this section we limit ourselves to the observations made with a conventional 3.2 cm scanning radar during the 1993 field trial. The scanning radar measurements were made about 15 km northeast of Akjoujt (19°45'N, 14°23'W) in western Mauritania, between 30 September and 9 October 1993 (Riley *et al.*, in preparation). Our radar was similar to the one we had used in previous studies of Acridoidea and of other large insects (e.g. Riley and Reynolds, 1983), and it could detect individual Desert Locusts in flight to a maximum range of approximately 3 km. *S. gregaria* which were flying at night were caught at a light-trap at the radar site, and we believed that these individuals were part of the population which was detected in flight at low altitudes by the radar. Some of the locusts taken at light showed the bright yellow coloration of sexually mature, gregarious phase individuals, while others exhibited a more solitary phase coloration. Whatever their colour, all these nocturnally active locusts were **behaving** as solitaries, i.e., they showed no signs of being in sensory contact with each other. The field trial thus provided an opportunity to observe the night-flight of mature Desert Locusts: previous radar observations had been mostly of immature individuals (e.g. Roffey, 1969).

Preferential flight by Desert Locusts on favourable winds

In order to survive in its arid environment, *S. gregaria* has, in both its gregarious and its solitary phase, evolved behaviour which tends to move it towards areas where rain has recently fallen, i.e., the strategy of downwind displacement (Rainey, 1951, 1963). Although simple downwind movement satisfactorily accounts for the great majority of *S. gregaria* migrations, there are a few regular seasonal movements which are less easily explained. For example, unlike other acridoid species in autumn in West Africa, *S. gregaria* solitaries do **not** appear to move south-westwards (following the southward retreat of the Inter-Tropical Convergence Zone): on the contrary, they move northwards, counter to the prevailing winds and towards the central Sahara (Farrow, 1990). Movements to the south would not be adaptive for locusts at this time of the year because they would take the insects out of their normal desert environment, and the question arises as to how *S. gregaria* avoids them, and how the northward movements are achieved against the direction of the prevailing winds. In the **late** autumn, the prevailing winds from the north are usually cooler and so would tend to limit or even suppress flight until occasions when warmer southerlies appeared, particularly ahead of cold fronts. This mechanism would seem to automatically favour movements to the north, and requires no sophisticated behaviour on the part of the locusts. However, earlier in the season air temperatures are high enough for locusts to fly in winds from **all** quarters, and this has led to the contentious hypothesis that *S. gregaria* must fly 'preferentially' on winds blowing in favourable directions. The timing of our studies allowed us to look for evidence that Desert Locusts selected favourable winds for their flights.

The predominant wind direction at Akjoujt over the observational period was from the northeast quadrant, with occasional winds from the southeast, south or southwest (4 out of 10 nights). We found that aerial densities of radar echoes attributable to solitarily-behaving Desert Locusts were distinctly greater when displacement directions were approximately **towards** the north, i.e., in a seasonally advantageous direction (Figure 36) (Riley and Reynolds, 1996). In other words, it appeared from the observations that the

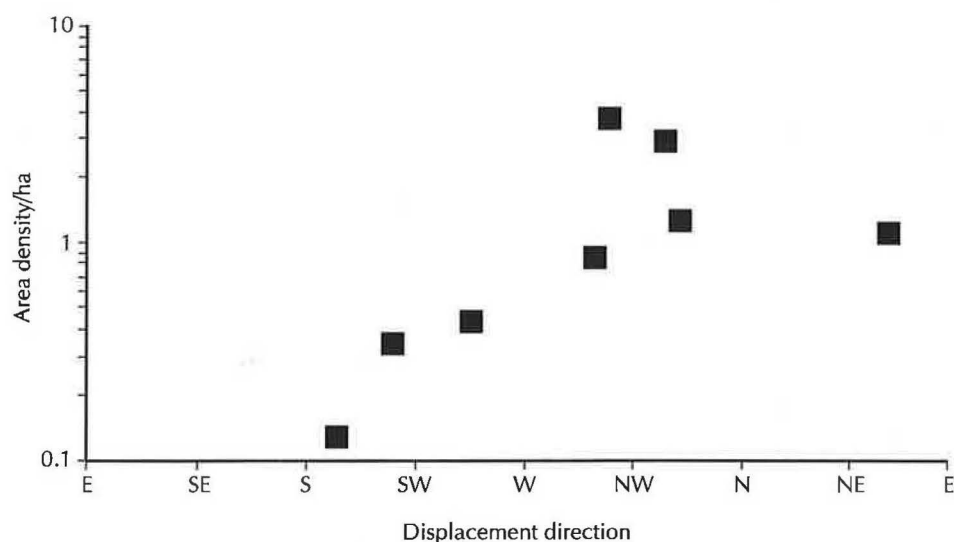


Figure 36 Relationship between the number of flying locust-sized insects and their direction of displacement, as observed on eight evenings between 2 and 9 October 1993, at Akjoujt, Mauritania

The number of insects is expressed as the sum of those airborne, at all altitudes above 40 m, over an area of 1 ha. The peak value for each night is plotted against the mean direction of displacement at the time the peak was observed.

locusts **did** fly 'preferentially' on winds from the south. We are continuing the analysis of our data to see if we can find any indication of the cues are used by the locusts to discriminate between southerly and northerly airstreams.

4.9 Long-term Automatic Monitoring of Aerial Insect Faunas

The complexity, cost and the form of the data output make 'conventional' entomological scanning radars unsuitable for **long-term routine** monitoring operations. By contrast, the new Vertical-Looking Radar (VLR) technique developed by the NRI Radar Unit (Smith, Riley and Gregory, 1993; Riley and Reynolds, 1993; Riley, 1993a; Riley, Smith and Gregory, 1993), under the ODA Innovative Research Program, makes possible the continuous monitoring of airborne insect movements for extended periods, e.g. over whole seasons. The inexpensive system can capture a wealth of data on individual migrants (e.g. altitude, direction and speed of movement, heading direction, and target size and shape), process it rapidly by microcomputer, and present it in a form readily comprehensible to non-specialists. The VLR is ideally suited to the routine surveillance of migratory pests (Riley and Reynolds, 1993; Drake, 1993), and in 1993 and 1994 we carried out field trials in Mauritania to evaluate the VLR as a monitor of solitary Desert Locust migration.

THE USE OF VERTICAL-LOOKING RADAR IN MONITORING DESERT LOCUST MIGRATION

Rationale for the proposed use of VLR in Desert Locust forecasting

During periods of recession, the Desert Locust exists at low densities, behaving in a solitary manner. Such locusts are found mainly in the remote and normally arid **recession** area, but if they encounter exceptionally favourable conditions (i.e., areas where widespread and heavy rains have fallen), they breed successfully and generate the gregarizing populations which give rise to local **outbreaks** (Roffey 1994). If an outbreak is followed by two or more successive breeding cycles of *transiens* to gregarious populations which are able to migrate between complementary breeding areas, there will be an enormous increase in numbers of locusts (Waloff 1966, Magor 1994a and b), which may lead to an **upsurge** or even a full locust plague.

Thus, the windborne nocturnal migration of behaviourally *solitary* locust populations is probably a critical determinant in the onset of outbreaks, and it is also of particular significance in the early stages of upsurges (Pedgley 1981). If it were practicable to monitor these movements using automatically operating VLRS this would make possible more accurate, reliable and rapid detection of outbreaks in key areas. Where monitoring in remote areas was required, the radar could run on solar power and report via a satellite telephony link to central forecasting services. It is envisaged that a network of radars could be used to confirm and update predictions of locust migration made by forecasting services, and also to detect any unexpected movements. This would increase the accuracy and reliability of forecasting, and so lead to more efficient control.

The VLR field trials in Mauritania

We deployed the VLR in Mauritania in order to evaluate the robustness of the system for continuous nightly observations under the range of weather conditions and background insect densities expected in a typical *S. gregaria* summer breeding area in West Africa. We needed to know, for example, if insect aerial densities frequently reached values high enough to cause breakdown in the VLR analysis procedure. Equally, if other insects of comparable mass but different shape from Desert Locusts were found to be present, we required evidence that the VLR could, in fact, distinguish between them. We also took the opportunity to test modifications to the prototype VLR software.

The trials were carried out in three widely separated localities: near Akjoujt (19°45'N, 14°23'W) and at Achram (17°23'N, 12°24'W) in September-October 1993, and near Aioun-el-Atrouss (16°38'N, 9°37'W) in the same months of 1994 (Riley and Reynolds, 1997). At Akjoujt, a conventional scanning entomological radar was also deployed in order to check the accuracy of the VLR flight trajectory and aerial density measurements. The integrity of the insect displacement speeds and directions produced by the VLR at Aioun was thoroughly checked by comparison with wind velocities determined from pilot balloon ascents. The trials were primarily intended to evaluate the capacity of VLR to monitor **nocturnal** flight by non-swarming locusts, so the radars were operated each day from dusk until flight activity declined to a low level, usually around midnight. Occasionally the VLR was set to run automatically until dawn. The field trials were carried out in collaboration with the Direction du Développement des Ressources Agro-Pastorales (DDRAP) of the Islamic Republic of Mauritania, and with the logistic support of Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ).

Figures 37a and b show a typical examples of insect displacement direction and speed data produced by the VLR from the Aioun-el-Atrouss site. Figure 37c gives a distribution of radar cross-sections from which mass can be estimated and, in this example, Desert Locusts could have accounted for only about 3 % of all the insects detected. For much of the time, the percentage of targets in the locust cross-section range was much lower than this, demonstrating that Desert Locusts comprised at most only a small part of the aerial fauna. This pattern was repeated at Achram, and also at Akjoujt, where the scanning radar data confirmed that the aerial density of locust-sized targets was very low (typically less than 5 locusts per 10^6 m³). This aerial density would result in the interception of only one or two Desert Locust-sized targets per hour by the VLR. Nevertheless, given the significance which is attached in forecasting work to the sighting, in certain circumstances, of even single Desert Locusts, the data acquired by the VLR would appear to be potentially very valuable (Riley and Reynolds, 1997).

In spite of the harsh environment, the radar hardware and software performed well during the experimental period, and the provisional results of our trials in Mauritania indicate that Desert Locusts could be reliably detected on the basis that their mass differed significantly from virtually all other airborne insects expected in their desert environment. Thus VLR has the potential to provide an inexpensive and effective means of detecting any significant increase in locust movement between complementary breeding areas, and it could be used to supplement (and to a certain extent replace) conventional survey data in operational Desert Locust forecasting.

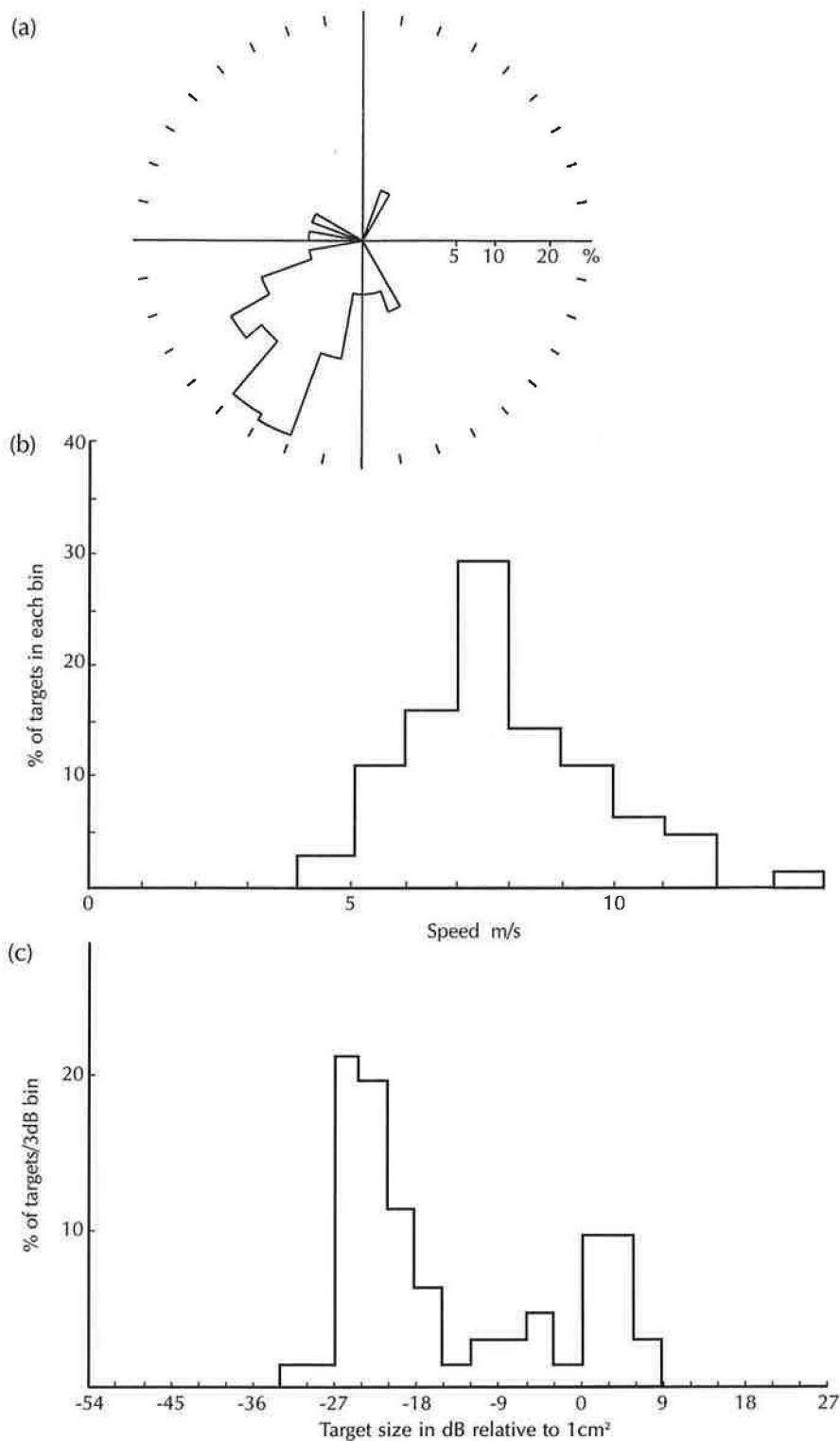


Figure 37

Distribution of (a) displacement directions (b) horizontal speeds and (c) a radar cross-section parameter, for 61 insect targets detected by the nutating vertical-looking radar at Aioun-el-Atrouss, Mauritania, on 27 September 1994

These insects were recorded by the VLR during the 5 minute period between 22:18 and 22:23 h in an altitude range between 150 m and 1000 m above the radar. In (a) north is vertical and the radial axis is scaled to produce an equiareal plot; (c) shows the distribution of the radar cross-section parameter σ_{xx} from which estimates of insect mass can be derived. Desert Locusts might typically have values of σ_{xx} in the region of 7 cm² i.e. ≈ 8 dB relative to 1 cm² so they could have accounted for about 3% of the total insects in this figure.

Funding was therefore sought to permit the installation of an operational monitoring system in Mauritania or another locust-affected country, and to train local operatives in its use. However, in spite of initial enthusiasm by UNDP and IFAD, budget reductions have meant that such funding has unfortunately not materialized.

PROSPECTS FOR THE OPERATIONAL USE OF VLR IN MONITORING PEST MIGRATION

The Chinese Ministry of Agriculture have recently approved a proposal by Nanjing Agricultural University to construct and install an experimental VLR for monitoring migratory insect pests, particularly the seasonal invasions of temperate China by rice pests from the south. NRI Radar Unit personnel will act as the main technical consultants for this project.

Interest in the VLR technique has also been expressed by the Agricultural Development and Advisory Service (ADAS), and the Institute of Arable Crops Research (IACR), Rothamsted, for operational pest management applications in the UK.

The technique has also been taken up in Australia, where V.A. Drake of the University of New South Wales, is currently carrying out an operational trial to monitor migrations of locusts in collaboration with the Australian Plague Locust Commission. Drake is also using a VLR in a study of *Heliothis zea* migration in a collaboration with the US Department of Agriculture's Areawide Pest Management Research Unit (APMRU) in Texas.

Finally, the Alliance for Aerobiology Research (AFAR) is interested in the role of VLR as part of their 'Bioflow' proposal, which would undertake long-term measurements of biotic flows of a range of organisms in the atmosphere over heights up to ~2 km throughout the USA (V.A. Drake, unpublished), perhaps in conjunction with the US National Weather Service's operational network of 'NEXRAD' Doppler weather radars.

THE OPERATIONAL USE OF VLR FOR BIODIVERSITY AND ENVIRONMENTAL PURPOSES

As well as its uses in pest forecasting and management, the VLR technique holds promise for applications in the fields of environmental impact assessment, environmental change and conservation of biodiversity. The method would appear to be particularly suited to rapidly detecting any gross effects on the insect fauna occurring over extensive areas, and would apparently have the advantage, over other techniques, of low manpower costs. Potential applications are described below.

Environmental impact assessment (EIA)

The environmental impact of activities which may cause short-term environmental disturbance, e.g. side-effects of large-scale pesticide spraying against (say) tsetse fly or armyworm, could be assessed by monitoring changes in the general abundance and diversity of the aerial insect fauna. Any gross effects should be reflected in changes in the numbers of airborne insects, and these should be readily detected by the radar. There seems no reason in principle why VLR should not be used to monitor the ecological effects of longer-term human activities e.g. deforestation, changes in land use, and pollution, or even

semi-natural events, such as climate change, which could be expected to produce long-term changes in insect biodiversity. Such projects may best be carried out in conjunction with a trap network such as the Rothamsted Insect Survey. In some cases, however, it may be easier to compare blocks of disturbed and undisturbed habitat simultaneously (e.g. logged areas and undisturbed forest) rather than study one block which is changing over a long time period.

Evaluation and comparison of relative diversity

Evaluation and comparison of the **relative diversity** of different ecosystems or habitats, can be used to establish priorities for conservation and the sustainable management of biodiversity, and to plan conservation areas.

It would appear that the biodiversity of extensive areas of different habitats (e.g. plantations versus natural forest) could be compared (in terms of the aerial fauna produced in each) by using radar-generated matrices of diversity (rather than absolute measures of species diversity). Radar monitoring may have advantages over more conventional trapping methods here. Firstly, surveys would be relatively rapid in that the VLR could monitor large numbers of flying insects (and perhaps a fair proportion of the fauna of an extensive area) in a relatively short time and this would be very likely to reveal gross differences in diversity between the habitats. Secondly, 'radar taxonomy', if this would suffice, would remove the need for detailed and lengthy identification of specimens by highly skilled and expensive taxonomic experts. Some developmental work would be required to determine whether **relative**, radar-generated indexes of diversity could be related to ecosystem type or quality.

Other 'environmental' research topics

Besides the monitoring of biodiversity and environmental impacts, studies of fundamental ecological processes occurring in fragile environments may be required. For example, there is practically no information on the amount of insect movement that occurs above the canopy in tropical forests, and VLR would be a highly appropriate technique for such a study.

4.10 Tracking Low-altitude Insect Movements with Harmonic Radar

Radar has been used successfully for over twenty-five years in studies of insect flight, but nearly all of these studies were designed to investigate one type of flight, viz. migration at high-altitude. However, much insect movement is non-migratory, and is concerned with searching for food, shelter, mates, egg-laying sites, avoiding predation, or maintaining the individual in a suitable habitat. These 'vegetative' movements usually take place near the ground and are often on a small scale compared to migration. Very fine-scale movements (over a few metres) can be tracked by video (Riley, 1993b) or followed by marking the insect's positions with flags and then surveying these with an electronic theodolite (Wiens, Crist and Milne, 1993). For movements over slightly longer distances (> 10 m), radar might be expected to have a role. However, until recently, it has been very difficult to employ radar techniques to observe insects flying at **low altitude** because the very strong radar returns from ground features and vegetation (**clutter**) obscure the tiny signals returned by insects, unless they are flying over extremely flat and featureless terrain (e.g. Loper, Wolf and Taylor, 1993).

We have recently developed a new harmonic radar system which has a maximum range in excess of 700 m and displays target range and bearing on a conventional radar PPI screen (Riley *et al.*, 1996). This system was designed to facilitate studies of short-range, low-altitude insect flight – specifically of tsetse flies, and it has already been successfully field tested with honey bees and bumble bees.

FIELD TRIALS WITH BEES

Trials were carried out in collaboration with the Bee Research Group at IACR-Rothamsted, Harpenden, UK, in August 1995 and in June and August 1996, initially with the idea of using bees simply as flying test-beds (Riley *et al.*, 1996; Carreck, 1996; Osborne *et al.*, 1997; Williams *et al.*, 1997). Tagged and numbered honey bees (*Apis mellifera*) and bumble bees (*Bombus* spp.) were released and tracked as they flew between nest and forage sites. The bees appeared unperturbed by the tag, the duration of foraging trips and the amount of pollen collected being the same as for untagged bees. Because

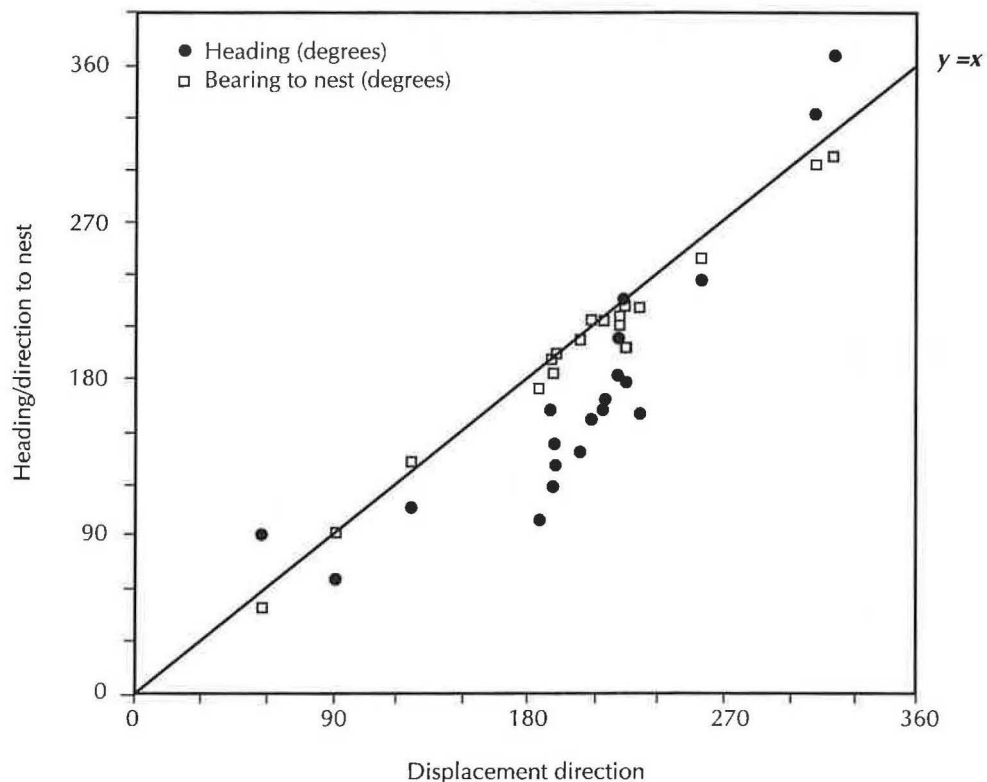


Figure 38 Harmonic radar data on bumble bee (*Bombus* spp.) flight

This figure shows how the dynamic flight behaviour of low-flying insects can be studied in detail by the new harmonic radar technique. The radar produced measurements of the homeward flights of bumble bees, and by subtracting the local wind velocity from the speed velocity of the bees, it was possible to calculate their airspeed and heading.

When the displacement directions were plotted against the direction straight back to their nests (open squares), they were found to be travelling over the ground in almost exactly the right direction to get back home (i.e. the squares lie on, or very close to, the $y=x$ line in the figure). Plotting their heading directions against the home direction (solid circles) showed that they were apparently laying off this direction in a way which prevented them from being drifted by crosswinds away from the homeward line. If this result is correct, it indicates remarkably sophisticated navigation behaviour on the part of the bees. However, the experiment needs to be replicated with more refined local wind measurements before it can be claimed that these provisional results are accurate.

the radar tracks the actual course of the bee, detailed information on the directness and range of flights is obtained. Heading and air speed of the bees can be calculated by subtracting the wind velocity from that of the bees as measured by the radar, and this yields additional information on flight behaviour such as compensation for unfavourable winds (Figure 38).

The trials clearly demonstrated the potential of this powerful technique, and although analysis of the data is not yet complete, it seems clear that valuable information on bee behaviour will be obtained, which can be used to improve conservation and management strategies of domestic and wild bee populations, especially in fragmented habitats.

The bee tracking experiments generated an enormous amount of interest by television, radio, newspapers and magazines, both in this country and abroad, and this publicity has generated many enquiries from scientific groups in Europe and the USA.

PROSPECTS FOR THE USE OF HARMONIC RADAR TRACKING

Harmonic radar tracking seems certain to have very wide application in studying 'vegetative' flight behaviour, or short-range dispersal, of large and moderate-sized insects in the field, and it is difficult to envisage all its possible future uses. Some research proposals with a 'developing country' focus include the following.

Tsetse flies

Trypanosomiasis spread by tsetse flies (*Glossina* spp.) is a major constraint to agricultural production in large areas of Africa because of its effects on human health and livestock production. Dr Glyn Vale of the Regional Tsetse and Trypanosomiasis Control Programme (RTTCP) has been a strong advocate of the development of harmonic radar, and our proposed collaboration with him and the Tsetse and Trypanosomiasis Control Branch (TTCB) of the Zimbabwean Department of Veterinary Services, remains the principal objective of the harmonic radar development effort.

In recent years, tsetse control by insecticide spraying has been largely replaced by the use of insecticide-impregnated baits and targets (which attract the flies by a combination of odour and visual stimulus) and the continual improvement of these techniques has been heavily dependent on research into tsetse behaviour. For example, certain types of flies are still under-represented in the traps, and there is a need for tracking of individual flies (Vale, 1993), so that opportunities for the further development of baits can be explored. If we are successful in further minaturizing the transponders so that they can be easily carried by the tsetse, one research objective would be the measurement of rates of progress of flies up odour plumes. Experiments using video and trapping have allowed progress in understanding how tsetse orientate with respect to these plumes, but the underlying mechanism is still unclear (e.g. Griffiths, Paynter and Brady, 1995). By greatly extending the range over which tsetse flight paths can be observed, harmonic radar should help resolve this question.

Harmonic techniques may also increase our knowledge about the behaviour of tsetse during periods when they are **not** attracted to traps or hosts, and are consequently difficult to find and study. A portable harmonic direction-finding system, currently under development, may have a role in locating the tsetse and discovering what they are doing during these periods.

Moths

Artificially synthesized pheromones have been used as lures in attractant traps for both monitoring and control of many insect pests. A particularly active area of research has been the use of the sex pheromones of pest Lepidoptera for control by mass trapping, 'lure-and-kill', or mating disruption. These techniques avoid the use of toxic chemicals and are to a great extent species-specific. Pheromone traps have also been used to **monitor** lepidopteran pests, with a view to predicting damage levels in crops so that insecticide applications can be made in a more rational manner. However, it is clear that the pheromone traps for some important species (e.g. *Helicoverpa armigera*) are far from efficient, and information on pheromone-following flight by individual moths would be very useful in the re-design and optimization of the traps.

We have already demonstrated (in collaboration with Peter Valeur of the University of Lund, Sweden) that our harmonic radar can track the noctuid moth species, *Agrotis segetum*, in the field (Riley *et al.*, unpublished observations), and there seems little doubt that the pheromone-following flights of other large pest noctuids, e.g. *Helicoverpa armigera*, could also be studied by this means.

Triatomid bugs

Triatoma infestans is the principal vector of Chagas' disease of which there are estimated to be 16–18 million cases in South and Central America, and a further estimated 90 million people at risk (World Health Organization, 1990). Control of the disease presently depends on control of the vector, but *T. infestans* often spreads back into areas from which it has been eradicated, partly by being carried on hosts and partly by flight. Knowledge of the flight behaviour of the vector is therefore of great importance in optimizing control strategies. It has been proposed that the NRI Radar Unit, in collaboration with Dr P. McEwen of the University of Wales, Cardiff, and others, would use harmonic radar to study *T. infestans* dispersal flights in the field, possibly in Argentina.

Bees

Finally, we mention the possible use of the harmonic radar technique to increase our knowledge of the foraging behaviour of honey bees in developing countries. The encouragement of bee-keeping by rural people in these countries addresses many desirable development objectives (Bradbear, 1990). The main collaborator here would be Dr N. Bradbear of 'Bees for Development'.

Section 5

Overview

Movement is a **critical** factor in the dynamics of migratory insect populations, and no rational management strategy for a particular insect pest is possible without some knowledge of whether it is migratory or not. Establishing unambiguously that a species is a long-distance migrant allows the focus of discussions to move forward to a quantitative consideration of the effects of the movements. 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. This was particularly the case where evidence for migration came from the capture of just a few individuals, whose behaviour could have been representative of only a tiny and anomalous minority of a given population, rather than of the population as a whole. Radar's unequivocal and graphic demonstrations of the migratory performance of whole populations have so transformed this situation that the uncertain state of our former knowledge is now not always remembered or appreciated.

As well as showing that a particular insect pest is migratory, the unique ability of radar to observe undisturbed high-altitude movement **while it is in progress**, allows us to quantify this process (in terms of aerial densities, altitudinal distributions, displacements, and the migratory flux of insects passing overhead). This information can then be used to develop models and other procedures for forecasting and managing pest outbreaks. The use of radar-derived height of flight data in the Chinese trajectory models of Brown Planthopper migration is just one example.

In this compendium we have shown how migration studies using relatively unsophisticated and inexpensive entomological radars, aerial netting and ground trapping, have allowed great strides to be made in our knowledge of insect pest migration in developing countries. However, this highly productive research era, which corresponded to the first quarter-century of radar entomology as a separate discipline, may be largely over. This is mainly because organizations supporting radar entomology facilities now tend to charge full overheaded costs for staff time, and this makes the traditional, labour-intensive radar entomology field study appear prohibitively expensive.

The way forward may lie in the deployment of inexpensive vertical-looking nutating radars (VLRs) which allow unmanned operation over long periods and provide automated data analysis (as discussed in Sections 3 and 4.9). This avenue was opened when NRI succeeded in developing an algorithm to analyse VLR signals (Smith, Riley and Gregory, 1993), and there are good prospects that insect monitoring radars of this type may be incorporated into **operational** pest forecasting systems, at least in China, where accurate forecasting is accorded high priority.

Much international interest has been shown in another recent technical innovation by NRI – the use of harmonic radar to track insects in flight at low altitude. This technique has many exciting potential applications in the study of both beneficial and pest insects, and it seems certain to provide new insights into the low-altitude flight behaviour of a variety of insects.

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