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Concentration of Flying Insects by the Wind [and Discussion]

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Concentration of flying insects by the wind

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The role of horizontal wind convergence in concentrating flying insects is examined. Because of the inverse relation between intensity and persistence of convergence zones, a tenfold increase in volume density is unlikely to be exceeded in a single atmospheric disturbance, and then only if the insects are not taken through the convergence zone. Radar has shown that the commonest disturbances associated with insect concentrations are windshift lines: modifications of the broad-scale wind flow due to buoyancy and blocking effects. Even in the absence of concentration, a tenfold increase in area density can be brought about by vertical circulations at windshift lines. Insect concentrations are likely to be most frequent and persistent at night, and over and near mountains, where searches are most difficult.

1. Introduction

If windborne insects accumulate in particular kinds of atmospheric motion patterns, in numbers and at volume densities to make air-to-air spraying effective, then the possibility arises of improving control by seeking out such patterns. This paper reviews several of the mechanisms that might concentrate flying insects, and discusses their application to the operational monitoring of insect populations. For an ecological discussion of the significance of aerial concentration on colonization by windborne insects, see Drake & Farrow (1989).

There is considerable evidence that many migrant insect species are windborne; for recent reviews see Pedgley (1982, 1983), Drake & Farrow (1988), and McManus (1988). The evidence continues to grow: it refers to not only small, weak fliers such as vectors of organisms causing serious diseases in crops (Kisimoto 1984: Liu 1984; Rosenberg & Magor 1987; Wada *et al.* 1987; Irwin & Thresh 1988), and man (Baker *et al.*, this symposium), but also larger, stronger fliers such as grasshoppers (Reynolds & Riley 1988), locusts (Symmons 1986; Casimir 1987) and moths. Among moths, there has been emphasis on various crop pests: armyworm moths in China and Japan (Chen & Bao 1987; Miyahara 1987; Hirai 1988; Chen *et al.* 1989), Africa (Rose *et al.* 1987; Pedgley *et al.* 1989) and North America (McNeil 1987; Johnson 1987; Pair *et al.* 1987), as well as bollworm moths in Australia (Wilson 1983), and green clover worm moths (Wolf *et al.* 1987) and celery looper moths (Peterson *et al.* 1988) in the U.S.A. Presumably all these windborne migrant species are open to concentration by the air motion.

2. Dispersion and concentration of flying insects

Insects moving like a cloud carried downwind may respond to each other as a coherent swarm. This happens with locusts and bees but it has not been demonstrated in other species, although large numbers of independently flying individuals may give the impression of a swarm. Instead, a cloud of insects might be expected to thin out as the mean separation between individuals increases under the influence of dispersion, like smoke or by individual flight behaviour. Field evidence in support of such thinning comes from radar studies of insect volume density decreasing downwind from a source (Riley *et al.* 1983; Riley & Reynolds 1983) and of observed variability in heading within a cloud of insects, particularly where they are likely to be largely of one species (Schaefer 1979; Greenbank *et al.* 1980; Riley & Reynolds 1983; 1986; Riley *et al.* 1981, 1983, 1987; Drake 1983, 1985*b*; Mueller & Larkin 1985; Drake & Farrow 1985; Chen *et al.* 1989). Mark-and-capture studies of distances flown by insects from a common source provide additional evidence, the dispersion then being dominated by day-to-day and hour-to-hour changes in the wind field (Li *et al.* 1964; Hendricks *et al.* 1980; Rose *et al.* 1985; Showers *et al.* 1989). There appears to be no theoretical study of dispersion of a cloud of insects having a variety of headings in a turbulent wind. Models developed for pollution studies might be adapted, as they have been for clouds of young caterpillars of the gypsy north, suspended on silken threads (Fosberg & Peterson 1986), but they would be even more complex than for particles, because of the need to incorporate insect flight behaviour.

The reverse of dispersion, concentration, might be expected if there is some mechanism to bring flying insects together. Concentration of insects *onto the ground* can be brought about by preferential settling, e.g. in areas sheltered from the wind. This is well known to occur in the lee of windbreaks (Pasek 1988), but it also occurs, on a larger scale, in the lee of hills. It may account, for example, for the association of African armyworm outbreaks with topography (M. J. Haggis, personal communication) due to concentration of the night-flying moths, similar to the concentration of day-flying sod webworm moths in New Zealand (Cowley 1987).

There is certainly evidence for the occurrence of dense insect clouds *in the air*: the sudden appearance of large numbers in flight, and the presence of innumerable radar echoes in the form of bands one or two kilometres wide and tens of kilometres long, moving at up to 10 m s^{-1}. Volume densities of moths and grasshoppers in these echo bands are typically 10^{-3}–10^{-4} insects m^{-3} (see, for example, Schaefer 1976, 1979; Riley *et al.* 1981; Pedgley *et al.* 1982; Riley & Reynolds 1983; Reynolds & Riley 1988). This contrasts with the much greater densities of Desert locusts in swarms: typically 10–10^{-3} insects m^{-3}, measured by radar (Ramana Murty *et al.* 1964) and by vertical photography (Waloff 1972). With typical depths 0.5–1.0 km, and therefore cross-sections of about 1.0 km^2, each kilometre length of band contains 10^5–10^7 insects. Some bands have been followed by radar for distances varying from 7 km (in 25 min, Pedgley *et al.* 1982) to 38 km (in 99 min, Schaefer 1976).

Increased volume density of flying insects has been associated with windshift lines, where there is a more or less well-defined boundary between two airstreams with different directions or speeds, or both. Such an association may be due to a change in the source of the insects, a triggering of take-off, a vertical concentration of individuals near the ground with the onset of rain, or a horizontal concentration of individuals by convergent winds. The first three are considered briefly; emphasis is put on the fourth.

A change in volume density with a change in wind direction can be identified by means of an hourly recording trap or by radar. An example of the use of radar comes from Muguga, near Nairobi, on the night of 17–18 April 1980, when a light trap caught many more armyworm moths than on the previous and following nights. Differences in trap catch could not be attributed to differences in trap efficiency (due to moonlight or wind speed), nor was there any significant rain. After the dusk take-off there were few echoes until just after midnight, when the wind changed fitfully from northeast to west and echoes moving from the west increased to a maximum at 01h45. There was no echo band and no windshift line (D. R. Reynolds, personal communication.).

There do not seem to have been any field studies of take-off being stimulated by a windshift line during the short time that it takes to pass overhead, although Bergh (1988) found increased take-off frequency in the laboratory with passage of cold fronts.

Large numbers of night-flying moths seen at lights or caught in traps are well known in rainy weather (Brown *et al.* 1969; Dickison *et al.* 1983, 1986; Tucker 1983; Tucker & Pedgley 1983). There is some radar evidence (Greenbank *et al.* 1980; Riley *et al.* 1983) to suggest that these large numbers can be due to descent to near the ground, or even landing, at onset of rain.

3. Wind convergence and concentration of flying insects

Rainey and co-workers have for long associated the concentration of flying insects with horizontal convergence of winds (Rainey 1951, 1963, 1972, 1974, 1976, 1980; Sayer 1962; Brown *et al.* 1969; Joyce 1973, 1983; Dickison *et al.* 1983). Horizontal wind convergence occurs where there is a net inflow into a given marked volume of air. Conversely, net outflow is divergence. Convergence and divergence are potentially mappable, as are other properties of the wind, such as speed and direction. A dense network of surface observing stations may be used, or Doppler radar where rain drops are tracers of the wind (Browning & Wexler 1968; Rabin & Zrnic 1980).

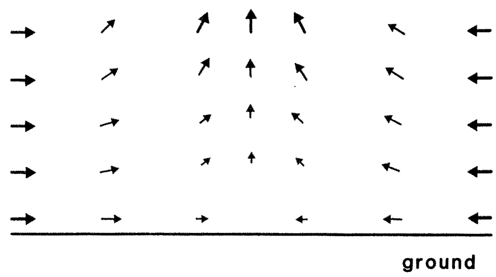

FIGURE 1. Vertical section through a region of horizontal wind convergence, showing vertical divergence and an increasing upward wind component with height. Arrow length is proportional to wind speed.

Near the ground, horizontal convergence is necessarily accompanied by vertical divergence (figure 1) because there is no significant accumulation of air (increase in air density). Vertical divergence implies an increase in the upward component of the wind with height. (Horizontal divergence is accompanied by vertical convergence and an increasing downward component with height.) Flying insects therefore have a tendency to be carried upwards where there is wind convergence, but their volume density would not increase unless there was also a tendency to resist being taken aloft, particularly where the upcurrent is sloping and there is no circulation to return descended insects into the convergence. Such a tendency would occur if insects actively avoided cold air, where temperatures are below a threshold for flight, varying not only between species but also, to some extent, between individuals within a species. Evidence that this does in fact occur comes directly from laboratory studies on many species and indirectly from trap catches in relation to air temperature. It is also provided by the frequent layering of night-flying insects recorded by radar on clear, quiet nights, once the dusk take-off period has been passed, and there are no persistent updraughts. Layering has been

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found with locusts (Drake & Farrow 1983), grasshoppers (Riley & Reynolds 1979, 1983; Reynolds & Riley 1988) and moths (Schaefer 1976; Greenbank *et al.* 1980; Drake 1984*b*, 1985*b*; Drake & Farrow 1985; Chen *et al.* 1989). Where there have been temperature soundings, maximum densities have been found in the warmest air, near the top of the nocturnal temperature inversion (Schaefer 1976; Riley & Reynolds 1979; Drake 1984*b*).

Convergence is the instantaneous rate of shrinking of unit horizontal area of a marked volume of air because of net inflow. Where wind direction is uniform over an area, convergence is readily seen to be due to downwind deceleration (figure 2*a*), but where the direction is not uniform (figure 2*b*) it is less readily identified. Convergence is measured in units of change of velocity per unit distance and is typically about 10^{-5} s^{-1}. With such an intensity of convergence, a given area will shrink by a factor of *e* (about 2.7) in about one day. The concentration rate of insects flying in such convergence is slow: a tenfold increase in volume density, for insects confined to a fixed depth in the atmosphere, would require a few days. However, there are parts of the atmosphere where convergence is much stronger, say 10^{-3} s^{-1}, often in strips known as convergence zones. Flying insects there could be concentrated much faster: a tenfold increase in volume density in about an hour. With such convergence the vertical velocity would increase upwards by 10^{-3} m s^{-1} in 1 m, that is, from zero at the ground to 1 m s^{-1} at a height of 1 km. Upward velocities of 1–5 m s^{-1} are characteristic of convergence zones with such an intensity, and may exceed the fall speeds of insects with their wings folded. Even stronger convergence does occur, as in tornadoes and so-called microbursts, but it is transient, often lasting only a small fraction of an hour.

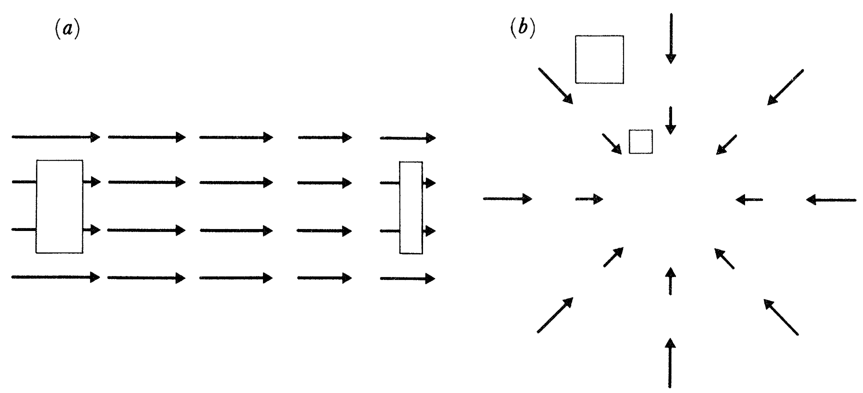

FIGURE 2. Wind arrows in two idealized convergent flow patterns with downwind deceleration, showing contraction of horizontal areas of moving volumes of air: (*a*) uniform direction; (*b*) radial inflow.

There is a tendency for stronger convergence to be associated with smaller and shorter-lived disturbances in the atmosphere (Fujita 1981), with the result that the time needed for a tenfold increase in volume density is comparable with the life-time of the disturbance. Hence an increase in volume density of about tenfold is to be commonly expected due to wind convergence within a single atmospheric system, irrespective of its duration, and only rarely a hundred-fold. Such increases in volume density assume the insects remain in the convergence zone, but winds may carry insects more or less quickly through the zone, with consequently less concentration. However, by comparing vertical profiles of volume density measured by radar in and near echo bands, increases of about fifty-fold have indeed been found (Schaefer 1976, 1979; Pedgley *et al.* 1982; Riley & Reynolds 1983). To compare densities at a given height (as measured by an aircraft, for example) is inadequate as an indicator of concentration when insects are fed from below into the convergence zone. Moreover, neither is an increase in *areal* density necessarily an indicator of concentration because it can be caused by a simple doming up of an insect layer without any increase in *volume* density.

Increased numbers of insects caught in traps that happen to be near convergence zones are sometimes used as evidence that concentration by wind convergence has taken place (Haggis 1971, 1979), but size of catch is also affected by trap efficiency (Douthwaite 1978; McGeachie 1989) and by insect flight behaviour, both of which can be modified by the weather accompanying convergence zones.

4. Atmospheric disturbances and insect concentration

Radar studies have clearly associated echo bands, or insects in line concentrations (the word is used here to describe the observed state, not a process), in the lowest kilometre of the atmosphere at night, with windshift lines and strong horizontal wind convergence. There are zones of strong horizontal wind convergence in three kinds of mesoscale atmospheric motion patterns (i.e. those with horizontal dimensions from a few tens to a few hundreds of kilometres); for a general review, see Atkinson (1981).

1. The leading edges of gravity currents (also known as density currents), where there is undercutting of warm air by cool air produced by evaporation of falling rain or by horizontal variations in the radiation balance of the ground, either on a large scale as at some cold fronts or the Inter-Tropical Front (ITF) or more locally as at coasts and over mountains (and possibly also at the boundaries of wet or cloud-shaded regions, see, for example, Ookouchi *et al.* 1984; Segal *et al.* 1986).

2. Overturning circulations in gravity waves in stably stratified air which has been displaced vertically, either by intrusion of gravity currents (Reid *et al.* 1979; Drake 1984*a*, *b*, 1985*a*), or by flowing over topographic barriers (Pedgley *et al.* 1982).

3. The edges of adjacent convection cells (polygonal or linear) caused by heating of the atmosphere over more or less homogeneous ground.

(*a*) *Gravity currents*

The structure and behaviour of gravity currents have been studied extensively in laboratory tank experiments, in the field (first using instrumented towers and dense networks of ground recorders, but later using Doppler radar and aircraft), and by simulation in numerical models. For reviews, see Fujita (1985), Simpson (1987) and Smith & Reeder (1988). Gravity currents in the atmosphere have depths of up to one or two kilometres, and at the leading edge there is convergence and ascent of both airstreams into a domed head containing an overturning circulation, or rotor (figure 3). Flying insects from both sides can be expected to ascend in a sloping curtain with a structure similar to that revealed by duststorms accompanying downdraught squalls in arid country (Lawson 1971). Such a structure is well demonstrated in a cross-section through a cloud of spruce budworm moths at a sea breeze front (Schaefer 1979), and in less detail for grasshoppers (Schaefer 1976) and African armyworm moths (Pedgley *et al.* 1982) at storm outflows. The vertical distribution of volume density found by Schaefer is consistent with a doming up, or even rolling up and mixing, of shallow, dense layers of insects near the ground from both sides of the front, similar to the vertical distribution of water vapour

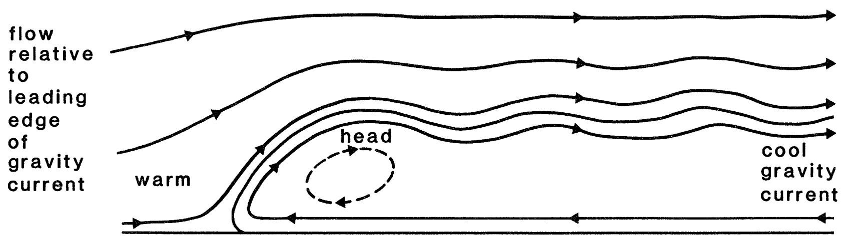

FIGURE 3. Schematic vertical section through a gravity current, showing flow from both sides into a zone of updraughts at the leading edge, and possible overturning in the head.

found by Simpson *et al.* (1977) at a sea breeze front. A result is that the area density increased about tenfold, whereas the volume density changed less. Another example of this rolling-up process is the reconstitution of swarms of the Desert Locust in northern Somalia flying into windshift lines (identified by Sayer (1962) as the ITF, but more likely to be gust fronts from adjacent rainstorms). Similarly, band echoes due to the presence of insect-feeding birds at altitudes of hundreds of metres in a sea breeze front are indicative of the effects of upward motion there on flying insects (Simpson 1967), and the same seems to be true for the leading edges of storm outflows (Harper 1960). Other echo bands due to insects have been reported in association with sea breeze fronts (Neumann & Mukammal 1981; Drake 1982, 1984*b*), storm outflows (Schaefer 1976; Riley *et al.* 1981; Reynolds & Riley 1988), cold fronts (Rainey 1979; Reid *et al.* 1979), and the ITF (Rainey 1976; Schaefer 1976). Gravity currents similar to sea breezes can develop along an escarpment bordering a plateau but their effects on flying insects have not been explored.

It is not known if the lobe-and-cleft structure (Simpson 1987) at the leading edge of a gravity current intensifies the concentration mechanism there. Nor are the effects on flying insects known where increased convergence occurs in vortices that sometimes develop along strongly sheared windshift lines. Such vortices vary in size from as small as dust devils to as large as tornadoes, and their accompanying circulations with dimensions from several kilometres to a few tens of kilometres (James & Browning 1979; Lemon & Doswell 1979; Hobbs & Persson 1982; Carbone 1982, 1983; Parsons *et al.* 1987; Mueller & Carbone 1987). Outflows from neighbouring rainstorms can collide, triggering new rainstorms and hence new outflows.

The process of insect concentration at a gravity current head has been modelled numerically. Mansfield *et al.* (1974) used the observed overturning circulation at a sea breeze front, and simple assumptions about aphid flight behaviour, to show that after two hours almost all the insects were being carried within the circulation. Symmons & Luard (1982) have shown the magnitude of concentration, by using some fairly arbitrary assumptions about both the structure of the wind field and insect behaviour. A two-dimensional (vertical plane), numerical, Eulerian model, based on a pollution diffusion model by using observed insect sources and wind soundings as inputs, is being developed to determine whether convergence simulates the distribution of brown planthoppers near the Bai-u front over China (F. Crummay, personal communication).

(*b*) *Bores and solitary waves*

When a gravity current enters a stably stratified fluid, a bore, like that on a tidal river, can be induced, as has been shown in laboratory tank experiments by Maxworthy (1980) and by Rottman & Simpson (1989). There is a sudden and sustained lifting of the streamlines, often in a sequence of waves (figure 4*a*). Such undular bores are smooth if the lifting is small, but they are progressively more turbulent as lifting increases. Tank experiments and numerical models show that an undular bore propagates away from the parent gravity current and evolves into a set of independently-moving solitary waves (figure 4*b*); for reviews, see Smith

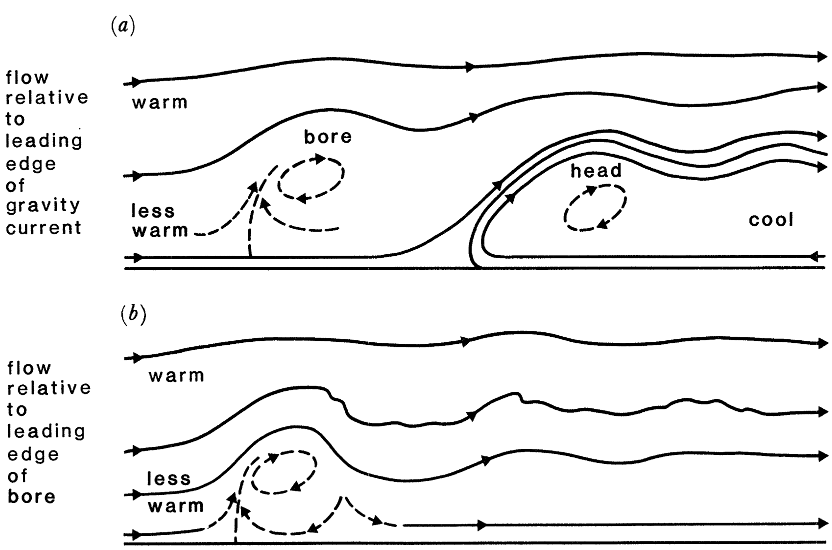

FIGURE 4. Schematic vertical section through an undular bore generated by a gravity current entering a stably stratified fluid: (*a*) smooth undular bore beginning to move away from the head; (*b*) turbulent undular bore that has propagated far from its source.

(1988) and Christie (1989). An atmospheric example that has been well documented in recent years is the Morning Glory of northeastern Australia, which seems to be generated by the collision of sea breeze fronts from opposite coasts of the Cape York Peninsula, in Queensland, and travels westwards for hundreds of kilometres at speeds of 5–15 m s^{-1}. Similar disturbances seem to be generated in nocturnal temperature inversions by sea breeze fronts (Simpson *et al.* 1977), by rainstorm outflows, and by horizontal variations in wind accelerations associated with formation of the nocturnal low-level jet. Little is yet known about the conditions for, or even the occurrence of, overturning circulations in such solitary waves, and their significance in concentrating flying insects is also unknown, but they may account for some of the echo bands reported from Australia (Drake 1984*a*, *b*, 1985*a*).

(*c*) *Mesoscale gravity waves*

Much larger gravity waves, with wavefront lengths of a few hundred kilometres and speeds of a few tens of metres per second, persisting for ten hours or more, occur occasionally in middle latitudes (Uccellini & Koch 1987). At the ground, these waves are accompanied by wind oscillations (superimposed on the large-scale flow) of amplitude about 10 m s^{-1}, with maxima under the crests blowing in the same direction as that of wave propagation, and under the troughs in the opposite direction. Maximum convergence is of the order of 10^{-4} s^{-1}. Implied vertical circulations extend throughout the depth of the troposphere, for many of the waves seem to have been set up by downdraughts although they are transmitted by marked low-level inversions. Their effects on insect concentration are unknown.

(*d*) *Topographic waves and vortices*

The motion occurring in a stably stratified airstream in the presence of a topographical barrier may take many forms, like those in a river flowing over and between boulders, and determined by the upstream profiles of wind and temperature as well as by the shape and size of the barrier. The structures of these disturbances are modified by diurnal patterns of heating and cooling and by the ever-changing large-scale wind systems (Alaka 1960; Nicholls 1973; Smith 1979; Baines 1987). If the airstream flows over a *long ridge*, narrow enough for the effects of the earth's rotation to be ignored (i.e. when it takes a small fraction of a day to cross it), a train of stationary gravity waves can form on the leeward side with their axes parallel to the barrier and with wavelengths typically up to 10 or 20 km. Beneath one or more wave crests, rotors may appear, if only intermittently, with associated convergence lines (figure 5(*a*)).

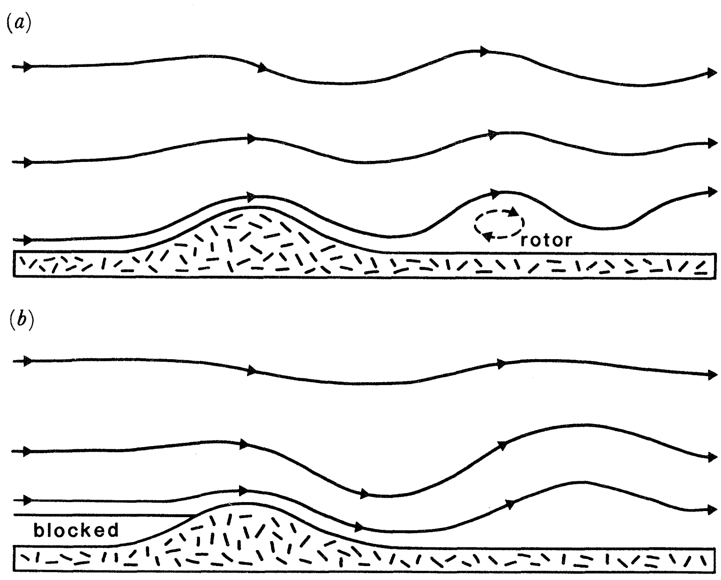

FIGURE 5. Schematic vertical section through a stably stratified fluid crossing a long ridge, showing: (*a*) lee waves and an overturning circulation (rotor); (*b*) blocking of the lower part of the upstream flow.

There is radar evidence for concentration of African armyworm moths in rotors (Pedgley *et al.* 1982). On the windward side, the lower part of the airstream may contain a similar rotor, again with an associated convergence line (figure 5*a*), or it may be brought to rest, or blocked (figure 5*b*). With parallel ridges, the flow can be more complex, depending on ridge spacing in relation to wavelength (Tampieri & Hunt 1985; Lee *et al.* 1987).

If the barrier is an *isolated hill* then much of the air that would otherwise be blocked is deflected around it, leading to a complex wake (figure 6) (Brighton 1978, Hunt & Snyder 1980). Waves may be induced in an inversion if it is at levels comparable with the top of the hill, perhaps with a horseshoe-shaped spiralling rotor in the first lee wave. Beneath this pattern,

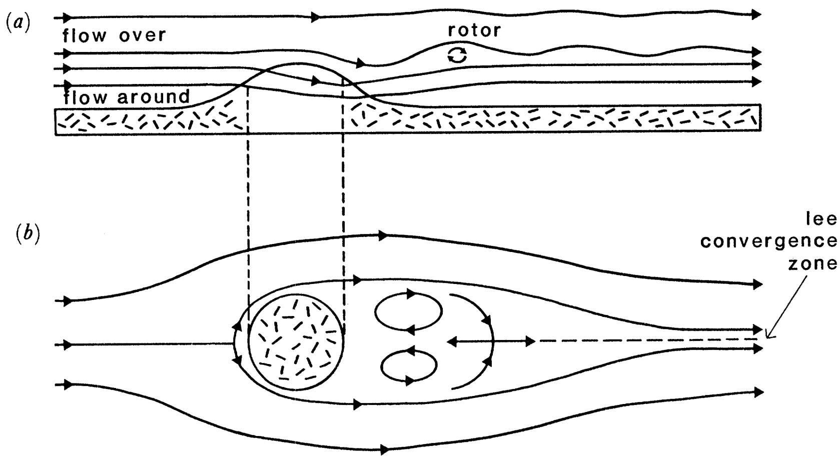

FIGURE 6. Schematic representation of flow of a stably stratified fluid over and around an isolated hill (based on Brighton (1978) and Hunt & Snyder (1980)): (*a*) vertical section showing the upper part of the stream flowing over the hill, and the lower part around; (*b*) horizontal plan showing separation of the flow on the upstream side, and a complex wake on the downstream side with vortices and a lee convergence zone.

the deflected flow, accelerating on either side of the hill, can be separated by shear lines from a zone of light winds (wind shadow), or by a lee convergence zone (Edinger & Helvey 1961, Walter & Overland 1982, Mass & Dempsey 1985*a*), or by contra-rotating vortices with more or less vertical axes and a zone of reversed wind blowing towards the hill. Vortices formed in a stably stratified airstream to the lee of isolated mountainous islands can be periodically shed as a Karman vortex street (Chopra & Hubert 1965). An example of similar shedding over land may be the Denver Cyclone (Wilczak & Glendening 1988), but the effects of such vortices on flying insects are unknown.

Complex interactions can be expected between gravity currents and topographic disturbances. A particularly complex and rapidly evolving wind field would be caused, for example, by downdraughts from adjacent evening storms triggered by a sea breeze front moving into a mountainous region.

(*e*) *Topographic convergence zones*

Another topographic effect is the channelling of stably stratified airstreams along valleys, leading to the formation of convergence zones. This has been studied over the Puget Sound (Mass 1981, 1982) and over the Red Sea (Pedgley 1966; Rainey 1976). Swarms of the Desert Locust, and its breeding, are concentrated on the lower land around the central latitudes of the Red Sea from November to January, before seasonal temperature rises are enough to allow daytime flight onto the adjacent plateaux and away from the zone's influence.

(*f*) *Slope winds*

When a nocturnal temperature inversion develops on sloping ground, the cooled air tends to drain downhill as a gentle katabatic wind. In a valley, katabatics from both sides can combine into a jet-like mountain wind, blowing down-valley with a speed up to 5 m s^{-1}, sometimes pulsating with a period of oscillation of the order of one hour. Evening onset of the mountain wind in a valley bottom can be sudden (Wilkins 1955; Dickson 1958; Thompson 1967; Tyson 1968) and it resembles a gravity current. The same is probably true where a katabatic wind reaches a gentler slope over nearby plains (figure 7*a*), as has been shown near Boulder, Colorado (Hootman & Blumen 1983; Blumen 1984), and appears also to happen over Tokyo (Ohara *et al.* 1989). Katabatics draining into an enclosed area become ponded, and because of their various origins the stratification becomes layered and conducive to the formation of bores and travelling waves (figure 7*b*). Concentration of insects has not yet been shown at the heads of katabatic flows, or in any waves they may induce, but the line concentrations reported from West Africa by Schaefer (1976) and by Riley & Reynolds (1983) may have been in the heads of katabatic fronts, Radar does sometimes reveal undulations in insect layers aloft (Richter *et al.* 1973; Pedgley *et al.* 1982; Gossard & Strauch 1983); these are presumably due to gravity waves but their origins are seldom known. They have separations varying from several hundred metres to a few kilometres, and speeds of 5–10 m s^{-1}.

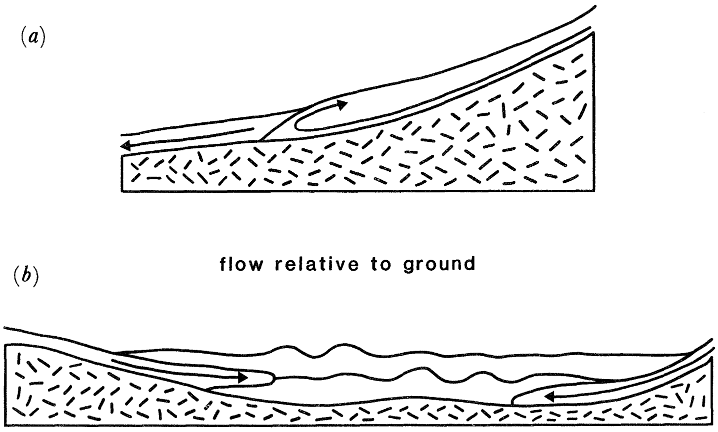

FIGURE 7. Night-time downslope katabatic winds: (*a*) forming a head at a change in slope; (*b*) entering ponded and strongly stratified cold air with generation of gravity waves.

Whereas gravity currents, bores and many waves are mobile, and may travel tens or hundreds of kilometres, the topographically linked waves and convergence zones are more or less stationary. There seems to have been little work so far on any breaking or reflection of travelling waves by topographic barriers, but Black (1979) gives examples of waves in shallow sea fog reflected from the shores at the head of the Bay of Fundy, Canada.

(*g*) *Cellular convection*

Daytime convection in the lowest few kilometres of the atmosphere is sometimes organized into polygonal cells a few tens of kilometres across, or in linear cells, or rolls, a few kilometres apart but tens of kilometres long. Most studies of polygonal cells have been over the oceans (Agee 1984, 1987). Similar convection over land seems to be much less common, but it has been reported from radar studies, in each of which the updraughts in cell walls have been located by means of the concentrations of insects: in the U.S.A. (Hardy & Ottersten 1969), in Australia (Schaefer 1976; Reid *et al.* 1979) in Niger (Schaefer 1976) and in India (Mazumdar *et al.* 1965). Convective roll vortices more or less parallel to the wind develop when slight instability is accompanied by wind shear in the vertical; for a review, see Brown (1980). Convergence of the order of 10^{-3} s^{-1} has been measured beneath upcurrents in such rolls. Although the effect on flying insects is unknown, some of the daytime radar echoes reported from Australia were almost linear, suggesting an effect of rolls. Harper (1960) identified echo bands, that we can now reasonably associate with roll vortices, as being caused by birds feeding on insects that were presumably being taken aloft at the convergence lines.

(*h*) *Coastal convergence lines*

When a wind over the sea meets a coast on the right-hand side (in the northern hemisphere) at a small angle a coastal convergence line may form due to greater friction over the land (Roeloffzen *et al.* 1986). Such lines have vertical circulations similar to those of sea breeze fronts, and indeed the two mechanisms may interact. Any effects on flying insects have not yet been shown.

5. Discussion

It is often difficult to be sure of the pattern of atmospheric motion that is associated with a given radar echo band. This is because some patterns are still poorly described, and because meteorological observations made during radar field studies are limited, being at best confined to autographic records of surface weather, together with a few soundings of wind and temperature, although aircraft observations are sometimes available. Reliance on surface records to distinguish kinds of night-time patterns is uncertain because temperature inversions more or less uncouple the surface flow from that aloft, even at heights of only a few tens of metres. Additional useful records would be in the vertical plane, obtained from Range Height Indicator radar displays of insect clouds and from frequent wind soundings, perhaps using remote sensing techniques such as Doppler radar.

How can an imperfect understanding of the mechanisms that may concentrate flying insects be used to improve the monitoring of insect populations? If the densities and numbers typical of line concentrations are not worth spraying, for logistic, economic or other reasons, then searching for individual concentrating disturbances is unlikely to be worthwhile. But that may not be true where the same insects are subjected to a sequence of such concentrations. That is most likely to occur where the motion is linked to topography, either coasts (sea breeze fronts and any associated rainstorms) or mountains (complex barrier effects and slope winds, and any associated rainstorms). Away from coasts and mountains, the distribution of convergent wind systems (such as downdraught fronts and bores) is likely to be so erratic in space and time that they would provide little guidance in locating insect concentrations for air-to-air control tactics. An exception is the ITF in Sudan, where it can be as well-defined as the leading edge of a gravity current. In some ways the ITF there resembles a sea breeze front, but on a larger scale. However, the ITF has a north–south diurnal oscillation in position of up to 200 km as well as more irregular movements over a few days of several hundred kilometres, reducing the chances of the same insects being successively concentrated, particularly for those species that fly for only a few days, and for only a part of each day. Another exception is the coastal front of northwest Africa (the 'trade front'), separating cool ocean air from hot continental air, which can persist for days or weeks and trap migrating Desert Locust swarms.

From this it follows that mountains, and particularly coastal mountains, are likely to be the places most favourable to the concentration of flying insects, because of the variety and frequency of suitable atmospheric disturbances. Such disturbances are likely to be most frequent at night, not only because of the static stability necessary for the development of bores,

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waves and katabatic flows, but also because gravity currents can persist from afternoon sea breezes and rainstorms. But the very complexity of both windfields and topography makes the operation of control aircraft a hazardous one, especially at night. It is difficult to predict the location of convergent wind systems likely to be present in given mountains on a given day or night: partly because the surface observational network is almost always inadequate, except for the larger systems; and partly because fine-mesh numerical models of wind fields have not yet been widely applied to mountainous areas, especially in low latitudes. However, simple diagnostic models, such as that of Mass & Dempsey (1985*b*) can usefully simulate wind fields in mountainous regions.

Even if a convergent wind system is located we do not know the chances of finding insects in numbers and densities worthwhile to control. Locusts already concentrated into swarms are known to become trapped, for hours or even days, in persistent and slow-moving convergence zones (often topographically linked) which therefore provide suitable sites for monitoring by aircraft. By contrast, short-lived zones (such as gust fronts) and mobile zones (such as cold fronts and the ITF) are much less suitable.

If insects do, in fact, settle on the ground from line concentrations before being dispersed again, and subsequent flight leads to an encounter with another concentrating motion pattern, then a high volume density may result. There is no direct evidence for such mass settling, but storm outflows seem to be a cause of concentration of African armyworm moths that lead to mass egg laying and hence outbreaks of caterpillars, which are known to be associated with night-time rainstorms (Tucker & Pedgley 1983; Pedgley *et al.* 1989). A similar occurrence with the fall armyworm in Canada has been noted (Rose *et al.* 1975), and the distribution of bollworm eggs in the Sudan Gezira may be similarly influenced by the concentration of parent moths (Haggis 1981). Meterological satellites have been used to help locate spreading downdraughts from storms and therefore have potential to help locate any associated armyworm outbreaks.

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Discussion

R. S. Scorer (*Imperial College, London, U.K.*). Meteorologists have been aware of the importance of wind patterns in the transport of any airborne migrating species, mainly through the work of R. C. Rainey and K. Williamson, as I have already described (Scorer 1958, 1978).

The essential mechanism for the concentration of numbers of insects is that horizontal

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convergence at the surface should support upward motion above, in which the insects resist being carried upwards. It is like the creation of rain in a shower cloud or front, where the amount of rain exceeds the total amount of water in the cloud by a large multiple because it is extracted from a much larger volume of air which flows in at the bottom and out at the top, having dropped rain in the process.

The horizontal convergence maintains the coherence of very large locust swarms, which are far bigger than could be held together by a flight behaviour in which random direction becomes inwards at the edges. Another most effective mechanism is that of shovelling up by a cold front, or any similar phenomenon such as a sea breeze front or cold outflow front from a storm. In this, again, the resistance to being carried upwards causes the collection on the 'shovel' as seen by Harper (1960) when (simultaneously by telescope and radar) he observed swifts soaring on the updraft of fronts and supposed that they were feeding on the insects lifted by the updraft.

The question of how resistance to being carried upwards is effected has several interesting aspects. If the air which is being cooled adiabatically in the updraft falls below what is presumed to be the threshold temperature for flight, the insects would automatically cease to fly actively. This raises problems in the context of layering of insect swarms (or 'clouds') at night. This phenomenon was discovered by Johnson (1957) and Taylor (1958) in the case of aphids already carried aloft by dusk. Their density was measured by traps carried aloft by the Meteorological Research Flight, and was found that after being spread through the full depths of the convection layer on a summer afternoon they often tended to accumulate in the warmer air as a layer just above the inversion produced by the cooling of the ground as the sun sets.

The effects connected with gravity waves comprise a very complex field for investigation. Thus, when potato beetles *Leptinotarsa decemlineata* (Say) were found in Czechoslovakia in the late 1940s, it was alleged that they had been put into the fields by enemy agents because they were found in three or four equally spaced rows. Förchtgott (1950) explained that this could have been because they were in lines where the wind was very light as a result of the occurrence of lee waves, the lines being parallel to the hill ridge which produced the waves. This is scarcely a case of clouds or swarms of insects being formed, and appears to depend on landing conditions preferred by a species that was being studiously hunted all over Europe at the time.

In my view, convergence may be quite alarming even over the sea. Convergence at a front of some sort seems quite capable of forming a locust swarm and the general convergence can be quite enough to prevent the dispersion of a swarm for many days even after the frontal character of the motion has ceased.

Smoke, unlike rain or locusts, is not concentrated in the same way because it has a fall speed much smaller than the updraft speed of the air; and the dispersion of smoke therefore is not a good guide to what would happen to a cloud of locusts, even in random flight. Pollution dispersion models are unreal in that they do not represent the motion of the air, and the models are quite artificial in containing diffusion coefficients designed to produce the observed results from a computation.

Because I see no significant aggregation being produced in the variety of gravity wave motion patterns, I would equally not expect to find them in waves reflected from mountains. Such reflections can occasionally be seen by satellite (Scorer 1986).

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D. E. Pedgley. Professor Scorer draws attention to two aspects of our ignorance: the behaviour of flying insects encountering a change in air temperature, and the potential for gravity waves to concentrate flying insects. His comments on the former point to the possibility that insects respond to falling air temperature by taking avoiding action rather than simply ceasing flapping flight below a threshold. Such avoiding action might be examined in a wind tunnel. As to the latter, it would be helpful first of all if field observations could establish, beyond reasonable doubt, that radar band echoes are in fact associated with gravity waves as well as gravity currents.

Professor Scorer also asserts that horizontal convergence maintains the cohesion of large locust swarms. I wonder what kinds of wind patterns he has in mind and the order of magnitude of the convergence needed. Micro-scale patterns (smaller than a few tens of kilometres) are too short-lived compared with flying time and, as a form of turbulence, would surely be dispersive. Mesoscale patterns seem to be too rare on the vast plains over which much of the long-distance migration take place for them to play any significant role. Macro-scale patterns (larger than a few hundreds of kilometres), although ubiquitous, have weak convergence. And is there any evidence that coherence is lessened when a swarm encounters divergence?

Concerning the formation of a swarm over the sea through wind convergence, alternative mechanisms need to be considered. For example, it is generally accepted that new-generation locusts form into swarms, some days after they have left widespread fledging areas and up to several hundred kilometres away, because of their behaviour.

J. F. W. Purdom (*Regional and Mesoscale Meteorology Branch, NOAA/NESDIS*). My comment assumes, as correct, Mr Pedgley's thesis that airborne migrant pests are concentrated within atmospheric convergence zones.

In his opening statement, Mr Pedgley points out that 'to make air-to-air spraying effective, then the possibility arises of improving control by seeking out such patterns.' Among other items, such seeking out would depend strongly on an accurate day-to-day weather forecast followed by an accurate 'nowcast' for the phenomena in question (the location of low-level convergence lines). Satellite and radar imagery are two of the most important tools available (Purdom 1982; Bader & Waters 1987).

Many of the convergence phenomena noted by Mr Pedgley have been routinely observed by satellite for many years, for example, thunderstorm outflow boundaries that appear as arc cloud lines (Purdom 1973, 1976, 1982). These boundaries have been observed to be a major controlling factor in afternoon thunderstorm development over southeast U.S.A. Convection associated with sea breezes and the ITCZ have been located by using satellite imagery since near the beginning of meteorological satellite era in 1961. Indeed, a project during the 1960s routinely used satellite APT imagery in the Desert Locust Control Organization for Eastern Africa in Asmara, Ethiopia. We are now well beyond those early days with once a day APT views of the cloud field. The ability to use frequent interval visible and infrared geostationary satellite imagery to monitor the location of such boundaries allows for their nowcasting, and by using the concept of 'convective scale interaction' makes it possible to nowcast favoured areas for deep convective development along such convergence lines (Purdom 1987). Satellite rainfall estimation techniques permit the location of regions along such convergence lines that should be experiencing heavier precipitation. That knowledge would help to identify regions where insects might land because of rainfall.

Some of the mechanisms that give rise to convergence zones are quite shallow, with a depth of 1–2 km. This is in agreement with aircraft flights through thunderstorm outflow boundary (arc cloud line) as observed by using satellite imagery (Sinclair & Purdom 1983). Those convergence zones were narrow, being some 5–10 km in width. It is well known that convergence in depth contributes to the vertical motion found along such convergence boundaries. However, when the air into which the convergence zone is advancing is stable, there is resistance to vertical forcing and that may contribute to such convergence lines.

As Mr Pedgley said, it is difficult to predict the location of convergent wind systems likely to be present in given mountains on a given day or night, because of inadequate surface observations and the lack of fine-mesh numerical models being applied to the problem. However, by averaging geostationary satellite imagery for the same time of day, each day over a particular season, and stratifying further by flow regime, it is possible to identify regions of preferred low-level convergence (in moist areas) by the higher frequency of convective cloudiness in a particular region. Such studies, undertaken over the mountainous region of western U.S.A., clearly show the influence of the mountains on afternoon convective development (Klitch *et al.* 1985). If such studies were undertaken by using Meteosat imagery, valuable information might be found that would be applicable for both planning and forecasting over the region observed by that satellite. When such satellite image climatologies are prepared for each hour of the day (by synoptic pattern), they may then be sequentially viewed by using an image animation device and compared with actual weather developing over the region at the same time. Although mesoscale models have not been widely applied to mountainous areas, mesoscale modelling of topographically induced thermally and mechanically driven circulations is well within the realm of today's technology. Tripoli & Cotton (1989) used a numerical model to study the development of convective systems over the mountains and their subsequent evolution and movement into the plains at night.

As Mr Pedgley points out, away from coasts and mountains, the distribution of convergent wind systems (such as downdraught fronts and bores) is likely to be so erratic in space and time that they would provide little guidance in locating insect concentrations for air-to-air control. While in some cases this might be true, it must be realized that small-scale features such as lakes, rivers, early cloud cover, and wet versus dry soil are known to give rise to local convergence zones that may trigger thunderstorm formation that in turn may lead to downdraughts that produce new convergence zones. In the mesoscale modelling work of Segal *et al.* (1986), the strength of the convergence zones that developed because of early morning cloudy and adjacent clear regions was found to be nearly as strong as those found along sea breeze fronts. By using knowledge of local effects on thunderstorm development, and the concept of convective scale interaction previously mentioned, nowcasting was done that allowed the aircraft investigations of arc cloud lines of Sinclair & Purdom (1983) to be successfully undertaken. I believe the same might be true for vectoring of flights for air-to-air control; however, having the proper real-time display and analysis equipment for this would be vital.

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J. E. Simpson (*Department of Applied Mathematics & Theoretical Physics, University of Cambridge, U.K.*). I would like to underline the probable importance of the effect of atmospheric bores on airborne insect behaviour. Ten years ago such bores seemed to be rare phenomena such as the Morning Glory in north Australia. Since then they have been thoroughly investigated in the laboratory and when looked for they appear to be of common occurrence. All that is needed for their formation is a reaction between a gravity current and a stable layer in the atmosphere. Such layers are almost universal during the night and the gravity current pushes through them, generating a bore disturbance which separates and travels ahead of it. One difference between a bore and a gravity current which is easily detected is the absence of any marked temperature change near the ground; another is the presence of waves, not usually found in gravity currents. Bores are of two types. In a strong bore with an increased height three or four times the undisturbed level, the flow is very similar to that in a gravity current. However in one in which the original depth is less than doubled the bore will take the form of a regular series of waves. This is the form likely to be identifiable in radar observations of insects airborne in bores.

P. G. Wickham (*Meteorological Office, Bracknell, U.K.*). There are many scales of atmospheric phenomena. Many that Mr Pedgley has mentioned, though significant physically, are difficult to observe in practice. Indeed the monitoring of any non-cloudy event presents great difficulties. The most useful scale, both in respect of its physical importance and its operational identification, is the mesoscale (5–50 km). Cloudy systems on this scale can be continuously monitored over the whole of Africa by meteorological satellites.

D. E. Pedgley. It is well known that satellites and radar are powerful tools for monitoring clouds and rain, particularly for research on the mesoscale structure and behaviour of weather systems. For day-to-day operations, however, their use is still restricted in many developing countries with arid or semi-arid climates by the limited availability of imagery and by the infrequency of clouds (let alone rain) at many of the convergence zones known or suspected to concentrate flying insects. Nevertheless, a promising start has already been made using half-hourly geostationary satellite imagery at night over eastern Africa to locate rainstorms that may be associated with the concentration of armyworm moths leading to caterpillar outbreaks. Such imagery has recently become available in real time through the introduction of PC-based image capture and processing facilities. Climatologies of such images may well point to preferred sites for outbreaks, but we have yet to learn how to distinguish clouds associated with moth concentration from other clouds. Numerical models, for example, of topographically modified wind fields, would be particularly valuable if simple enough also to be run in the field on PCs, using current synoptic data as input.

R. B. B. Dickison (*Department of Forest Resources, University of New Brunswick, Canada*). I support Mr Pedgley's judgement that many of the convergence lines leading to concentration of airborne insects would not be accompanied by cloud, and would therefore not be detected on satellite imagery. Marine flows for example are so shallow that the induced vertical motion is usually not sufficient to reach the lifting condensation level of the atmosphere above the layer.

R. M. Morris (*Meteorological Office, Bracknell, U.K.*). The only practical way of exploiting operational Numerical Weather Prediction techniques to monitor and forecast the movement and behaviour of flying insects is to use a moveable nested grid mesoscale model, which could simulate the essential topographical and atmospheric details. Such a model is capable of depicting fine shear lines and localized convection. Forecast vertical profiles of wind, temperature and humidity could be exploited given knowledge of the behaviour of the insects under specific weather conditions.

V. A. Drake (*Division of Entomology, CSIRO, Canberra, Australia*). It seems to me that ecological and meteorological constraints, together with more general public-health and environmental considerations, may severely limit the use of spraying insecticides into convergence zones as a method of managing populations of insect pests. For most crop/pest systems, targeting of the often relatively few pests that are in a position to cause immediate crop loss seems likely to be more economical, less ecologically damaging, and less likely to induce resistance to the insecticides used than attempting a broad-scale and indiscriminate control of the entire pest population. Increasing concern about spray drift onto populated areas, non-target food crops, and biodiversity conservation reserves will also limit opportunities for emitting insecticide into convergence updrafts, even though total deposition may be reduced when the latter technique is used (Schaefer 1980). Convergence-zone spraying is therefore most likely to be useful over extensive, relatively uniform, low-value agro-ecosystems where human habitation is sparse, biodiversity is relatively low, and heavy conventional applications of insecticide are currently

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required. Obvious candidate targets include spruce budworm and gypsy moth in North American forests and grasshoppers, locusts, and armyworms in African grasslands.

The practical difficulties of locating and spraying insect concentrations in convergence zones appear considerable, mainly because suitable features occur irregularly, and often also infrequently. In New Brunswick, for example, concentrations of spruce budworm moths in sea-breeze convergence lines, which in many respects appear almost ideal as targets for air-to-air spraying, penetrate far inland only once or twice each moth-flight season (Neumann & Mukammal 1981). If control were attempted only on these occasions, not only would aircraft and personnel be standing idle for long periods, but the few sprays carried out might be insufficient to reduce infestation levels below the economic threshold; moreover, it is possible that in some years no opportunities for convergence-zone spraying would arise. On the other hand, if such sprays are made only as a supplement to some more general insecticidal control scheme, the additional economic benefit obtained from them may be quite small, and the necessary investment in the equipment and patrol flights necessary to locate convergence difficult to justify. Such considerations may have led Schaefer (1980) to emphasize routine air-to-air spraying of insects flying in stable airflows rather than opportunistic spraying into convergence zones.

I see little prospect of convergence-zone spraying finding application in Australia. In coastal eastern and southwestern Australia there are extensive forests, large areas of which are exploited for timber and pulp production, and sea breezes, which frequently penetrate far inland, sometimes accumulate large numbers of insects at their leading edge (Drake 1982). Insects cause few problems in these forests, however, except in the far southwest where the jarrah leafminer (*Perthida glyphopa* Common) perhaps deserves investigation to determine whether adult dispersal flights (Mazanec 1989) ever result in concentrations forming at sea-breeze fronts. In the main agricultural zone further inland, pest problems occur mainly in high-value crops that occupy only a very small proportion of the whole area, and timely conventional spraying of individually monitored field and orchard populations appears more appropriate than any attempt at broad-scale control. Migrating insects frequently become concentrated at convergence zones in this region (Schaefer 1976), but the convergence zones, which arise in mesoscale disturbances of a variety of types, occur irregularly, and many of the resulting concentrations are too weak, too localized, too short-lived, or located too close to storm activity to be practicable spray targets (see my comments on the paper by Riley & Reynolds, this symposium). In addition, ground-survey, phenological, and aerial-sampling observations, indicate that concentrations do not necessarily consist predominantly of economically important pests. In the pasturelands even further inland, where broad-scale population suppression of Australian plague locusts (*Chortoicetes terminifera* (Walker)) is regularly undertaken by spraying of hopper bands and swarms (Symmons 1984), the infrequency and unpredictability of suitable target concentrations would probably make convergence-zone spraying impracticable. Air-to-air spraying in stable airflows might have some application in this region as it could be undertaken as a supplement to daytime swarm control, with the same aircraft flying additional night-time sorties on occasions when conditions were suitable for long-distance migration following a mass take-off flight at dusk (Hunter 1981).

An additional problem with any form of broadscale air-to-air control is that the level of population suppression achieved, and thus the economic or social benefit derived, will be more than usually difficult to establish.

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D. E. Pedgley. Dr Drake draws attention to a variety of constraints in the strategy for the management of windborne insect pests based on air-to-air application of insecticide in atmospheric convergence zones. These constraints are real; nevertheless, there may be regions and seasons where the strategy is workable with species such as those mentioned by Dr Drake.

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