

Recent Insights from Radar Studies of Insect Flight

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Abstract

Radar has been used to study insects in flight for over 40 years and has helped to establish the ubiquity of several migration phenomena: dawn, morning, and dusk takeoffs; approximate downwind transport; concentration at wind convergences; layers in stable nighttime atmospheres; and nocturnal common orientation. Two novel radar designs introduced in the late 1990s have significantly enhanced observing capabilities. Radar-based research now encompasses foraging as well as migration and is increasingly focused on flight behavior and the environmental cues influencing it. Migrant moths have been shown to employ sophisticated orientation and height-selection strategies that maximize displacements in seasonally appropriate directions; they appear to have an internal compass and to respond to turbulence features in the airflow. Tracks of foraging insects demonstrate compensation for wind drift and use of optimal search paths to locate resources. Further improvements to observing capabilities, and employment in operational as well as research roles, appear feasible.

Flight boundary layer (FBL): a layer of the atmosphere, usually close to the ground, where the wind is light enough for the insect to make progress in any direction

VLR: vertical-looking radar

INTRODUCTION

The predominant and most significant mode of transport among insects is powered flight in the adult stage (38). Although there are some notable exceptions to this generalization, e.g., ballooning Lepidoptera larvae (6) and marching bands of Mormon crickets, *Anabrus simplex* (106), the great majority of long-range insect movements are accomplished by flight. Insects fly for many reasons, but one useful and rather general distinction that can be made is between station-keeping movements, in which the individual remains within its current habitat patch, and movements that take it away, permanently or for an extended period, from this home range (27, 52). Probably, the most common form of station-keeping activity is foraging, in which movements are directed toward the acquisition and exploitation of resources (e.g., host plants, shelter, or mates). Such movements, e.g., odor-mediated anemotaxis in mate-searching male moths (10), cease when appetitive cues associated with the sought-after resource are encountered; they produce characteristically erratic flight trajectories made up of numerous short stages in different directions. Foraging insects need to maneuver precisely; this requires good control of their track, and thus foraging flights typically occur close to the vegetation canopy, within the insect's flight boundary layer (FBL) (107).

Movements that take an individual beyond its home range can be further divided into ranging and migration. Ranging is movement over an area in order to explore it and locate a new home range; like foraging, it stops when the sought after resource is found. Migration, in contrast, entails a temporary inhibition of responsiveness toward the appetitive cues that would otherwise arrest the individual's motion (27, 52). Migratory movement is sustained, characteristically undistracted, and produces rectilinear tracks; its function is to relocate the individual to a habitat that is (or will soon be) better endowed with resources than the current one. For many insect species, the most efficient way to achieve sustained (i.e., long-distance)

movement is to utilize the fast winds above the insect's FBL (33). Consequently, migrating insects typically fly at high altitudes, sometimes as high as 2 or 3 km above the ground (11, 44). This strategy would seemingly often result in displacement in unfavorable directions, however, and indeed some large day-flying species (e.g., many migratory butterflies and dragonflies) migrate predominantly within their FBL (103) and maintain considerable control over their movement direction, though at the cost of significantly increased journey durations.

Movement plays a central role in all facets of the population dynamics, ecology, and evolution of insects, and thus knowledge of insect flight strategies should underpin many entomological disciplines. A recent theoretical framework (62) proposed that the primary challenge for movement ecologists is the characterization of the external factors, internal states, motion capabilities, and navigation capacities of their study organisms. These are difficult challenges indeed for small, flying organisms such as insects—even if studies are restricted to foraging flights—as all but the shortest flights quickly take the insect out of visual range. The scale of the problem increases dramatically in the case of long-range migratory flights, many of which take place at heights beyond the reach even of powerful optical devices.

The remote-sensing capability of radar provides a solution to the seemingly intractable difficulty of collecting ecologically relevant movement information from distant flying insects, and entomological radars have made a huge contribution to several distinct areas of movement research (16, 17, 31, 35, 84). During the 1970s and 1980s, the application of scanning radars to the study of high-altitude insect migration resulted in numerous insights into the migration ecology of a range of agricultural pests (81). The development of two new entomological radar techniques in the 1990s, namely vertical-looking radar (VLR) and harmonic radar, ushered in a new era of radar entomology in which descriptive observation gave way to hypothesis-driven analysis and even some experimentation. A synthesis of the

important findings emerging from the last 10 years of radar entomology studies is thus timely. Developments in radar technology continue, and the new opportunities that these developments provide for entomologists are also outlined in this review.

EARLY ENTOMOLOGICAL RADARS AND THEIR CONTRIBUTION TO MIGRATION STUDIES

Insects were first positively identified as a source of radar echoes in 1949 (24), and the detection of a locust swarm in 1954 alerted entomologists to the technology's potential for their discipline (68). However, it was not until 1968, when G.W. Schaefer deployed a radar designed specifically for locust observation to the Sahara, that findings of real entomological value were generated (97). Most early entomological radars were of the scanning pencil-beam type, in which the beam is directed upward at a series of elevation angles and turned steadily in azimuth. Targets appear as bright marks (paints) on a display known as a plan-position indicator (PPI), and by following the paints over a series of scans, it is possible to estimate target speed and direction (97). Observations have been made mostly with units transmitting at a wavelength of 3.2 cm using components from marine radars, but versions operating at 9 mm have been produced for the purpose of studying smaller species such as planthoppers (85).

A number of other radar designs were trialed in the 1970s and 1980s (81), but only an aircraft-mounted type with a beam that pointed directly downward saw much use (45, 116). The speed of the aircraft enabled transects to be obtained, allowing the lateral extent of a migration to be determined. A study in the southern United States, for example, showed that a cloud of moths originating from a cropping region remained extant for over 400 km as it drifted downwind (116). Despite such successes, no airborne entomological radar survives; and since the early 1990s, use of scanning radars has

also declined. The main reason is that radar entomologists have increasingly recognized the need for long-term datasets and have sought methods that are less labor-intensive in order to acquire these at practicable cost. The new VLRs also provide more precise information about target identity and this has further encouraged the switch away from scanning systems. However, scanning observations have continued in China (42), where the radars are now partially automated and PPI images are acquired and analyzed digitally (22).

The early scanning radars were used mainly to study the migrations of pest species, including grasshoppers and locusts; noctuid, pyralid, and tortricid moths; and planthoppers. The principal findings have been

- that migratory flight occurs by day and by night, with the former commencing around midmorning (69) and the latter with a mass takeoff at dusk (32, 89);
- that migrants regularly attain heights of a few hundred meters and flight at 1 km is not unusual (32, 83, 89);
- that movement is almost always approximately downwind (32, 37);
- that during daytime, when the atmosphere is typically convective (i.e., mixed by thermally driven updrafts and downdrafts), insects become concentrated in plumes of rising air (69);
- that in the stable atmosphere, which typically forms at night over land, insects are distributed nearly uniformly in the horizontal but frequently concentrate around particular heights (i.e., form layers) in response to features of the temperature or wind profile (30, 37, 80);
- that in a stable atmosphere most larger insects exhibit some degree of mutual alignment, often in a direction different to that in which they are moving (29, 83, 89);
- and that the steady nighttime migrations in stable conditions are sometimes disrupted by atmospheric disturbances, especially sea breezes, thunderstorm outflows, and flows down sloping terrain, that not only change the direction of a

PPI: plan position indicator

movement but also gather the migrants into line concentrations that propagate across the landscape (28, 90).

These features of insect migratory flight have continued to be observed as scanning-radar studies have been undertaken on further species and in additional regions (5, 42), and appear universal.

The contribution of radar to the study of a particular species has often been to establish that high-altitude migrations occur, that they do so frequently, and that a significant proportion of the population is involved (e.g., 19, 32, 40, 45, 81). Radar observations provide various measures of the intensity of a migration, such as the cumulative number of migrants passing per unit length of a line drawn in whatever direction the investigator chooses (32, 80). Comparison of this number with infestation levels in the destination region allows the ecological significance of the movement to be determined. Multidisciplinary programs with radar observations occupying a central role have contributed to the recognition of the migratory circuits of several pest species, both in temperate regions (42) and in the semiarid subtropics (26, 32, 80).

NEW-GENERATION ENTOMOLOGICAL RADARS

Vertical-Looking Entomological Radar

Since the late 1990s, most radar observations of insect migration have been made with a design in which echoes are recorded electronically as targets pass through a stationary upward-pointing beam. Each echo shows a gradual rise and then fall, over a period of a few seconds, as the insect causing it traverses the beam. Echoes are partitioned by range, which corresponds to height in this configuration, so profiles of insect numbers are accumulated. The number of traverses in each range bin is readily determined by computer analysis of the digitized recordings, and a migration rate for the bin altitude can be estimated from this. Year-long datasets were first achieved with a radar of this type op-

erating in Texas in 1990 (4). The speed of the target can be determined from the rate of the rise and the fall, and for larger species the wing-beat frequency can be extracted by Fourier analysis (36).

The most sophisticated variant of this design (16, 21) incorporates target interrogation, in which the polarization of the transmitted wave is rotated continuously and, synchronously, the beam is nutated (wobbled slightly) to produce an additional time variation in the echo. The now rather complicated form of the echo contains information about the target's movement, heading direction, its size and its shape, and analyses have been developed to extract all these parameters (48, 100). The ability to discriminate between targets of different size, shape, and wing-beat frequency, and thus to accumulate samples of track directions, headings, and speeds for specific target classes, is unique to this radar design and enables significantly more precise biological analyses.

VLRs operate automatically, under microcomputer control, so it is practicable to install them in locations—perhaps far from the researcher's home laboratory—where insect activity of particular interest is most likely to occur (**Figure 1a**). Datasets extending over several years, and with millions of individual traverses recorded, are now available for sites in the United Kingdom and Australia. These have provided unprecedented opportunities for empirical, large-sample studies of insect migratory behavior (see below). The Australian radars are also developing an operational role, as their outputs are routinely drawn upon by the Australian Plague Locust Commission in support of its operations aimed at forecasting and managing locust outbreaks.

Harmonic Radar

Harmonic radars rely on a rectifier circuit (which in biological applications is incorporated into a tag worn by an individual animal that is to be tracked) that generates an echo with exactly half the wavelength of the transmitted wave. As there are few naturally occurring

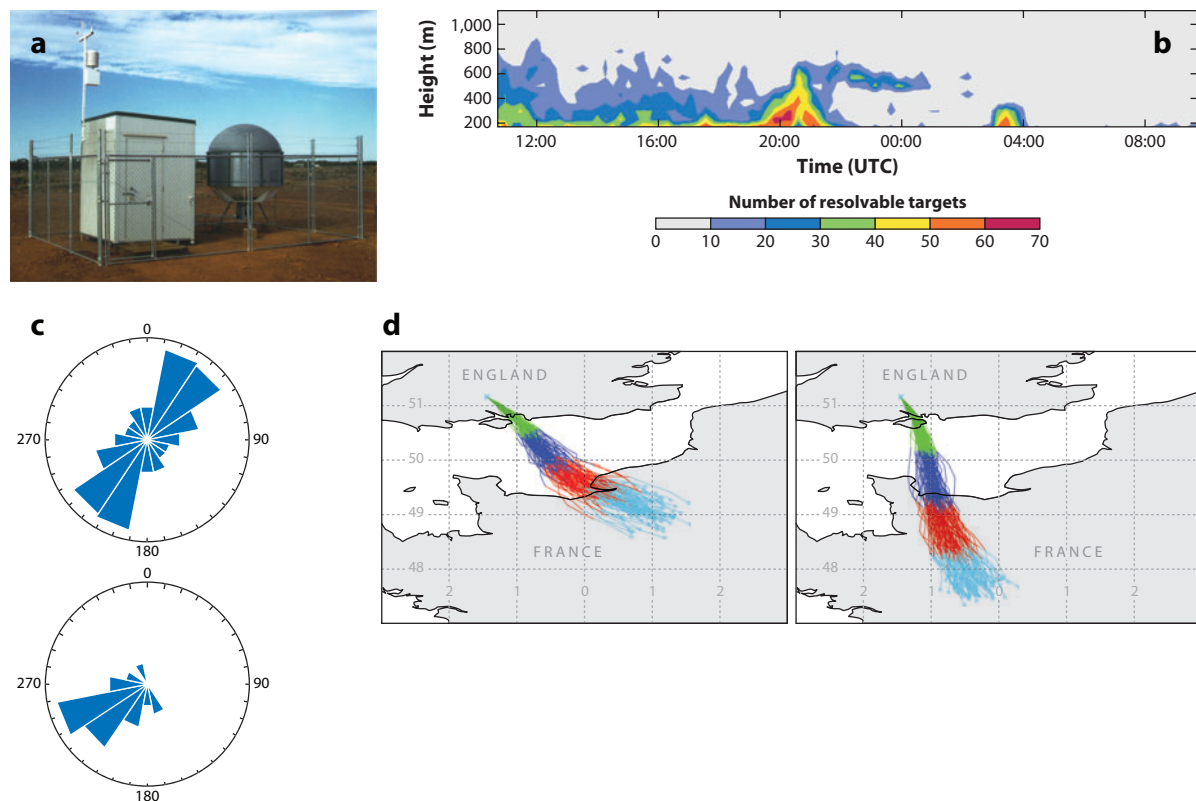


Figure 1

(a) A vertical-looking entomological radar (VLR) for automatic monitoring of high-altitude insect migration. This unit is situated at Thargomindah, in the remote inland of Queensland, Australia (photo courtesy of V.A. Drake). (b) Time/height plot of insect numbers recorded by a VLR at Malvern, England, on June, 25–26, 2003. The color scale bar refers to the number of resolvable insect targets detected at each sampling height during each 5-min sampling period. The figure shows many of the typical features in the vertical profile, namely, the extended daytime flight period and the activity peaks at dusk and dawn. On this occasion, an elevated layer formed after 2200 h and persisted until dawn. Modified with permission from Reference 82. (c) Circular distributions of (top) body alignment and (bottom) displacement direction of insects recorded by a VLR during a single night's migratory flight of *Autographa gamma* moths over the United Kingdom. Although there is a 180° ambiguity in the body alignment directions, other evidence shows that the migrants were orienting themselves toward the southwest, close to the direction of their windborne displacement. (d) Simulated 8-h migration trajectories for (left) 100 inert particles and (right) 100 *A. gamma* moths released from a VLR site in southern England on August 10, 2006. The different colors represent successive 2-h sections of trajectory from 2000 to 0400 coordinated universal time (UTC). The coastlines of southern England and northern France and lines of latitude and longitude are shown. The effect of flight heading and altitude selection by the moths produces improvements in both distance covered and direction (i.e., moth trajectories were 24° closer to the seasonally preferred direction of 180°). Modified with permission from Reference 12.

rectifiers, a receiver operating at the harmonic wavelength detects the echo from the transponder without being swamped by echoes from terrain features and vegetation. The particular advantage of harmonic tags for entomological applications is that they operate passively and therefore do not require a battery; this means that, with modern microelectronic components, they can be made light enough

to be carried by medium-sized insects such as honey bees (*Apis mellifera*) and noctuid moths without any obvious effects on behavior. Their main limitation is that the returned signal contains no identification information. Another constraint is that terrain and vegetation, although not sources of echo, still act as barriers and create shadow areas within which tags are undetectable.

The harmonic principle was first successfully employed in entomological work in the form of handheld direction finders (54). These relatively low-cost devices allow tagged insects to be relocated once or twice a day; individuals are then identified by reading a number on the tag. Harmonic direction finders continue to be used in studies of the lifetime tracks of individuals through their habitat (115). A harmonic radar, in contrast, measures ranges as well as direction. The unit developed for entomological applications in the early 1990s (92) (**Figure 2a**) is similar in many respects to the conventional scanning entomological radars then in use: It transmits with a wavelength of 32 mm, has a narrow beam (and so locates the target quite precisely), completes a scan in 3 s, and presents its output on a PPI display. This radar is capable of detecting transponders to a range of around 900 m; its spatial resolution is ~5 m. The signals returned by the tags have a wavelength of 16 mm, and to match this optimally the transponder antennas, which are constructed from fine wire with the diode and an inductive loop at the midpoint, are 16 mm long. They weigh 1–12 mg and are mounted dorsally, pointing upward (**Figure 2b**); this provides reasonable performance and minimizes obstruction of the insect's normal activities.

Development of a true harmonic radar is technically demanding and until recently only a single unit has been available. In addition, the lack of identification means that only one or two insects can be followed at a time, and because of the shadowing problem observations have been possible only in flat and relatively open landscapes. Nevertheless, a range of species have been studied, both by observing natural behaviors and through manipulative experimentation.

RADAR STUDIES OF WINDBORNE INSECT MIGRANTS

Long-range windborne migration, the process by which migrants ascend above their FBL to be transported downwind, occurs in all the

major orders of insects and has evidently evolved many times (11, 44). Migration allows species to exploit temporary breeding habitats and escape adverse seasonal conditions, and provides the potential to breed continuously throughout the year. Utilization of fast, high-altitude air currents enables individuals to cover enormous distances (hundreds or even thousands of kilometers) with just a few days or nights of flight. These strategies often benefit migrants relative to less mobile species, and consequently many migrant species have become hugely abundant and often these are now important pests of crops (34) or vectors of animal or plant diseases (79). Windborne insect migration occurs on a colossal scale, far exceeding (at least in numerical terms) the migratory flux of birds (12, 16, 46, 50). Yet in comparison to birds we know relatively little about the behavioral adaptations of insects that undertake long-range movements (1, 2, 50). The new VLRs, however, have opened a window onto this previously inaccessible realm and have already produced some important findings. Concurrent work with scanning radar in China has also contributed and is also summarized here.

Diurnal and Seasonal Patterns of Migratory Activity

Over ten years of continuous VLR observations in southern England, in conjunction with a dedicated aerial-sampling program (20), have revealed that even in the comparatively cool Atlantic climate of the United Kingdom the magnitude of the migratory flux is immense. A bioflow of 3 billion insects crossing any 1-km stretch of the southern English countryside has been estimated for a typical summer month (16). This figure exceeds the total number of migratory passerine birds involved in the entire Palaearctic-African migration system (46)! The radars have shown that numbers aloft increase dramatically as temperature rises, and have not indicated any reduction in numbers at the highest temperatures experienced in a typical British summer (21, 99, 118).

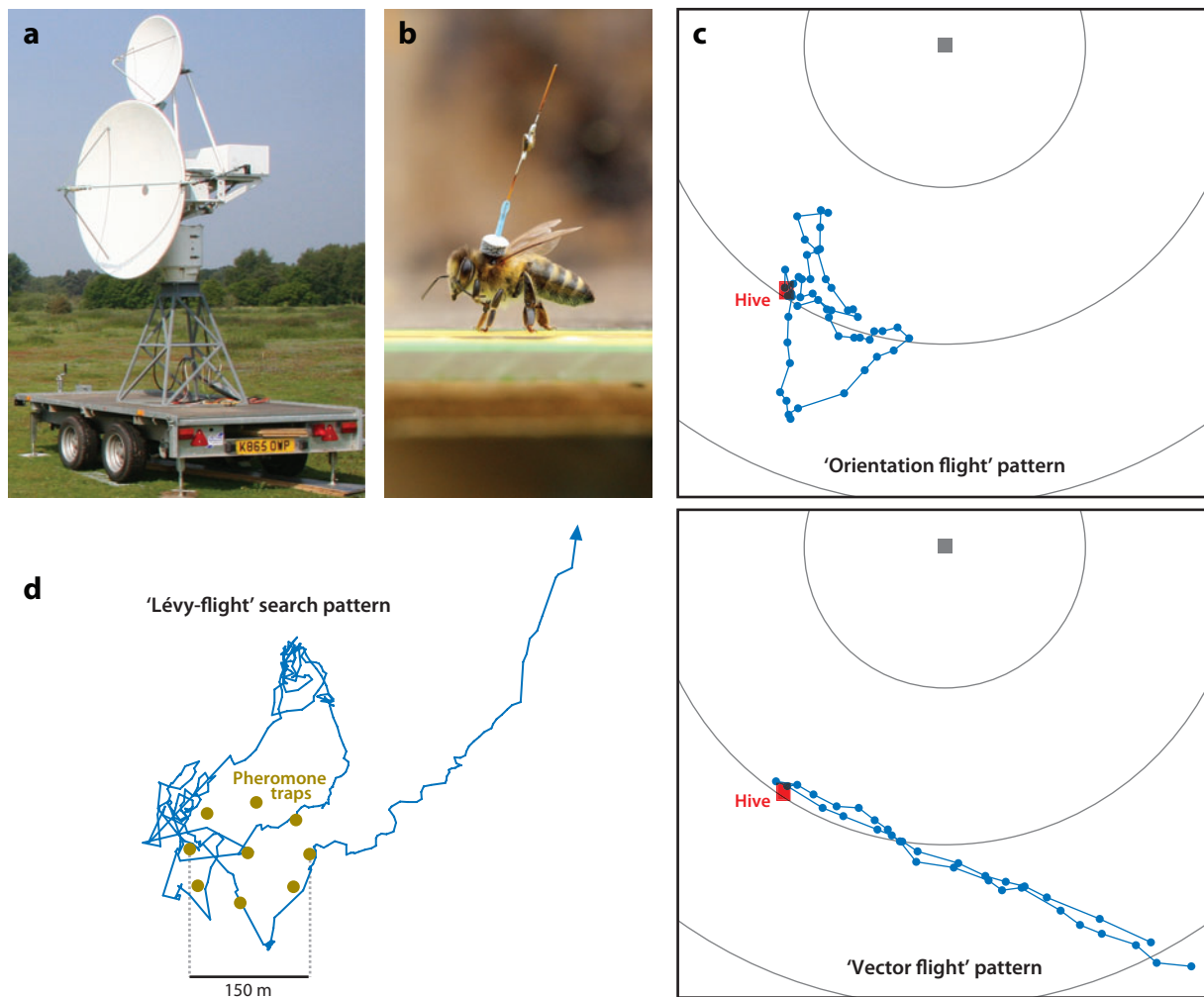


Figure 2

(a) The scanning harmonic radar for following individual low-flying insects tagged with transponders (photo courtesy of A.D. Smith). (b) Honey bee wearing a radar transponder (photo courtesy of M. Garcia-Alonso). (c) Two examples of honey bee flight tracks: (top) an orientation flight by a young (6-day-old) worker bee; (bottom) part of a vector flight to a forage patch from which the bee returned with a pollen load. The latter flight goes out of range before returning along the same path. The hive is marked by a red square; the radar range rings are at 116-m intervals. Modified with permission from Reference 9. (d) A Lévy-flight search pattern recorded from a male *Agrotis segetum* moth during a pheromone-confusion trial. The ring of pheromone traps (dark yellow dots) is 150 m across. Modified with permission from Reference 73.

The diurnal pattern of insect flight activity over England is highly consistent (16, 21, 82, 99, 120). There is generally a discrete take-off of crepuscular species during the dawn twilight period (**Figure 1b**); this flight tends to be short-lived, although occasionally it continues

for some time (82). Day-flying migrants take off from mid-morning onward, as atmospheric convection develops, and generally descend in the late afternoon (**Figure 1b**). Occasionally, small numbers of day-flying species continue their migration into the night (20). However,

Atmospheric boundary layer (ABL): the

bottommost 1–2 km of the atmosphere, within which the air is slowed by surface friction; usually it is mixed by thermal updrafts and downdrafts by day but is stable (though turbulent) by night

nocturnal migration is typically initiated by a mass takeoff at dusk (**Figure 1b**), stimulated by falling light levels, and the nocturnal migrants usually fly throughout the night, sometimes concentrated into narrow altitudinal layers (16, 78, 82, 117, 120). There is almost no overlap between these three phases of migratory activity, which, at least in the United Kingdom, involve different taxa. By day, microinsects such as cereal aphids and their hymenopteran parasitoids—which are all too small to be detected by the VLRs—predominate but large species including carabid beetles and hoverflies are also abundant (19, 20). The dusk peak is composed partly of crepuscular insects such as lacewings and small Diptera that fly for a relatively short period of an hour or two around sunset (13, 20), and partly of the nocturnal migrant fauna that flies throughout the night. The dominant large nocturnal migrants are generally noctuid moths (12, 14, 15, 30, 40, 42, 43, 120), with grasshoppers and locusts also abundant in the semiarid subtropics (32, 35, 80, 89, 90).

Migration is associated with spatiotemporal habitat variation, which in temperate regions is driven primarily by the (relatively) regular and predictable seasonal pattern of temperatures, whereas in warmer semiarid and arid regions it is usually rainfall that is limiting and this is often erratic. In the former case, insect migrations in spring and early summer are toward higher latitudes, with populations tracking the poleward extension of the growing season of their plant hosts; a reverse movement occurs in autumn. Radar has helped to document migration circuits of this type and to identify behavioral adaptations that facilitate the migrations for several moth species that are serious agricultural pests in North America and China, including *Helicoverpa zea* (112), *H. armigera* (42), *Spodoptera exigua* (40), and *Mythimna separata* (43). In Australia, VLR observations revealed that northward movements of Australian plague locusts, *Chortioctes terminifera*, were more frequent and intense than had previously been realized, leading to recognition of a semiregular seasonal to-and-fro movement between winter

and summer rainfall regions at temperate and subtropical latitudes, respectively (26, 35).

Selection of Flight Altitude and Layer Concentrations

An hour or so after the dusk emigration, the vertical profile of insect aerial density usually assumes a relatively stable state where (in the absence of disturbances) changes occur only gradually. These midevening profiles, when the aerial population has come into equilibrium with the atmospheric boundary layer (ABL), may assume various forms, but one of the most common is the concentration of the migrants into layers of shallow depth (~100–150 m) but broad horizontal extent (30, 33, 44, 71) (**Figure 1b**). Early radar observations established that nocturnal insect layers are a frequent phenomenon in subtropical regions, and more recently it has been demonstrated that they also often occur in temperate regions (40, 41, 42, 78, 117, 118, 120). The vertical stratification of insect aerial density is often paralleled (and presumably influenced) by the stratified nature of the nocturnal ABL. In fine weather, a nocturnal temperature inversion usually forms in the first few hundred meters above the ground, and insect layers frequently occur near the inversion top where warm, fast-moving airflows provide optimal conditions for long-distance transport. In the relatively cool nighttime conditions of temperate regions, layers are often confined to the warmest zone of the atmosphere because the cooler airstreams above or below are unsuitable for insect flight (78, 117, 118). When air temperatures are warmer, however, migrants can select their flight altitude, and moths in particular are often found at the altitude where the air is moving fastest, thereby maximizing their nightly displacement (12, 14, 15, 117).

The cues and sensory mechanisms involved in layer formation may be similar to those used to achieve orientation and are discussed further below. One recent suggestion that is specific to layering is that a turbophoretic mechanism tends to advect migrants into regions with low turbulence, which typically coincide with zones

of maximum air temperature and/or wind speed (71). Accumulation in layers through passive turbophoresis would be very slow, but if the migrants can amplify the effect by actively initiating ascents or descents in response to turbulent vertical air motions, then concentration into layers that match those regularly observed appears plausible (71, 72).

In fair weather over land, thermal convection is usually well developed by midmorning, and the resulting up- and downdrafts often become organized into systems of cells. Insects tend to be concentrated into regions of convective uplift typically ~ 0.5 –1 km across (69, 97) that move along with the large-scale air flow. Daytime migration is thus highly heterogeneous, at least on the small scale, and time-height profiles from VLRs show this process well (120) (**Figure 1b**). In contrast to the nighttime situation, daytime layers are reported only occasionally (21, 51, 99). They may originate from the dawn takeoff, are usually found in the stable air above the convecting region of the atmosphere, and are liable to be disrupted later in the day as the convective plumes extend upward (82).

Common Orientation in Relation to the Wind

Perhaps the most surprising finding to emerge from the earliest radar entomology observing campaigns was that the body alignments (i.e., flight headings) of large nocturnal migrants, such as grasshoppers and noctuid moths, often showed a high degree of common orientation (83, 97) (**Figure 1c**). Prior to this discovery, it had been assumed that nocturnal insects flying at high altitudes would orient themselves at random due to the presumed lack of environmental cues to which they could respond (72). Radar studies have since documented the ubiquity of common orientation among large nocturnal migrants and have shown that they often maintain headings that are relatively close to the downwind direction (29, 41, 72, 80, 81, 90, 97, 117). Downwind orientation is potentially highly adaptive for large insects, as addition of

their air speed to the wind speed significantly increases their displacement distance in a given time.

The question of how nocturnal migrants flying at altitudes of several hundreds of meters, and under low illumination levels, can select wind-related flight headings has proved difficult to resolve. Determination of the wind direction by visual perception of their movement direction relative to ground features (a type of optomotor reaction) seems an exceptionally challenging task given the low rates of optic flow and the dim nighttime illumination (88), although some nocturnal insects have extremely sensitive visual capacities (88, 108, 109). It seems unlikely that a visually mediated mechanism can explain all the observed patterns of nocturnal common orientation, but a wind-mediated mechanism similar to that already considered for layer formation (see above) may be able to do so (72), and a common mechanism for these two phenomena might account for the frequency with which they occur together.

How an actively flying insect could distinguish turbulent accelerations from those produced by its wing-beating is unclear. There is growing evidence that insects' antennae, via their action on Johnston's organs, play important roles in the stabilization of flight (96), regulation of migratory activity (58), and detection of extremely subtle environmental cues (110, 121); that the antennae might be capable of detecting faint turbulent flows is therefore at least plausible. An intriguing prediction from the proposed model is that nocturnal migrants attempting to orient themselves downwind will be misled by the change of wind direction with altitude (the Ekman spiral) that occurs in the boundary layer and will show a consistent offset to the right of the wind direction in the Northern Hemisphere and to the left in the Southern Hemisphere. Radar observations of medium-sized insects migrating over England at night have demonstrated a highly significant bias in their offsets that is indeed to the right of the downwind direction (72); an obvious test of the theory is therefore to determine whether similar migrants in the Southern

Hemisphere exhibit a corresponding bias to the left.

Selection of Seasonally Beneficial Tailwinds and Optimal Migration Trajectories

Many species of insect undertake seasonal migrations to higher latitudes to take advantage of temporary breeding habitats, and then escape the onset of harsh winter climates by returning to lower latitudes in the fall (44). To cover the huge distances required within the short developmental window (between assuming the fully flight-capable adult form and sexual maturation) available to most species, insects predominantly make use of the fast airstreams at higher altitudes. Simple reliance on windborne transport would seemingly often lead to displacement in highly disadvantageous directions and could cause the progeny of spring migrants to become trapped at high latitudes at summer's end—the so-called Pied Piper phenomenon (55). However, large-scale return migrations of windborne migrants are now well documented (12, 14, 40, 42, 59, 98). As wind speeds aloft are typically faster than insect airspeeds, a mechanism that ensures regular transport in seasonally beneficial directions would be highly adaptive. Initiating migratory flights only on occasions when the wind is blowing in a broadly favorable direction, and then letting the wind do the rest, appears a good strategy, especially for weak flyers, but it is dependent on a means for identifying suitable winds. In some species, return migrations in the fall are achieved by responding to particular meteorological conditions associated with winds blowing toward the equator, such as cold air temperatures (59), though this appears to be a high-risk strategy given the characteristically unpredictable weather of the temperate zone.

Recent radar observations indicate that large moths employ a sophisticated behavioral repertoire to exploit wind transport to move in the seasonally appropriate direction. The orientation strategies of the silver Y moth, *Autographa gamma*, which migrates annually

between north Africa and northern Europe, have received particular attention (12, 14, 15). *A. gamma* evidently has a compass, and it uses it not only to select nights with favorably directed winds, but also to align its flight heading so that it partially compensates for crosswind drift while maximizing its displacement speed (14, 15). Thus, these moths are clearly not at the mercy of the wind, and analysis of their flight trajectories indicates that selection of appropriate orientation and height of flight can increase displacement distances in favorable directions by up to 40% compared to passive movement downwind (12) (**Figure 1d**). These findings imply that this species is able to complete its migrations between summer-breeding and winter-breeding regions in as little as three or four nights. Similar behavioral mechanisms have been found in other large insects that engage in seasonal windborne migration (12). The compass utilized by nocturnal insects remains to be elucidated, although a magnetic mechanism (67), perhaps calibrated by the twilight pattern of polarized light (61), appears most likely. Day-flying migrants such as butterflies use a sun compass to maintain seasonally beneficial flight directions when migrating within their FBL (58, 60, 63, 103), and they possibly use it also to select favorable winds when migrating at high altitudes (12, 104).

BEHAVIORAL RESEARCH WITH HARMONIC RADAR

The relatively short working ranges of scanning harmonic radars have led to these units being used exclusively for the characterization of local movements, especially foraging flights. Even with this limitation, harmonic radar has almost as many potential applications as there are species capable of carrying the transponders and that inhabit reasonably open landscapes (92, 93). Harmonic radar has already contributed to studies on bee neuroethology (9, 56, 57, 87), pollinator ecology (8, 65), odor-mediated anemotaxis (73, 77, 94, 105), optimal searching strategies (73, 75–77), and short-range dispersal (64, 66).

Contribution of Harmonic Radar to Studies of Bee Behavior

Honey bees provide convenient subjects for manipulative behavioral experiments (101), and researchers studying them quickly adopted harmonic-radar technology when it became available. A second unit, recently commissioned in Germany, is also being applied to the study of bee flight (56).

Orientation flights by naïve honey bee foragers. The ability to learn the precise location of sites that a foraging individual will return to, such as a nest or reliable forage patch, is an essential component of the navigational capacity of central-place foragers such as honey bees. Beekeepers have known for many years that honey bees make repeated orientation flights that allow inexperienced worker bees to learn the hive location with respect to landscape features, and such flights are a prerequisite for successful homing of foragers. However, little was known about the nature of these exploratory movements beyond the immediate vicinity of the hive until a pioneering harmonic radar study recorded the paths of inexperienced workers throughout their first flights (9) (**Figure 2c**). The radar tracks revealed the ontogeny of the orientation flights of naïve bees: The area covered, and the maximal range from the hive, progressively increased on successive trips, but this was achieved by faster flight on later trips rather than an increase in flight duration (9). Furthermore, the progressive changes in flight behavior were related to the number of trips an individual engaged in rather than to the worker's age. This flexible timeframe for completing the series of exploratory flights allows bees to cope with variable weather conditions and forage availability (9).

Vector flights and drift compensation in social bees. Honey bee and bumble bee workers have to solve the challenging problem of returning swiftly and efficiently to their nest site after long and convoluted foraging excursions into often unfamiliar territory. Social bees were

believed to achieve this by a mechanism known as path integration, which involves the continual updating of the flight vector that would take them home by integrating all the distances covered and angles steered during each component of the outgoing trip (23). Direction of travel is ascertained from the sun's azimuth (or, alternatively, from patterns of polarized sky light), and distance traveled is gauged by the passage of movement-induced optic flow over the bee's retina—the so-called odometer (102). Whereas the use of path integration for returning directly to a nest was established many years ago in pedestrian foragers such as desert ants, *Cataglyphis fortis* (111), the practical difficulties of quantifying the return trajectories of flying insects prevented investigation of whether social bees used the same procedure. A study by Riley et al. (87) provided the first direct quantification of goal-oriented homeward flights in foraging honey bees and established that they do indeed rely on path integration to make a bee-line back to their hive (**Figure 2c**). Bees captured at an established feeding station, and then displaced before release, embarked on the vector flight that would have taken them directly to their nest if they had not been artificially displaced. During these vector flights, they ignored unfamiliar landscape features along the new route, and so in essence they were flying in automatic pilot mode (87).

In contrast to pedestrian central-place foragers, social bees have to compensate for the effects of crosswind drift if they are to maintain direct routes between foraging sites and their nest. This appears to be a difficult task, as fine-scale variation in wind speed and direction may be considerable at the heights at which social bees fly. However, visualization of the complete vector tracks of returning bumble bees, *Bombus terrestris* (91), and honey bees (86, 87), with harmonic radar demonstrated that both species can compensate for lateral wind drift, even when flying in strong crosswinds, by heading partly into the wind and moving on an oblique course over the ground. They most likely gauge the degree of compensation necessary by adjusting

Lévy flight: a power-law step-length distribution characterized by frequent short steps and a small proportion of much longer ones

their headings until the direction of the optic flow they experience occurs at the angle to the sun's azimuth corresponding to their intended track (91).

The honey bee waggle dance and forager recruitment. The astonishing discovery by Karl von Frisch that worker honey bees engaging in the waggle dance transmit a coded, abstract message to their hivemates communicating the location of a new food source was one of the great breakthroughs of twentieth-century biology. Although there was some initial skepticism, recent experimental studies provide convincing evidence that the dance language contains information on the distance to the food source (as measured by the amount of optic flow experienced en route) as well as its direction (39, 102). What was missing was direct quantification of the actual flight paths of bees recruited by the waggle dance, and so harmonic radar was used to provide this description and thus to test how effectively recruited bees translate the encoded information (86). In this experiment, bees were trained to visit an artificial feeder lacking odor and visual cues, and then harmonic radar was used to track the flights of naïve bees recruited by the waggle dance performed by the trained bees. The flight paths of naïve control bees took them from the hive directly into the vicinity of the feeder, but, crucially, experimental naïve bees that were released from a displaced location undertook vector flights directly to the vicinity of where the feeder would have been if the bees had not been displaced (86), thus confirming von Frisch's claim that the dance communicates both distance and direction information.

Contribution of Harmonic Radar to an Understanding of Movement Ecology

The ability to track individuals over distances of several hundred meters that harmonic radar provides has revealed features of insect foraging and dispersal flights that can be understood as adaptations to the particular environment or

as consequences of the particular population history.

Optimal searching patterns in honey bees and moths. One of the most exciting recent developments in animal movement research has been the development of biologging technologies that allow high-resolution quantification of the entire movement trajectories of individual animals, and the concomitant development of sophisticated analytical techniques for interpreting the movement behaviors captured by these techniques (62, 74, 95, 113). Size and weight constraints generally preclude the use of most tracking devices for studies of long-range migration in insects (but see Reference 114 for an exception), but harmonic radar has made characterization of insect foraging flights possible and a significant development of our conceptual understanding of insect searching strategies has ensued.

There are several situations in which foraging honey bees have to conduct searches when they have no prior information of where the resource will be found, for example, searching for a new forage patch or locating their hive after becoming disoriented due to the accumulation of errors in their path integration system. Theoretically, the optimal strategy for locating patchily distributed resources in an uncertain environment is a type of scale-free, random searching pattern known as a Lévy flight (74).

A reanalysis of radar-derived flight trajectories by A.M. Reynolds demonstrated that honey bees employ Lévy-flight searches when trying to locate profitable food sources (76, 77) or find their hive after artificial displacement (75). When they have some limited knowledge of where the resource is expected to be, they deploy a looping search strategy, with randomly directed movements from a central point, but if this fails they eventually switch to a freely roaming search to cover more ground (75).

Many insects have to systematically search for randomly distributed resources that advertise their presence with attractive odors, e.g., male moths searching for conspecific females that release sex pheromones. There have been

numerous studies on the upwind anemotaxis used to follow an odor plume to its source (10), but few investigations of the behaviors employed to find the plume in the first place. Landscape-scale harmonic radar studies of male *Agrotis segetum* moths indicated that when odor filaments of sufficient concentration are encountered, males that are flying downwind change course and start flying crosswind, while crosswind fliers start moving upwind (73); the effectiveness of such a plume-locating strategy could be demonstrated using realistic modeling of plume structure, pheromone-detection thresholds, and wind conditions. More complex search patterns were also noted, including a type of Lévy flight (73) (Figure 2d). Investigation of further flight-capable insect species for Lévy flights and other optimal searching strategies would appear worthwhile.

Dispersal rates in butterfly metapopulations. Dispersal capability is a key factor in the survival of insect populations, particularly for those species that exist as metapopulations in spatially fragmented landscapes where there is a distinct probability of local extinction (47). Dispersal is achieved through a suite of morphological, physiological, genetic, and environmental factors, and individual variation in dispersal rates can be affected by any and all of these. These complex interactions have been extensively studied in metapopulations of the Glanville fritillary butterfly, *Melitaea cinxia*, in the Åland Islands (Finland) by Hanski and colleagues (47). In an experiment in the United Kingdom, harmonic radar was used to track free-flying *M. cinxia* females in order to record their tracks over periods of several hours. The results confirmed that variation in dispersal was associated with population history: Females from newly established (1-year-old) isolated Finnish populations were more dispersive than those from older (>5 years) isolated populations (66). Previous work had also indicated that variation in the gene encoding for the enzyme phosphoglucose isomerase (*Pgi*) was associated with individual variation in flight metabolism in this butterfly (64). The radar tracking

demonstrated that the higher flight metabolic rate translated into higher dispersal rates in the field, with heterozygotic *Pgi* individuals moving longer distances and flying at lower ambient temperatures than homozygous individuals (64). The radar studies thus helped to establish connections between organizational levels ranging from molecular variation in a single gene, via flight physiology, to landscape-scale patterns of butterfly movement.

FUTURE PROSPECTS

The increasing availability, affordability, and reliability of radar, signal processing, and microcomputing hardware, and the rapidly increasing power of the last two, will allow further development and wider deployment of entomological radar technology. In the case of harmonic radar, modification of the receive antenna to produce a pair of vertically overlapping beams would allow the target's height of flight to be inferred. For vertical beam radars, separate transmit and receive antennas, and perhaps use of frequency-modulated continuous wave (FMCW) rather than pulse transmission, would largely eliminate the ~150-m blind zone just above the ground of current designs. Incorporation of Doppler processing would allow observation of target ascent and descent; this appears to be the most promising technique for studying the rather cryptic and poorly characterized termination phase of migratory flight.

The size, shape, and wing-beat frequency values determined for each individual insect by a VLR with full target interrogation capability are already allowing inferences to be drawn about the identity of the detected targets (13, 18, 25). With a priori information on the local migrant insect fauna, assignment of target numbers, speeds, and directions to broad taxonomic classes (e.g., large grasshoppers, large moths, small moths)—and sometimes even to a particular numerically dominant species—is possible. Fully automated monitoring of locusts, and perhaps also of some pest moth species, can thus be envisaged. Extending the rather small

FMCW: frequency-modulated continuous wave

current dataset of measurements of the radar properties of known species (49), and investigating intraspecific variance, would help to develop identification confidence.

As millimeter-wavelength radar technology becomes more affordable, deployment of 9- and 3-mm-wavelength VLRs alongside current 32-mm units at each observing site can be contemplated. Flight activity could then be monitored for insects ranging in size from sphingid moths and locusts, through planthoppers (~1–2 mg; 85), to aphids, small Diptera, and minute parasitic wasps (~0.05–0.5 mg). Radars operating at 9 and 3 mm have been developed for atmospheric observations and on warm cloudless days detect insects in large numbers (119). The great profusion of small taxa will present a target identification challenge that will be best tackled by sampling, at least occasionally, with a balloon-borne net (20).

An alternative way of exploiting the falling hardware costs would be to install additional 32-mm-wavelength VLRs in a network to explore how migratory activity varies over a region. A chain of these units across a prominent migration route, for example, the Mississippi flyway in North America, would reveal the timing and lateral extent of migration events and how these vary with season, wind, and weather; additional units at higher or lower latitudes would strengthen knowledge of distances moved and the seasonal advance and retreat of populations. Similar networks can be envisaged for Europe and eastern China, while in Australia an additional five or six VLRs would provide comprehensive coverage of the inland region where locust outbreaks most frequently develop. On a smaller scale, operating a mobile unit for a few weeks at varying distances from a long-term observing site would establish the scale over which a VLR's observations are representative.

Finally, modern weather surveillance radars, especially those with dual-polarization capability, routinely detect insects in fine warm weather and are being deployed in networks covering entire countries. Dual polarization can discriminate insects, with their elongated

bodies held approximately horizontal, from both hydrometeors and birds (3); it also reveals patterns of common orientation (70) (a phenomenon long familiar to radar entomologists, see above), which helps to establish the biological identity of the targets. Weather-radar observations of insect activity are beginning to contribute to forecasts and “now casts” of migratory pest incidence (53).

Turning from technology to biology, the orientation behavior observed in nocturnal windborne migrants (12, 14, 15) clearly warrants laboratory investigation to determine its neurophysiological basis; identification and characterization of magnetoreceptors (67) and of sensory organs for detecting turbulent air motions are obvious priorities. The association of layer concentrations and common orientation, and the variation of orientation with height and time, can be examined with archival VLR datasets, but FMCW radars, with range resolutions of only 1–2 m, and simultaneous meteorological profiling of wind, turbulence, and temperature may be needed to fully resolve the causes of these phenomena. Observations from a VLR network (see above) would establish whether seasonally advantageous flight headings occur throughout a species' range and how these headings vary with longitude and latitude or according to local geography. A radar on the Falsterbo Peninsula in southwest Sweden, for example, might resolve whether high-flying insects take the shortest sea crossing to Denmark by flying west—as low-flying red admiral butterflies, *Vanessa atalanta*, have been observed visually to do (7)—or steer a southward course more in accordance with their presumed long-range goal. VLR network data might also elucidate how some seasonal migrants are able to move differentially on winds from certain directions, avoiding displacement in highly disadvantageous directions (e.g., poleward in the fall). Is this achieved by sensing a cue (e.g., the relative humidity of the airstream) while still on the ground, or do potential migrants have to take off and then rapidly terminate their flight if they sense that they are being displaced in the wrong direction?

CONCLUSIONS

Radar has now been used by entomologists for over 40 years. After a brief but exciting discovery phase, the focus of its application became careful studies of economically significant pests, usually undertaken in conjunction with simultaneous trapping, survey, and visual observation campaigns. The aims of this research were primarily to establish whether these pests were migratory and to determine the scale, direction, timing, and frequency of movements and the conditions in which they occur. Almost in passing, behaviors modulating the incidence of migratory flight and the displacements achieved were recognized. More recently, technical developments and a new radar design allowed more precise observations to be accumulated over much longer periods, while the introduction of harmonic detection extended radar work into a new field—the study of foraging and searching flight. As the entomological use of radar has matured, behavioral questions have increasingly been targeted, and descriptive and quantitative analyses of observations have been supplemented by formal hypothesis testing and, in the case of harmonic radar,

manipulative experimentation. However, observations with a more ecological focus continue in regions where migrant insect pests have a significant economic or welfare impact, and in this more applied context the new automated units may be able to fulfill an operational role—most likely for locust management.

Radar continues, as it began, to reveal remarkable insect behaviors that appear to represent sophisticated evolved adaptations. It is now clear, thanks in good part to radar work, that insects are highly effective migrants and foragers. Over the past decade, radar-led research has refined our knowledge of the strategies and sensory capabilities employed by insects in flight. Some specific and bold hypotheses have been developed to account for the observed phenomena, and these have been tested with both new and archival radar datasets. Much of this research is at an early stage and it is reasonable to suppose that there is still much to learn. The potential of current entomological radar types is surely far from exhausted, and further technological advances can be expected to provide additional opportunities for those willing to grasp them.

SUMMARY POINTS

1. Entomological radars have made a huge contribution to understanding windborne insect migration.
2. Two new designs, VLR and harmonic radar, have significantly enhanced the observational capabilities of researchers studying high-altitude migration and low-altitude foraging flight, respectively.
3. VLRs have shown that windborne migrant moths use environmental cues to select flight headings and flight altitudes that optimize their migratory trajectories.
4. Harmonic radar has demonstrated that social bees navigate to their goal by path integration (with wind-drift compensation) and progressive learning of landmarks, and confirmed that honey bees communicate both direction and distance information through the waggle dance. Harmonic radar has also shown that insect foragers employ Lévy-flight optimal search strategies.
5. Further technological improvements will enable radar entomology to remain in the forefront of research into insect flight behavior.

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