

RECENT APPLICATIONS OF RADAR TO ENTOMOLOGY

J R Riley, J W Chapman, D R Reynolds* & A D Smith describe how new applications of advanced radar systems have been used to reveal the flight patterns of both high and low flying insects

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Abstract

This paper describes recent applications of vertical-looking radar to monitor migratory insect movements at high altitude, and of harmonic radar to record the flight paths of low-flying insects. Examples are given of how these radars have revealed novel information about the flight of bees, butterflies, moths and carabid beetles. The paper also briefly mentions some technical innovations designed to improve the performance of these radars.

Introduction

In a recent article in the influential American publication *Bioscience*, Jason Chapman pointed out that: *Millions of metric tons of insects are aloft in Earth's atmosphere at any one moment* (Chapman *et al.* 2003). This is an alarming figure, given that a significant proportion of these insects are likely to be pests of crops or vectors of disease (Reynolds *et al.* 2006), and at first sight it also seems rather unlikely – after all (rare locust plagues aside) the sky never seems to be *that* full of insects. But it turns out that the discrepancy between Chapman's claim and common experience is not hard to explain, because most of these airborne insects are invisible, either because they are flying much too high to be seen, and/or because they are flying in the dark. This 'invisibility' meant that the true magnitude of insect aerial movement became apparent only after radar was introduced to entomology in the late 1960s. It is, therefore, not surprising that almost all of our current knowledge of the flight behaviour of high-altitude insect migrants has been derived over the past four decades from the use of this powerful technique. The aim of this paper is to show how radar entomology is now being carried forward by the continuing evolution of two novel techniques: *harmonic radar* for observing low-flying insects, and *vertical-looking radar* for long-term monitoring of high altitude insect abundance and movement. The effectiveness of these techniques is illustrated by a summary of some of their recent applications to studies of insect flight at high and at low altitudes.

It is now 57 years since it was first shown that radar could detect individual flying insects (Crawford 1949), but 20 years elapsed after this demonstration before the first biologically useful radar studies of insect flight were made. These

pioneering studies (Schaefer 1969; 1976) of locusts, grasshoppers and moths were successful enough to stimulate the evolution of radar entomology into a discipline in its own right (Riley 1980, 1989; Reynolds 1988, and see <http://www.pems.adfa.edu.au/~adrake/trews/>). Most of the early observations were made with simple, 3-cm wavelength marine radar transceivers connected to parabolic reflectors that were equipped with a tilting mechanism, and mounted on a rotating platform. This arrangement generated a narrow radar beam (typically 1–3° wide) that scanned in azimuth at about 20 revolutions per minute and could be set at any desired angle of elevation. Any airborne insects (of sufficient size) that were intercepted by the rotating beam registered as individual 'dots' on a conventional 'plan position indicator' (PPI) radar display. Typical working ranges extended up to 1.5 km for individual grasshoppers and moths, and to several km for dense concentrations. Analysis of photographic records of the PPI display gave values for the direction and speed of the insects, their aerial density, and their altitude. A clue to their identity could be obtained by stopping the rotation, and recording the amplitude of the radar 'echoes' returned by any targets that flew through the stationary beam, because these signals were often modulated at the targets' wing-beat frequencies (Riley 1974).

Over the following years, data acquired in this way (mostly on pest species of grasshoppers, locusts and moths) have vastly increased our knowledge of the high altitude flight behaviour of long-range insect migrants (see reviews in Reynolds 1988; Riley 1989; Reynolds & Riley 1997, 2002). But powerful though the early scanning radars were, they suffered from three major constraints. Firstly, the labour-intensive nature of both the observations and the analysis made long-term studies impractical; secondly, target identification capacity was very limited; and thirdly, low-flying insects could not be reliably detected because of the obscuring effect of strong radar echoes from ground features (clutter). We describe below how all three of these limitations have been eased by two new technical developments – *vertical-looking radar* and *harmonic radar*.

Vertical-Looking Radar for Monitoring Insect Flight at Altitude

Outline of the Technique

Vertical-looking radars (VLR) developed for entomological observations are mechanically much simpler than the conventional scanning radars used in earlier studies, in that they project a narrow, conical beam vertically upwards from a



Figure 1: A vertical-looking radar installed at Rothamsted Research. The radar is controlled by a personal computer, and operates 24 hours a day throughout the year, monitoring the passage of overflying insects in the altitude range from approximately 150m to 1200m above ground level.

stationary reflector (Figure 1). The radar beam is offset slightly from the vertical and the beam, together with its plane of polarisation, is rotated continuously. This produces a narrow-angle, conical scan system which yields a wealth of information about overflying targets (Chapman *et al.* 2002a). Individual insects pass through the beam, and analysis of the radar signals reflected from them yields their speed and direction of movement, their body alignment, and estimates of mass and body shape (Smith, Riley & Gregory 1993). Wingbeat frequency can sometimes also be extracted from the returned signals (Drake, Wang & Harman 2002a). Because both the operation of the radar and the analysis of the data are performed by a computer, long-term (months or years), continuous observational programs can be undertaken (Chapman, Reynolds & Smith 2003). Computerised operation also means that radar can be set up for surveillance in remote areas, but controlled and interrogated from the home laboratory hundreds of kilometres away (Drake, Wang & Harman 2002b).

Some Recent Applications of Vertical-Looking Radar

Diamondback Moth (Plutella xylostella) Immigration into the UK

A great advantage of VLR is that flight monitoring can be maintained automatically for 24 hours a day, for months and even years on end, so the technique can be used to detect unpredictable and short-lived migration events. In this study, data acquired on the insect fauna overflying a VLR at Rothamsted, Harpenden, UK, over a three year period, were used to investigate the immigration of the diamondback moth (*Plutella xylostella*), a serious world-wide pest of cruciferous

vegetables. The species was identified by a combination of size and shape data extracted from the radar signals, combined with short, but intensive periods of aerial trapping from balloons. The radar data on aerial density, and on direction and speed of movement of *P. xylostella*, were supplemented by records of the temporal variation in the species' abundance derived from the Rothamsted Insect Survey's network of light traps. Taken together, these results showed that a major immigration from Holland to the UK occurred in early May 2000, and that immigration from mainland Europe is responsible for the annual re-establishment of the UK population of the species (Chapman *et al.* 2002b)

Nocturnal Layering of Insects (mainly Noctuid Moths) over the UK

The capacity of VLR to sustain monitoring for extended periods also means that long-term, systematic investigations of general flight behaviour can be undertaken. The focus of this study was the altitudinal distribution of insect fauna over the UK, over time scales ranging from instantaneous vertical profiles, updated every 15 minutes, to long-term profiles aggregated over whole seasons. Aerial density data from VLRs in two geographically separated sites revealed that, on occasions during warm nights in the summer months when intense insect layers developed, the insects were flying preferentially at the top of strong surface temperature inversions. In other cases, layering was associated with higher-altitude temperature maxima, such as those due to subsidence inversions, and sometimes double layers were present (Reynolds *et al.* 2005). The radar data showed that the layers were formed by insects of a great variety of sizes, but peaks in their mass distributions on certain occasions pointed to a preponderance of noctuid moths.

This work was carried further by comparing radar measurements of insect density profiles, with concurrent meteorological profiles generated by the UK Meteorological Office's Unified Model (UM) for the 'air column' above each radar. Three factors were identified that appeared to determine the heights at which nocturnal layer concentrations formed. These were: the altitude of the warmest air (as described above); heights that corresponded to species' temperature preferences for sustained migration (ceiling layers); and occasionally, on nights when air temperatures are relatively high at all levels, the heights at which wind-speed maxima associated with the nocturnal jet occurred (Wood *et al.* 2005).

Diurnal Migration in the Carabid Beetle (Notiophilus biguttatus)

Because the characteristic mode of locomotion of carabids (Coleoptera: Carabidae) is by walking or running, they are generally considered to have rather limited mobility. This is certainly true for some species (or morphs within the species) as they are morphologically or behaviourally flightless. However, when we used VLR (together with traps at 12 m and 200 m above ground), to document high altitude movements of insects over agricultural land in southeast UK, we discovered that the long-winged (macropterous) form of the carabid *Notiophilus biguttatus* was one of the most common

airborne insects in its size range (~5 mg). This observation was an unexpected and revealing result in view of the conclusions of an earlier, classic Dutch study by den Boer and colleagues that had firmly classified *N. biguttatus* as a poorly dispersing species which tended to become isolated in remnants of natural habitat. We believe that the discrepancy between the two studies implies that a very recent adaptation of the beetle's migration syndrome has occurred, that allows the species to better exploit the mosaic of temporary habitat patches making up the increasingly intensive agroecosystems of northern Europe (Chapman *et al.* 2005).

Some Recent Technical Developments

Efforts to enhance the performance of the VLR technique have been recently directed towards a better theoretical characterisation of the radar-reflecting properties (backscattering) of insects at ventral aspect (Dean & Drake 2005), with a view to improving target identification. In our laboratory, we have been examining the use of fast A-D converters that should enable us to achieve a higher accuracy of signal acquisition, so that radar backscattering cross-sections can be measured with greater precision, with concomitant improvements in the estimation of the body mass of detected insect targets. We have also been using sensitive radar cross-section measuring equipment (Riley 1985; Hobbs & Aldhous 2006) to describe the ventral-aspect radar cross-sections of insect species that we expect to overfly our radars.

The possibility of using VLR to monitor the migratory movements of small insects (down to 2mg) has also been investigated, and it seems clear that this should be feasible, provided that the technical resources needed to produce a millimetre-wavelength radar can be realised (Riley, Smith & Reynolds 2003).

Harmonic Radar for Studying Low-Flying Insects

Outline of the Technique

When an insect flies within a few metres of the ground, its radar returns are normally completely hidden in the much more powerful echoes from ground features and from vegetation, and it therefore cannot be detected by radar. However, this difficulty can be overcome if the insect is fitted with a small electronic device (a transponder) that picks up the interrogating radar signal, and immediately emits a signal at a different frequency, and one to which the radar receiver has been selectively tuned. Such a frequency change can be conveniently achieved if the transponder has non-linear electrical characteristics, because the non-linearity introduces currents at multiples (harmonics) of the frequency of the original radar signal, and these currents re-radiate harmonic frequencies of this signal (Vogler, Maguire & Steinhauer 1967). We, therefore, modified one of our conventional scanning radars to use this 'harmonic radar' principle with the specific objective of recording the host-finding flight of tsetse flies, as a contribution to a UNDP insect pest research program in Zimbabwe. The radar was found to work very effectively out to ranges of just under 1 km (Riley *et al.* 1996; Riley &



Figure 2: A honeybee fitted with a transponder. The transponder, which does not need a battery to operate, can be detected by the Rothamsted scanning harmonic radar at a range of just under 1 km. The combination of transponder and radar allows records of insect flight trajectories over hundreds of metres to be made.

Osborne 2001; Riley & Smith 2002), and understandably, a key contribution to its success was the development of transponders weighing only a few milligrams (Figure 2). Field trials showed that tsetse flew normally with these transponders attached, but changes in funding priorities meant that the technique was never used for the purpose for which it was originally designed. However, it was enthusiastically taken up in the study of other insect species, and we provide an outline of these applications below.

Some Recent Applications of Harmonic Radar

Orientation Flights by Honeybees

Beekeepers have known for many years that when honeybees (*Apis mellifera*) first leave their hives, they carry out a series of familiarisation or 'orientation' flights before becoming foragers at about three weeks of age. However, very little was known about the nature of these flights until they were recorded by harmonic radar. It was then discovered that the bees flew out in loops of increasing length, but that their flights were not evenly distributed around the hive. As the bees became more experienced they tended to hold trip duration constant, but flew faster, and so covered more ground than in previous trips, gradually building up their familiarity with the environment in the vicinity of the hive (Capaldi *et al.* 2000).

Vector Flights by Honeybees

The capacity of bees to fly in straight lines is so well known that the term 'bee-line' has passed into everyday English language as being synonymous with 'straight'. Nevertheless, the distance over which straight flight is maintained, and indeed, even the degree of linearity itself, remained largely a matter of conjecture until harmonic radar made it possible to record the bees' actual flight paths. These recordings demonstrated that bees captured at an established feeding station, but then released elsewhere, embark on the previously-learned straight 'vector' flight that would have taken them directly home from the station had they not been artificially displaced. Almost all the bees maintained accurate compensation for lateral wind drift, and most completed the full length of the vector flight before starting to search for their hive. Our results showed that during their 'vector' flights, bees tend to disregard landscape cues, at least initially, and rely on the 'optic flow' of the ground beneath them to judge distance, and their sun compass to judge direction (Riley *et al.* 2003).

Flights of Honeybees that have been recruited by a 'Waggle Dance'

The 'dance language' of honey bees (von Frisch 1967) is perhaps the most celebrated example of animal communication yet revealed (Dyer 2002), and is thought by many to be one of the great discoveries of 20th century biology. The novel factor in this process is that the dancer generates a specific, abstract, symbolic message that describes the location of a new food source, and her message is displaced in space and time from her discovery of that source. Von Frisch concluded that bees 'recruited' by the dance subsequently used the information encoded in it to guide them directly to the food source. This conclusion carried the startling implication that, although bees are invertebrates with tiny brains, their communication system is more complex than in any other non-primate species (Gould 1975).

However, a major problem with von Frisch's results was that recruited bees took far longer to arrive at food sources than would be expected by direct flight from the hive, and this fact, together with limitations in his experimental protocol, caused scepticism about the 'dance language' hypothesis. In particular, it was claimed by Wenner and others (Wells & Wenner 1973; Wenner 2002 and <http://www.beesource.com/pov/wenner/index.htm>), that von Frisch's results could be explained if bees became recruits by memorising odours that had become attached to the dancer at the food source. In this model, the recruits then fly out of the hive and locate the food source by tracking down the wind-borne odours emanating from it. A detailed exposition of the resulting controversy can be found in Gould (1976), who independently provided strong support for the von Frisch hypothesis by ingeniously manipulating dancing bees so that they dispatched recruits to inappropriate destinations. More recent work (e.g. Srinivasan *et al.* 2000; Esch *et al.* 2001) on the response of recruits to distance information encoded in the dance, also supports this hypothesis. However, what was lacking was a definitive demonstration that recruits in the field fly as predicted by von Frisch, rather than by Wenner.

This demonstration was finally provided by harmonic radar recordings of the flight paths of recruits leaving their hive, and also of the flights of recruits that had been artificially displaced from the hive before commencing their first flights to the feeder. In the first case, the recruits undertook a straight flight that took them directly into the vicinity of the feeder; in the second, they flew directly to where the feeder *would have been*, had they not been displaced. Overall, the radar data provided the first quantitative and direct description of the degree to which recruits translate information encoded in the waggle dance into flight to the vicinity of the designated destination (Riley *et al.* 2005). Our results showed that although this process is highly effective, most recruits would not reach the intended food sources without the use of odour and visual cues in the final stages of their flight. Together with earlier studies, particularly those of Gould, Srinivasan and Esch, these results provide a final and definitive vindication of the von Frisch hypothesis (Gibbons 2006).

Compensation for Wind Drift by Bumble Bees

The ability of bumble bees (*Bombus* spp.) and honeybees (*Apis mellifera*) to find their way between their homes and distant food sites is very impressive, and in the case of honeybees, some of the mechanisms underlying this intriguing phenomenon are understood. However, the lack of a means of observing flight for more than a few tens of metres precluded the acquisition of detailed information about navigational performance *en route* from source to destination. Harmonic radar is an ideal tool to overcome this constraint, and it has been used to describe the response of bumble bees to the navigational task of returning to their nests in winds of different strengths and from different directions.

The flight tracks of individual bees foraging from their nests over arable farmland were recorded, typically over distances of 200 to 700 m, and in winds from a variety of directions, in the speed range 0.1 to 7 ms⁻¹ (measured at 2.7 m above ground). Outgoing tracks were sometimes truncated when the bees flew over the radar horizon formed by hedgerows or tall crops, so their ultimate destinations could not be fixed with certainty, but incoming tracks shared a common and precisely defined destination (the nest). The majority of bees maintained direct outward and return routes between their nest and forage areas, and they did so even in winds that had a strong cross-track component. In a few cases, they slightly over-compensated for lateral wind drift, and flew in a very shallow curve on the upwind side of their intended tracks.

Subtraction of the local wind vector from the bees' velocity demonstrated that they achieved compensation by flying obliquely over the ground, and laying off their courses into the wind by up to 55°. It was noted that the observed corrections for wind drift would be achieved if the bees were simply adjusting their headings so that the direction of optomotor flow across their retinas was maintained at an angle relative to the sun's azimuth which corresponded to their intended track direction. The bumble bees' average air speed in calm conditions was 7.1 ms⁻¹, and they responded to favourable or adverse winds by adjusting their heights of flight and to a lesser degree, their air speeds (Riley *et al.* 1999; Riley & Osborne 2001).

Bumble Bee Foraging Behaviour

Bumble bees play a vital role in the pollination of many crops and wild flowers, but plans for their conservation require a knowledge of the spatial scale and dynamics of their foraging flights which is very difficult to obtain using conventional methods of observation. The foraging flights of these insects have, therefore, been studied by harmonic radar, and two features of particular interest emerged. Firstly, the bees' outward and return trips were often remarkably straight over hundreds of metres, and sequential foraging trips were often along almost the same flight path and to the same destination. Secondly, bees did not necessarily choose to go to the forage sources closest to their nests, a result that highlights the difficulty of making assessments of gene flow in bumble bee-pollinated crops and wild flowers (Osborne *et al.* 1999).

Butterfly Flight Paths

Qualitative descriptions of the local flight behaviour of brightly coloured, day-flying butterflies can be obtained fairly easily from direct visual observations, but producing quantitative data on even short flight paths is difficult. Harmonic radar brings with it the considerable advantage of yielding geometrically accurate measurements of flight paths on scales of a kilometre or more, and in a form that can be overlaid directly onto digital maps of the landscape over which the insect is flying. This combination of techniques has been used to investigate the flight of five species of butterfly over an agricultural landscape. Flight paths were analysed for straightness, displacement distance, ground speed, foraging, and the influence of linear landscape features on flight direction. Two main styles of flight were identified: fast linear flight; and slower nonlinear flights associated with foraging and looping. The loops appeared to perform an orientation or familiarisation function, and were often associated with areas of forage. In the absence of forage, linear landscape features did *not* have a guiding effect on flight direction, and only dense tree-lines acted as barriers. Overall the results provide tentative support for non-random dispersal, and for an effective visual range of 100-200m for the species studied (Cant *et al.* 2004).

*The Flight of Male Turnip Moths (*Agrotis segetum*) in the presence of Airborne Pheromones*

Male moths are known to fly distances of many hundreds of metres in response to the airborne sex pheromones emitted by calling females, but only a few metres of these nocturnal flights are accessible to infra-red and low-light film and video recording techniques (Riley 1994). By contrast, harmonic radar has been used to describe moth flight tracks of up to 7.7 km, and to investigate the flight of male moths flying above plots treated with high doses of artificial pheromone (Svensson *et al.* 2001). A recent analysis of this data has demonstrated the complexity, but also the effectiveness, of the moths' plume-location strategies (Reynolds *et al.* 2007 in press). It was found that disruptive doses of sex pheromone can have a marked influence upon male moth flight patterns.

Recent Technical Developments

Our original harmonic radar used a conventional PPI display (Riley *et al.* 1996), but making photographic records of this medium was rather unsatisfactory, and the subsequent extraction of flight trajectory data very laborious. As a part of a process of continuing technical development, we have produced an interface device that allows the radar data to be acquired and stored by a PC, and simultaneously displayed on the computer's screen (Riley & Smith 2002). This process greatly facilitates both direct observation and subsequent data analysis.

In studies of the flight performance of low-flying insects, it is often desirable to know their height above the ground, but in current versions of scanning harmonic radar, all we know is that a detected insect is somewhere within the vertical width of the radar beam. This beam-width can range from the ground up to 15m, so height estimation is rather imprecise. In order to improve on this, we have constructed a prototype receiving antenna that generates two vertically offset, but overlapping, beams each feeding a separate receiver channel. The downside of this arrangement is that it introduces additional complexity into the radar display and recording system because of the need to compare the relative amplitudes of the radar returns from the two beams accurately. Nevertheless, trials with this system have allowed us to estimate the vertical distance of a target from the beam axis, and thus to derive its altitude with much greater precision than was previously possible. Although these initial results are promising, we have yet to evaluate the system over a variety of terrain types, so that we can establish whether interference between direct and ground-reflected signals (the Lloyd's mirror effect) is likely to degrade height-finding performance.

Conclusions

The example applications described in the preceding paragraphs demonstrate that harmonic and vertical-looking radar are exceptionally powerful tools for investigating insect flight. There are, however, some significant limitations to what the techniques can offer.

Harmonic radar requires a clear line of sight, and so would be of little use in forests, in undulating terrain or in an urban environment. In addition, all transponders 'look the same' on the screen, so only a few insects can be tracked at the same time if their tracks are not to become confused. The current lower limit for transponder weight is about 3mg, so the technique as it stands is normally suitable only for insects weighing above, say, 20mg, although we found that some smaller strong-flying insects (e.g. tsetse) can also be tracked.

The ability of VLR to identify any particular species depends on that species having a mass, body shape or wing-beat frequency that is significantly different from others airborne at the same time. Even when this condition is met, some supplementary evidence (e.g. from aerial trapping) will usually be needed for confident identification. This is especially the case if aerial densities become so high that signals from nearby targets interfere with each other, because in these circumstances mass and body shape data cannot be extracted.

In spite of these limitations, both techniques offer an unmatched window on insect flight behaviour, and there is little doubt that they will continue to contribute to new discoveries about this intriguing and many-faceted phenomenon.

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Since 2001, when NRI withdrew from the field, radar entomology in the UK has been carried forward by the Rothamsted Radar Entomology Unit (RREU) under the leadership of *Dr Jason Chapman*. Alan Smith joined the RREU, and Joe Riley continued to contribute to the subject as a Rothamsted Research Fellow. Don Reynolds also maintained very active collaboration with the RREU, particularly in long-term, automatic monitoring programmes to investigate high-altitude insect migration over the UK.