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2 authors:

V. A. Drake
UNSW Canberra

Roger Farrow
None

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THE INFLUENCE OF ATMOSPHERIC STRUCTURE AND MOTIONS ON INSECT MIGRATION

V. A. Drake and R. A. Farrow

Division of Entomology, CSIRO, G.P.O. Box 1700, Canberra, A.C.T. 2601, Australia

INTRODUCTION

The importance of weather as an influence on insect migration has long been appreciated (47). The relation of migration to meteorological factors has been the subject of three reviews in recent years (94, 103, 147) and was also considered in detail in a more general treatise on insect migration (76). The long-distance transport of migrants by large-scale wind systems has received particular attention, because such movements frequently initiate outbreaks of agricultural pests or insect-borne plant and animal diseases (94). However, insect migration can be affected by a wide variety of meteorological phenomena, and in recent years much new information has appeared on how migrants interact with small-scale weather features and with the vertical structure of the atmosphere. Our aim in this review is to identify the various features of the atmospheric environment that affect insect migration, and to indicate how migrating insects respond to these features and how their migratory flights are influenced by them.

An analysis along these lines was first made by Wellington (146), although, writing over 40 years ago, he had few relevant entomological observations to draw on. Rainey (104) described some additional atmospheric features that affect migrating insects in a 1976 paper, which was based mainly on his own pioneering research on migration meteorology (e.g. 101a, 102). Our coverage is more comprehensive than Rainey's, although we treat individual atmospheric features and their associated entomological phenomena in much less detail. For each of the atmospheric features that have been shown to affect insects during migratory flights, we first provide a brief description

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of the meteorological phenomena and then summarize the entomological observations. The behavioral and ecological implications of the observations are considered together at the end of the review, where some suggestions for future investigations are also presented.

Research on migration meteorology has been greatly stimulated in recent years by the growing use of radar for observing insect flight. Some radar systems designed for meteorological research (e.g. 108, 133), and especially several developed specifically for entomological applications (e.g. 120, 121), have proved extremely effective for showing how insect migratory behavior is related to atmospheric processes. Radar observations of migration in small-scale atmospheric features can be extremely graphic, as the feature often appears in its entirety on the radar screen (e.g. 33, 35, 97, 120). Radar has also provided new and more detailed information on some aspects of migration in large-scale weather systems (28, 39, 40, 154).

In addition to the radar work, more conventional case studies of weather factors affecting long-distance migration have continued to appear since Pedgley's 1982 review (94) (e.g. 30, 31, 45, 67, 69, 88, 92, 95, 96, 129, 130, 132, 137, 141, 148, 153). It is now possible to identify some common features of these migrations and to place them in an ecological context by relating them to seasonal and random variations of habitat availability. Here it is not possible to treat this aspect of the subject as comprehensively or critically as the considerable literature would allow, although we attempt to cite most of the more recent work and a few key studies from earlier periods.

The atmospheric features that most affect migration are *stratification,* i.e. the formation of a layered structure, waves, and circulatory motions. These features are interrelated, and they can all be influenced by, and may even arise from, features of the surface topography. The features range in size from *microscale* (horizontal dimensions of the order of 1 km) through *mesoscale* (order of 100 km) and *synoptic scale* (order of 1000 km) to *planetary scale,* i.e. the dimensions of the general circulation of the earth's atmosphere (see e.g. 48). In the vertical dimension, insect migratory flight is almost completely confined to the lowest 2 km of the atmosphere, a zone that corresponds approximately with the *planetary boundary layer* (PBL). We first describe the PBL and the role of its structure in insect migration. We then consider, in order of increasing size, the various atmospheric motions that migrants encounter.

THE PLANETARY BOUNDARY LAYER

Structure

The phenomena generally referred to as "weather" are almost completely confined to the bottom 10–15 km of the earth's atmosphere, a zone known as the *troposphere*. The PBL (20, 86), which occupies the lowest 1–2 km of the troposphere, is defined as the zone in which the earth's surface has a direct effect on the atmosphere. The PBL exists in two forms: In the *convective* form, the PBL is vertically mixed throughout by thermally driven circulatory air motions, while in the *stable* form it is highly stratified. Migrating insects are strongly influenced by the structure and internal motions of the PBL in both of its forms. Thermal convection is described, along with other internal motions of the PBL, in the following section.

In both the stable and the convective PBL, the wind speed in the *surface layer* (20, 86, 93), i.e. the lowest few tens of meters, increases approximately logarithmically with height. Above this layer the wind continues to increase with altitude, but in the extratropical regions it also shows a gradual change in direction, clockwise in the northern hemisphere and counterclockwise south of the equator. This phenomenon, known as the *Ekman spiral,* is due to the variation with height of the balance between the deflecting force of the earth's rotation (the *Coriolis force*) and the forces arising from friction and the gradient of atmospheric pressure (8). Near the top of the PBL the direct effect of friction is negligible and the wind is usually approximately *geostrophic,* i.e. it has the speed and direction expected from the local gradient of atmospheric pressure. Except in the tropics, the Coriolis force causes the geostrophic wind to blow almost at right angles to the pressure gradient, i.e. along the *isobars,* the lines of equal atmospheric pressure.

The wind near the bottom of the surface layer, i.e. within a few meters of the surface, is light. There is therefore a zone, known to entomologists as the *flight boundary layer* (134), in which the airspeed of a flying insect is greater than the wind speed, so that the insect is capable of moving in any direction and of carrying out the "trivial" (128) movements required for feeding, reproduction, and finding shelter. Insects migrating on fixed compass bearings or along particular terrain features, by day or night, are restricted to this zone when the wind direction is unfavorable, although these migrants, mostly butterflies (Lepidoptera), will fly at higher altitudes when the wind is behind them (6, 55, 56, 88, 90, 118, 151). Upwind migration is occasionally possible at high altitudes when winds are light (110).

Migrations above the surface layer are generally close to downwind, because the insects' airspeeds are usually much less than the wind speed. In middle latitudes, the speed and direction of these migrations change gradually with height up to altitudes of about 500 m. The variation follows that of the wind and is in the direction expected for the Ekman spiral phenomenon (34, 39, 40).

STABLE PBL The stable form of the PBL (20, 86) occurs when the earth's surface is cooler than the air above it. This happens when a warm wind blows over a cool sea, and also over land areas on clear nights, when the ground rapidly loses heat by radiation. Air in contact with the surface is cooled and becomes denser than the air above, i.e. the surface layer becomes stable. The surface air is also slowed by friction, so that the wind changes with height; this phenomenon is known as *wind shear*. This shear causes *turbulence* (gustiness), i.e. a random component to the wind, which produces some mixing, but only over a short vertical distance because the stability of the surface layer tends to suppress vertical motion. These processes, at least over flat terrain, typically produce a zone extending 100–300 m above the surface in which temperature increases rapidly with height (a *temperature inversion*). The usual Ekman spiral increase of wind speed and variation of wind direction with height are confined to this zone. The term "stable PBL" refers only to this zone, but insects fly much higher into a deeper upper zone, whose structure depends on its state before the onset of stability. Over land areas, where the upper zone will usually have formed part of the convective PBL during the daytime, the temperature above the inversion typically decreases with height at a rate of about 1°C per 100 m (the *dry adiabatic lapse rate*) and the wind is approximately geostrophic. It is convenient to describe migration in both zones under the present heading.

Over land areas the PBL usually becomes stable around sunset. A shallow temperature inversion forms near the surface at first and gradually becomes deeper. Insect migratory flight is rarely observed at sunset (154), but numerous species commence their migrations soon afterward in a dusk takeoff flight (e.g. 34, 64, 111, 114, 115, 120). These nighttime migrations in the stable PBL are undertaken not only by nocturnal insects such as moths, but also by grasshoppers and locusts and by planthoppers, which are also active during the daytime. In addition, many microinsects (e.g. aphids) and ballooning spiderlings that probably start migrating well before dusk continue their flights into the night (11, 44, 46). The duration of these nighttime migrations is variable: Sometimes most migrants fly for less than 1 hr (38, 115), but many flights continue for several hours, and occasionally a migration is still underway at dawn (e.g. 34, 37, 64).

Nocturnal flights at the bottom of the surface layer, i.e. within and immediately above the vegetation canopy, appear to be mainly trivial. At heights of 5–10 m, however, a variety of insects (15), especially moths (76a, 80, 87, 130a; V. A. Drake & R. A. Farrow, unpublished information), fly in the persistent and rectilinear manner characteristic of migratory movements (76). These migrants fly downwind, and in some instances they increase their flight altitude during the early evening (130a), probably in association with a deepening of the temperature inversion layer (80, 87).

Observations at higher altitudes, made mainly with radar, suggest that the horizontal distribution of migrants is usually approximately uniform after the takeoff period (34, 120). In the vertical direction, however, the migrants are frequently found concentrated into layers. Layering has been observed during nighttime (33, 34, 38, 64, 87, 106–108, 111, 120, 130a, 142, 154) and early-morning (46, 62, 74a) migrations over land, and during day and night migrations in warm winds over the sea (36, 40). The insects undertaking these migrations are mainly grasshoppers (38, 107, 111), moths (34, 40, 64, 87, 130a), and, perhaps less commonly, microinsects (46, 74a). The migrations are at least approximately downwind (34, 36, 40, 87, 130a).

The formation of concentrated layers of insects indicates that migrants are affected by the highly stratified nature of the stable PBL. An insect layer is sometimes located near the top of the surface inversion, where simultaneous measurements of the temperature profile have established that the air is 5–10°C warmer than at the surface (34, 87, 111, 120). Such layers are typically 50–200 m thick and have their lower boundary 100–200 m above the surface. There is sometimes a sharply discontinuous change in insect density at the lower boundary, where the density is close to its maximum value, but only a gradual decrease in numbers with altitude at higher levels (34).

Not all layer concentrations are associated with the surface inversion. Several layers may be present simultaneously (19, 40, 46, 64, 74a, 106–108, 111, 154); as many as five have been reported (120, 142). The topmost layers may be at altitudes as high as 1–2 km, and occasionally a single layer is found at comparable heights (39, 106). These high-level layers, which are usually about 50 m thick, indicate that there is often stratification in the zone above the stable PBL, i.e. in the upper zone where temperature generally decreases with height, and that insects respond to this stratification. Some of these insect layers may be associated with temperature inversions (19, 108, 154), but others appear to be located near zones of wind shear (62, 120). The source of the air may also be important. For example, more migrants are found at higher altitudes in air that has passed over a likely source of insects than in an undercutting airflow that originated in a different region (120) or even at sea (5). It is also possible that some layers mark the flight ceilings of particular species, i.e. the height at which temperature has fallen to the species' flight threshold (39, 111).

LOW-LEVEL JET The wind profile of the stable PBL frequently exhibits a wind speed maximum at an altitude of a few hundred meters (53, 83). This effect, which is generally known as the *low-level jet* (LLJ), has a number of forms (127) and can arise from a number of causes, some of which may act in combination. LLJs caused by the deflection of large-scale airflows by mountain ranges (e.g. 149) or by the temperature differences of land and sea along coastlines (e.g. 29, 72) and LLJs associated with cold fronts (e.g. 17, 52, 85) tend to persist through day and night and have a long, thin form for which the term "jet" is appropriate. LLJs occurring in the absence of these features are found only at night over inland areas that are flat (126) or at least have no major topographical features (139). They are caused by two mechanisms, one involving the Coriolis force (12) and the other involving large-scale terrain slope (71). Both mechanisms are driven by the diurnal variation of surface heating and cooling and the resulting diurnal changes in the PBL. This second type of LLJ is broad horizontally and might better be termed a *boundary layer wind maximum* (12). The wind is typically strongest just below the surface inversion, at an altitude of 200–400 m, and the jet may be *supergeostrophic*, i.e. the wind speed may be greater than that expected from the local pressure gradient.

Observations of insects migrating when an LLJ is present show that a layer concentration may form near (154) or just above (37, 120) the level of the maximum wind. As the surface temperature inversion is expected to extend just above the wind maximum, the latter observations suggest that layering in an LLJ indicates a response to temperature rather than to wind speed. The important role of long, thin LLJs in the long-distance transport of migrants is described below in the section on synoptic-scale weather features.

Internal Motions

In addition to the general horizontal airflow, which forms part of the system of large-scale air movements in the troposphere, and LLJs, a variety of smaller-scale air motions can occur within the PBL. A common feature of these internal motions is that the air in them moves vertically as well as horizontally. Before describing the various types of motion, we introduce two general classes of airflow that occur in the atmosphere in a number of forms.

Many but not all atmospheric motions are *circulations,* i.e. patterns of airflow in which air masses displace each other in a cyclic manner. These motions are usually driven thermally; more buoyant warm air displaces cool, denser air in one part of the circulation while the opposite process takes place elsewhere. An important feature of circulations is that they can exhibit *convergence* (27a). In particular, a localized region of rising air will suck in air at its base, producing a convergent airflow near the surface; this will be matched by a divergent flow at higher altitudes. This form of convergence is potentially of great importance for windborne migrants because insects that avoid being carried upward may never reach the region of divergence and will therefore collect in the lower part of the region of ascending air. Insects may actively avoid ascent, or, if they are carried up to altitudes where the temperature is below their flight threshold, their failure to ascend may be simply passive. Migrating insects are therefore likely to become concentrated in zones of convergence that persist for any length of time (101a, 104).

A type of air motion that occurs in the PBL in a number of forms is the *density current* (or *gravity current*). This is a horizontal flow of cooler, denser air that intrudes into and displaces a neighboring, less dense air mass (124).

The current is usually located immediately above the surface and is typically a few hundred meters deep. At the leading edge of a current there is a zone of strong horizontal convergence and rising air; this frontlike interface advances at about 75% of the speed of the normal component of the undercutting flow. Immediately behind the front the undercutting airflow forms a *head,* i.e. it is deeper here than elsewhere. The convergence at the front causes a line concentration of windborne insects to form along it. Insects flying both ahead of and behind the front are carried into it, and will collect there if they avoid ascending with the air (120, 131). Insects overtaken by the front will experience a marked change in the direction of their movement.

THERMAL CONVECTION The PBL is convective when the earth's surface (land or sea) is warmer than the air above it (20, 86). Air warmed at the surface rises for 1–2 km until it encounters a *capping inversion,* a stable layer through which the rising air cannot penetrate. Cooler air is displaced by the rising air, and a nearby region of descending air completes the circulation. These relatively large-scale vertical motions mix the PBL so that the average temperature decreases with height at about the dry adiabatic lapse rate. The mixing also causes air slowed by the friction effect of the surface to be spread throughout the PBL, so average wind speeds are considerably less than would be expected from the pressure gradient. Winds near the surface are variable because of the horizontal components of the convective airflows. Convection occurs over land on clear days, when the surface is rapidly warmed by solar radiation. It can also occur when a cool wind blows over a warm sea, but insect migration has not been observed in this situation.

The daytime insect population of the atmosphere over land areas has been extensively investigated by trapping from aircraft, tethered balloons, and kites (75, 76). Insects are regularly found at altitudes of up to about 2 km. These high-altitude catches consist mostly of microinsects, and it is generally inferred that they are carried to these heights by convective upcurrents. Calculations and aerial sampling suggest that a small proportion of first-instar moth larvae that migrate on silk threads are transported distances of the order of 20 km with the aid of convective lift (50, 138). Trapping studies have shown that a greater proportion of the airborne insect population is present at higher altitudes when the lapse rate (76) or turbulence (57) indicates that convection is present. Trapping data obtained mainly during the daytime, when the PBL would often have been convective, showed that insect density averaged over a period of 1 hr or more decreases continuously with height and can be described empirically by an inverse power law (75).

Butterflies occasionally ascend in regions of convectively rising air *(thermals)* (54–56, 65) and sometimes make true soaring flights, i.e. ascend while gliding in circles (54, 56). The monarch butterfly, *Danaus plexippus,* in

North America soars only when the wind direction is favorable for its southward autumn flights (56); it may ascend to altitudes of over 1 km (55). Swarming desert locusts, *Schistocerca gregaria,* also fly in thermals and sometimes reach the top of the convective layer at heights of 1–2 km (103). Ascent and descent rates for insects in thermals, measured with radar, are of the order of 3 m s^{-1}, and an individual insect has been observed to rise 450 m in 3 min (9, 117).

Thermals may be distributed at random, but in strong winds they become aligned parallel to the wind and form *streets* (66). These indicate that the convective circulations have become organized into longitudinal roll vortices, with adjacent rolls turning in opposite directions (122). In light winds, thermals may be organized in a honeycomb pattern of polygonal cells, often inaccurately called *Bénard cells;* the borders between cells are usually regions of rising air, while the cell centers are regions of descent, but the opposite circulation has also been reported (3, 66).

Radar observations of insects migrating in convective conditions show that the migrants have a highly heterogeneous horizontal distribution. Concentration of the insects into parallel bands aligned downwind (152) and into patterns intermediate between parallel bands and polygonal cells (66, 107, 120) are frequently seen and are clearly due to the insects' location in regions of convectively rising air. Concentrations in the form of plumes apparently associated with isolated thermals also occur, although not commonly (117). The concentrations may form by convergence, and insects have been seen moving toward walls from both sides (120), but behavioral effects, e.g. cessation of flight if there is no lift, could also be important. The insects forming these concentrations have been identified as dragonflies, locusts, and butterflies (107, 120), but microinsects are probably also present.

Over land areas, a shallow convective zone is formed near the surface each morning and gradually extends upward through the pre-existing nocturnal inversion, which acts as a capping inversion (20). Thermals impinging on the stable zone from below will distort it, causing temporary "hummocks" and buoyancy waves. Layer concentrations of insects migrating in the stable zone are gradually lifted during the morning as the convection deepens; the layers are distorted by the convective motions and may finally break up (19, 35, 46, 108). High-altitude layer concentrations occasionally seen later in the day (19, 39) are presumably formed by insects that have flown up into the stable air above the zone of convection.

If convectively rising air reaches heights where the temperature is below the threshold for moisture condensation, so that a cloud forms, the upcurrent will be strengthened by warming from the release of the latent heat of condensation. This process may lead to showers and ultimately to thunderstorms that extend far above the PBL. Convective storms have strongly convergent low-level inflows, which may concentrate flying insects into the storm, where they may be washed out and deposited by heavy rainfall (28, 68).

SEA BREEZES A *sea breeze* (3, 144) is a mesoscale circulation that forms along a coast during the day. Its principal feature is an onshore wind that extends from the surface to 500–1000 m, and a return flow out to sea at higher altitudes. The breeze is driven by the temperature difference of the land and sea surfaces, and there may be a reverse circulation, the *land breeze,* during the night. Similar airflows occur near lakes and even inland, where a "pseudo sea breeze" can form at the escarpment of a plateau (144). The onshore breeze meets the prevailing wind at a zone of convergence, the *sea-breeze front,* where air rises. Development of the front, which usually moves rather slowly during the day and is typically about 20 km inland by mid afternoon, is most marked when the direction of the prevailing wind is offshore.

Afternoon sea breezes can alter the direction of movement of windborne day-flying insects. Swarms of desert locusts have been maintained in a coastal hinterland by sea breezes, even though the prevailing synoptic-scale winds were offshore (102). *Lymantria dispar* (gypsy moth) larvae dispersing on silk threads during the afternoon may be kept airborne by the lift at the sea-breeze front and may be concentrated by the frontal convergence; infestation levels of this species are sometimes found to be highest about 10 km inland from the coast (84).

Sea breezes sometimes penetrate far inland during the late afternoon and evening. They then take on the character of density currents, forming a well-defined front with a head. Their rate of advance then increases to about 5 m s^{-1} (125). These currents may still be moving forward as late as midnight, by which time they will have advanced 50–100 km from the coast (3, 91, 125); penetrations of 400 km can occur in favorable circumstances (26). Such currents may eventually become detached from the coastal circulation, which late in the night is likely to be of the land-breeze type.

Intense line concentrations of night-flying insects sometimes form in sea breeze density currents, apparently in the region of the head (33, 64, 91). An insect concentration at least 40 km long has been observed moving 25 km inland in 1 hr, and the migration toward the inland on the sea-breeze airflow continued after the front had passed (33). Convergence at the front is sufficient to account for the insect concentration found there (64). Moving line concentrations in the heads of flows tentatively attributed to sea-breeze currents have been observed around midnight 400 km inland in southeastern Australia (V. A. Drake, unpublished data). This type of airflow may account for the sudden late-night westward redirection of migration that occasionally occurs in this region (34, 38).

STORM OUTFLOWS The strong vertical motions within a convective storm include downdrafts of cool air. When these reach the surface they are deflected horizontally and spread outward as a density current. These *outflows* (58), which are usually strongest on the forward side of a moving storm, advance at speeds of the order of 10 m s^{-1}. Migrating insects are rapidly collected into a line concentration by the convergent wind fields at an outflow's leading edge (97, 120). The concentrations coincide in position with the head of the flow and have a sharply defined forward boundary. The insect density in the concentration may be 1–2 orders of magnitude greater than in surrounding areas. Outflow line concentrations have been followed for distances of over 20 km.

WAVES An atmospheric wave is a coherent pattern of air motions in which temporary displacements are followed by the return of the air to its original position in the general flow. The movements are often repetitive, and the pattern will usually *propagate* (change its position). The waves that affect migrating insects are *buoyancy waves* (or "gravity waves"), i.e. waves in which the effect of gravity on air masses of differing densities provides the restoring force required for wave motion. These waves occur in a stable atmosphere; the air displacements are in the vertical direction, and the waves propagate horizontally. True wave motions are not circulatory and do not exhibit convergence.

Small-scale waves that are an atmospheric analog of waves on the surface of a deep sea can occur at density interfaces. These waves propagate along density stratification features in the stable PBL. They are *evanescent,* i.e. their amplitude falls off rapidly above and below the level where the density changes. They are frequently generated by wind shear, and are then known as *Kelvin-Helmholtz waves* (60). Migrating insects have occasionally been observed flying close to waves of this type propagating along stratification features a few hundred meters above the surface (59). The insects [individuals (4) or layer concentrations (120)] move up and down with the wave.

Waves that propagate in a layer of stable air and have a wavelength much greater than the layer depth are known as *long waves;* they are akin to waves in shallow rather than deep water. Waves of this type propagating in the surface inversion layer sometimes have very large amplitudes (e.g. 61) and are now usually identified as *solitary waves* (21, 22, 32). They usually have the form of *waves of single elevation,* i.e. as the wave passes, the stable layer first increases in height and then returns to its original height. When these waves are of large amplitude they contain a closed horizontal vortex circulation. Solitary waves often occur in trains; the first wave has the largest amplitude and travels fastest (at speeds around 10 m s^{-1}), and each successive wave is somewhat smaller and slower than its predecessor. The speed differences cause the waves to become separated, so that the train evolves into a series of independent individual disturbances that maintain their shapes for long periods. The direction of propagation may be completely different from the direction of the general airflow, which is not usually permanently altered by the passage of the waves. Boundary-layer solitary waves probably originate when density currents flow into a surface-based layer of stable air, and are often located at the leading edge of a *bore,* i.e. a propagating sudden increase in the depth of this layer (23, 27).

Insects have been detected migrating in or near large-amplitude long waves propagating in both the nocturnal (35, 62) and the marine (36) boundary layer. Insects migrating in layer concentrations are repeatedly lifted and then returned to their original altitude by passing trains of solitary waves of elevation (35). Insects can also become concentrated in the leading, large-amplitude waves of a train (36, 62), where they are presumably entrained in a vortex circulation. Other observations of propagating parallel line concentrations of insects (35, 114) can probably also be accounted for by this effect. The general direction of migration is not permanently changed by the passage of the waves, and the original direction may even be restored between individual waves of a train (35, 36). This lack of a change in direction distinguishes line concentrations in solitary waves from those that form at a density-current front. Multiple line concentrations associated with wind shifts (120) probably occur when a density current has only partially evolved into a train of solitary waves.

TERRAIN-INDUCED MOTIONS A number of types of air motion can arise if the surface terrain is not flat. The simplest is that caused by the deflecting action of a hill or similar obstacle on an existing airflow (144). The air on the upwind side of such an obstacle is forced to ascend; migrating butterflies have been observed to use this updraft to gain height by soaring (56). Downwind from the obstacle a train of stationary (i.e. nonpropagating) buoyancy waves *(lee waves)* may form (3, 60, 122). When these waves are of large amplitude they may contain a stationary closed horizontal vortex circulation (a *rotor*). Heavy infestation by Colorado potato beetles, *Leptinotarsa decemlineata,* has been associated with deposition of insects in the calm-air portions of a train of lee waves (49). The unsteady small-scale wind systems, containing rotors, that were observed to affect moths flying below and downwind of an escarpment (97) were probably due at least in part to lee-wave motions.

Sloping terrain can also induce circulatory air motions. These motions are driven thermally, by changes in the density of the air near the ground due to heating of the surface by day and to cooling by night (3, 144). Near the surface there is a downslope drainage flow of cool air (a *katabatic wind*) at night and an upslope flow of warm air (an *anabatic wind*) during the day. In mountainous regions these slope flows combine in valleys to produce winds that blow up a valley by day and down it by night. Well above the surface the circulations are completed by winds blowing across and along the valleys in the opposite directions. These winds, especially the reverse flows at higher altitudes, are reinforced or opposed by the large-scale airflow over the region and by the deflections and wave motions that arise in that airflow because of the uneven terrain. The resulting wind system may be very complex.

Moths that persistently fly into a light wind have been observed to move upslope in katabatic flows at night (7, 63). These movements do not appear to be trivial, since the moths vacate their habitat of origin, and since they may initiate long-distance downwind migration when they reach the ridge tops (7). Transport on anabatic winds may account for the frequent appearance of grasshoppers in mountainous areas at altitudes well above their resident range (1) and the movements of desert locust swarms toward and up mountain slopes (102). Gypsy moth larvae migrating on silk threads in ridge-and-valley terrain are carried aloft by updrafts at ridge tops and are transported directly to the next ridge top by the prevailing large-scale wind (84); the updrafts probably have an anabatic component, although deflection of the general airflow may also contribute.

Katabatic winds may spill onto a plain, and they can develop on very gentle slopes when these are sufficiently extensive. In both cases, the winds may take on the form of a density current, with a frontlike convergence zone at the leading edge. Some moving line concentrations of insects probably arise in flows of this type (120). Katabatic effects may also reinforce a density current that was initially driven by some other mechanism. This may be a factor in the deep penetration of the sea-breeze currents that influence insect migration in inland Australia (see above).

SYNOPTIC-SCALE WEATHER FEATURES

Synoptic-scale motions extend above the PBL and form major disturbances of the general circulation. These disturbances take the form of large-scale waves and vortex circulations in which the air is displaced horizontally. Convergence in these systems is localized at fronts, which produce disturbed weather over regions of mesoscale size. We first consider the effects of fronts on migrating insects and then examine the large-scale airflows.

Intertropical Front

The *intertropical front* (ITF) is the boundary between the opposing trade-wind and monsoon airflows that arise in the low latitudes of each hemisphere (8, 41, 119). It is aligned approximately east–west around the tropics, with some deviations where particular wind systems are strengthened by topographical features. It moves northward and southward with the seasons, and there are also medium-scale movements lasting a few days and a smaller diurnal oscillation. The ITF slopes back over the moister monsoon air mass for a distance of 100–200 km; the region of overlapping flows is known as the *intertropical convergence zone* (ITCZ). The front itself is usually marked only by a change in the direction of the surface wind, which is typically light, but large convective storms often form 10–100 km away on the equatorial (monsoon air) side.

Line concentrations of night-flying insects have been observed at the ITF (120). Both the low-altitude convergence and the resulting insect concentration observed when the monsoon air mass was advancing appear similar to those found at the leading edge of a density current. Day-flying locust swarms accumulate at the front when it is nearly stationary, converging on it each day from their overnight roosting sites and coalescing into a single linear swarm coincident with the front; the locusts fly up in a sheet in the ascending air at the sloping interface between the monsoon and trade-wind air masses (119). Catches in traps on aircraft and towers also indicate that flying insects are more numerous in the immediate vicinity of the ITF (104).

Topographical effects in East Africa produce two semipermanent zones of wind convergence similar to but distinct from the ITF. These also have a concentrating effect on desert locust swarms and other insects (104).

Temperate-Zone Fronts

Synoptic-scale fronts (8, 16a) in the temperate zones form part of the two *polar fronts* of the northern and southern hemispheres. These *polar fronts* mark the boundaries of planetary-scale airflows originating in the subtropics and in high latitudes. They are distorted and broken up by synoptic-scale waves and vortices that carry frontal segments eastward. The fronts are termed *warm* when the following air is of subtropical origin and *cold* when it originates from higher latitudes. The ascent of air at these fronts produces a zone of rain and disturbed weather that is typically a few hundred kilometers wide. Fronts typically advance at speeds of 10–15 m s^{-1} (17, 52, 99).

In temperate latitudes conditions are generally more favorable for insect flight on the warm-air side of the polar front. The arrival of a cold front can completely change the direction of a major migration (39, 40). The front itself may be preceded by a series of squall lines, which may form a prefrontal trough of low pressure and one or more low-level jets (17, 52, 99). The jets blow along the length of the front and act as a *conveyor belt* (16a), carrying subtropical air and sometimes also migrating insects (116, 143, 150) toward higher latitudes. The prefrontal squall lines and the front itself provide the stormy weather and associated high humidity and electrical and microbarographic activity with which the initiation of migratory flight has been associated (10, 24, 68a).

Although synoptic-scale fronts are zones of strong horizontal convergence, they have not been reported to produce line concentrations of insects similar to those found at sea-breeze and density-current fronts. This may be because rain at the front washes the insects out, or simply because radar cannot detect insects in rain. Another possible explanation is that the insects may be repeatedly swept ahead of the front by outflows from frontal storms. High concentrations of insects have been detected at gust fronts ahead of a cold front (136). Observations of unusually high densities of migrant insects immediately behind cold fronts (28, 40) or in their general vicinity (28a, 104) suggest that concentration by convergence may occur, but it should be noted that observations of this type could sometimes arise from increased flight activity by local populations stimulated by disturbed weather at the front. Migratory activity that is associated with the passage of a front but that is probably related primarily to the airflows immediately ahead of or behind it is described below in the section on anticyclones and depressions.

Gust fronts and squall lines ahead of a cold front may be a source of density currents that can propagate far ahead of the front and perhaps evolve into a bore with an associated train of solitary waves, if the front stalls (21, 52, 99). This mechanism may account for the formation of a moving multiple-line concentration of grasshoppers observed a few hundred kilometers ahead of a slow-moving cold front (112).

Tropical Disturbances

The trade-wind and monsoon airflows of the tropics are relatively persistent, but large-scale propagating disturbances occur, the most notable being easterly waves and tropical cyclones (8, 109). Invasive movements of locusts in northern Australia have occurred during the development of tropical troughs (43), and moth flights from Australia to New Zealand sometimes occur on the winds of tropical cyclones (51). On a somewhat smaller scale, but perhaps of greater significance for migrating insects, are movements of the ITF and similar convergence zones that last for a few days and cover distances of the order of 100 km. Thus, incursions of westerly winds into East Africa have brought an eastward extension of armyworm moth *(Spodoptera exempta)* infestation, and probably also invasions of several other moth species (104). Similarly, mass migrations of grasshoppers in the Sudan occurred when a southerly monsoon airflow was replaced by northerly trade winds (120), and movements of a variety of insect species to an island off the east coast of tropical Australia coincided with periods when the northwesterly monsoon replaced the southeast trade winds (45). Because major disturbances occur infrequently in the tropics, winds are generally lighter than in temperate regions and typical migration distances are probably not as great. Trajectory calculations in tropical regions should be made from streamline charts (45).

Anticyclones and Depressions

In temperate regions the wind regime of the general circulation is unstable, and distortions in the form of waves along the polar front and associated vortex circulations dominate the pattern of airflows (8). *Cyclonic* vortices form in low-pressure areas *(depressions)* along the front, and counter-rotating *anticyclonic* vortices occur in high-pressure areas. In the northern hemisphere the circulation around an anticyclone turns clockwise (when viewed from above, as on a synoptic chart), and that around a depression turns counter-clockwise; the rotations are opposite south of the equator. These disturbances move, rather irregularly, toward the east. A depression and its associated fronts pass over a point typically about once each week, bringing disturbed weather, often some rain, and finally a drop in temperature. The wind direction at a point changes cyclically as the depressions and anticyclones pass by; the wind turns suddenly to originate from higher latitudes when the cold front passes, and then gradually changes back, sometimes passing through a full 360°, to originate from lower latitudes again as the next depression approaches. Toward the subtropics, anticyclonic circulations predominate and the generally fine and warm conditions are disturbed only occasionally by the strongest cold fronts. The whole belt of depressions and anticyclones moves northward and southward with the seasons.

Wind speeds in temperate-zone synoptic airflows are usually sufficiently high that migration is close to downwind, and migration trajectories can be calculated from synoptic data (94, 123). Wind speeds of 10–20 m s^{-1} are common above the stable PBL, and insects flying for several hours can be transported 100–500 km overnight (38, 39, 42, 131, 154). Smaller movements, perhaps in a variety of directions, occur in the light winds near the center of an anticyclone (39). The number of migrants and the distance moved is usually greatest in the warmer winds that originate in lower latitudes, and immigration into higher latitudes occurs principally on such winds (18, 42, 46, 67, 70, 74a, 82, 88, 95, 100, 105, 129, 153). These warmer winds are typically located, in both hemispheres, on the west side of an anticyclone and to the east of an approaching depression and cold front. Migrations in these winds may occur in the warm sector of a depression (28a, 30, 69, 79, 87), or in the conveyor-belt winds (40, 131, 150) and LLJs of the long, thin type (31, 78, 116, 143) that form ahead of a cold front. Migration can also be intense immediately behind a cold front (28a), although it usually falls to low levels after a few hours when the cold airflow from higher latitudes has become well established (39, 40); movements toward lower latitudes can occur in these conditions (39, 137). Mass immigrations (14, 28a, 68, 68a) and higher rates of capture of immigrants (51, 130, 150) on days when cold fronts pass probably occur because the winds ahead of or behind the front are suitable for carrying the migrants from their source regions. Immigrants recorded far from their origin immediately following the passage of a cold front (51, 79) are likely to have been carried for long distances by warm-sector winds before having been overtaken by the front. Migrations of exceptional length, e.g. from Australia to New Zealand (51, 140) and perhaps even across the Atlantic (74), usually occur in airflows that are close to cold fronts.

GENERAL CIRCULATION

The major wind systems of the general circulation that are used by migrating insects are the easterly *trade winds* and the *equatorial westerlies* (or *monsoons*) of the tropics, and the highly disturbed westerly airflow of temperate regions (8, 109). The tropical and temperate systems are separated by a semipermanent zone of high pressure, the *subtropical anticyclonic ridge*. The seasonal movement of these systems is associated with the annual patterns of temperature and rainfall that characterize the regional climates of the world.

Insects migrating on these wind systems tend to be displaced in particular directions. Thus, in the trade-wind belt, migrants swept out over an ocean usually originate from the landmass to the east rather than from the west (13, 101) and desert locust upsurges lasting several years tend to spread westward from an origin in the east (145). A consistent westward component to the direction of planthopper migration was recorded in the Philippines during the dry (trade-wind) season (115). Conversely, in the temperate zone, transoceanic movements are usually from west to east (51, 74, 140). Invasive movements into Japan on both temperate and monsoon wind systems have an eastward component (69, 79, 92). The convergent wind systems of the tropics carry insects toward the ITF from both north and south (103), while in temperate latitudes the greater warmth of airflows originating from lower latitudes probably results in a net movement of insects toward the poles (46); this is an example of "rectification" (77) by temperature.

Finally, we note that global-scale disturbances of both the atmospheric and oceanic circulations of the *El Niño–Southern Oscillation* (98) type may influence insect migration. These events lead to persistent changes in the weather patterns of widely separated regions (*teleconnections*). When these disturbances result in exceptional rainfall in semiarid regions, large populations of migratory insects may develop (90). This process may account for the frequency with which migrations of butterflies occur in Europe and North America in the same year (151).

BEHAVIORAL AND ECOLOGICAL IMPLICATIONS

Nocturnal Migration

The prevalence of nocturnal migration, at least among large insects, suggests that nighttime conditions may be particularly favorable for migratory flight. This may be simply because migrants avoid predation by birds at night, or because the absence of solar radiation makes it easier for the migrants to avoid thermal stress (103). Another possibility, however, is that the steady airflows found when the atmosphere is stable provide the best conditions for some types of migration. This is suggested particularly by the formation of insect layer concentrations immediately above the surface temperature inversion, where the combination of relatively warm air and geostrophic (and sometimes supergeostrophic) winds is probably optimal for long-distance migration downwind (34). The formation of layer concentrations at higher altitudes, and especially in zones of wind shear, suggests that a different combination of conditions, not yet identified, may be optimal for some migrants.

The wind speed above the surface inversion is often considerably greater than the migrants' airspeeds, so that heading direction will have only a minor effect on the migration trajectories. Moths flying above temperature inversions sometimes fly "unenergetically" and glide (80, 87), and perhaps merely maintain their altitude and rely entirely on transport by the wind to achieve displacement. On the other hand, the frequent occurrence of collective orientation at high altitudes (113) indicates that heading direction is often of some significance to the migrants and that nocturnal migration is not confined simply to movement downwind but may include some element of navigation, which is most effective in light winds.

Nocturnal migrations usually commence at dusk, when the PBL is already stable and there are no vertical air motions. Many of the larger migrant species can attain altitudes of 500–1000 m in less than 1 hr under these conditions (34, 38, 111, 120). It is therefore not necessary to assume that long-distance migrants are dependent on ascending air to gain height at the beginning of their flights, as some authors have implied (2, 92, 137, 140).

Daytime Migration

Daytime migration in convective conditions is particularly prevalent among microinsects. Thermals provide a frequently available means for insect larvae and spiderlings that migrate on silk threads to be carried aloft, and for all insects to gain height with minimal expenditure of energy. Migration in the convective PBL is downwind, but much slower than in the geostrophic airflows found in stable conditions. Many species that migrate by day are capable of sustained flight (76), and it is unlikely that these are dependent on convective updrafts to keep themselves aloft. These species might be transported further if they migrated at night, so they may fly during the day for some reason unrelated to air motions, e.g. because nighttime temperatures are too low or because they use visual cues to terminate their flight in a suitable habitat. Similar factors may account for the apparent prevalence of daytime flight by insects migrating in a fixed compass direction or along topographical features, as it is not clear that surface-layer air motions are more suitable for flight into an opposing wind during the daytime than during the night.

Convergence and Concentration

There is no doubt that convergent wind systems on a wide range of scale can concentrate migrating insects, with densities often increasing as much as 10 or 100 times (120, 121). It is less clear, however, that this process is always of ecological or behavioral significance to the migrants. Concentration processes are potentially important for insect populations because an increase in density may be sufficient to boost the population from an endemic to an epidemic equilibrium state (25). Concentration may also produce localized outbreaks of a pest species from widespread subeconomic infestations (76a). However, there is little reason to suppose that insects in moving concentrations, such as those in convective updrafts or in the head of a density current, are usually deposited together at the end of their flight; nor, except in the case of swarming desert locusts, do they appear to respond to each other while flying in the concentration. Mass deposition has been observed when a line concentration has become stationary (64), and it may occur when two line concentrations intersect (120), but these are probably infrequent events. Storm outflows may produce localized deposition (76a), but washing out of insects concentrated by thunderstorm inflows (28, 68, 68a) probably occurs more frequently. Washing out is perhaps the most likely mechanism by which small-scale convergence could initiate local outbreaks. In the absence of any mechanism for simultaneous deposition of insects, the degree of concentration of immigrants on the ground will depend on the speed of movement of the zone of convergence. The ground concentration will be high only if the zone moves slowly. Gypsy moth infestations associated with afternoon sea breezes are an example of concentration of surface populations by a relatively slow-moving convergence zone.

Ecological significance has been established for concentration by one convergent wind system, the ITCZ (101a, 104). Surface populations can build up in this zone by convergence because the ITF remains approximately stationary for long periods. Moreover, because the accumulating insects remain in the same general area, they can take advantage of improved growth conditions that arise locally from rainfall associated with the convergent airflows. In contrast, the warm and cold fronts of temperate regions are fast-moving, and their rainfall is spread over a wide area. Any concentration effect of these fronts is much less likely to be ecologically significant, even in low-rainfall areas.

Small-Scale Air Motions

Motions arising from topographical influences can be expected to be of local importance because they tend to affect a particular locality consistently in the same manner. Thus, in coastal regions the sea breeze may help to prevent day-flying insects from being carried out to sea (119). Lee waves may provide lift for medium-range movements away from a mountain ridge, and slope and valley winds would appear to be of potential value for insects undertaking altitudinal migrations.

Density currents have considerable potential for influencing nighttime migrations over extensive plains because they affect the altitudinal range in which most migration occurs and because they cause major changes to migration trajectories. Also, their frequency of occurrence, of the order of one per night (120), is sufficiently high for migrants to have a reasonable chance of encountering them. Storm outflow currents are relatively variable in direction, and may be important for mixing populations over distances of the order of 20 km. Sea-breeze currents move consistently inland and can probably transport insects up to 100 km in one night; they may have a particular ecological importance in regions such as southeastern Australia where the synoptic-scale wind systems that are most favorable for migration carry insects in a coastward direction. Their significance is greatest in regions relatively near the coast, as they reach these regions regularly, and early in the evening when migration is still at its peak; further inland, much migration will already have been completed by the time the sea breeze arrives. Currents of katabatic origin can be expected to have a similar effect in regions of large-scale terrain slope. Forecasts of insect-migration trajectories that fail to take account of sea-breeze or katabatic currents are likely to be seriously in error.

Most types of wave motion displace migrating insects only temporarily and do not have a major effect on migration trajectories. Insects that become entrained in the closed circulation of a solitary wave may have their tracks significantly altered, but such events are probably not common (35). In any case many insects appear to continue their flights without being affected (36). Waves therefore probably have little direct ecological significance. It has been suggested, however, that Kelvin-Helmholtz waves may provide the cues necessary for insects to maintain a preferred orientation (113). If this is confirmed, it will indicate that waves have a very considerable behavioral significance.

Long-Distance Migration

The trade-wind and monsoon airflows of the tropics and the more variable winds of synoptic-scale disturbances in both the tropics and temperate regions provide the means for long-distance insect migrations. These movements allow migrants to exploit temporarily favorable habitats (128) in widely separated regions. In the tropics, long-distance migration is associated primarily with the seasonal movement of the ITCZ and its band of rainfall (16, 41, 81, 103, 111). In cold temperate regions, spring movements toward the poles carry populations to habitats that are just becoming warm and where host-plants are just commencing active growth (2, 18, 30, 31, 69, 70, 78, 79, 82, 100, 129, 143, 148, 153); the immigrants arrive before the overwintering population, if there is one, has reached the adult stage. Reverse movements sometimes occur in autumn (130, 137), and patterns of seasonal population movements may form a closed loop (89). However, migrations into high latitudes sometimes appear to take populations into regions from which they cannot return, because the temperature of airflows toward lower latitudes is below the species' threshold for flight (94). Infrequent invasions of species well outside their normal range (51, 95) probably have no long-term effect on the dynamics of the main population. In warm temperate regions, where temperatures rarely fall so low as to completely inhibit migration, movements in different directions on the changing winds of passing synoptic-scale disturbances may redistribute populations almost randomly. This mechanism may be effective for ensuring species survival in semiarid areas in which erratic rainfall produces a patchy distribution of ephemerally favorable habitats (39), and may lead to a reticulated space-time pattern of population distribution (135).

Long-distance migration in a particular region is an adaptation to both the seasonal variations of habitat favorability in the region and the availability of winds suitable for transporting migrants in the required directions. Migration systems therefore depend on particular topographical and climatic factors, and are unique to each region (39). These factors have been tentatively identified for the few systems for which there is a significant body of observations. Movements in East and West Africa associated with the ITCZ have already been described. In the interior of North America, where winters are severe, a number of species migrate northward in spring on warm southerly airflows which often persist for several days and in which a well developed LLJ frequently forms over the Great Plains (2, 18, 31, 67, 70, 78, 100, 105, 129, 143, 153). Similarly, in northern China and Japan, which also experience harsh winters, immigrants arrive from the south or southwest each spring on warm winds which are usually located on the southern, warm-sector side of northeastward-moving temperate or monsoon-front *(baiu)* depressions (69, 79, 82, 92); *baiu* migration probably occurs mainly in a strong prefrontal LLJ (C. Kitamura & H. Seino, personal communication). In southeastern Australia, populations of migratory species build up in the warm, semiarid interior following rains and migrate south or southeast toward the cooler continental periphery on the warm winds ahead of a cold front (40, 42, 46, 73, 132); the migrants occasionally perish after flying out to sea (39, 42). Conditions in inland Australia are often sufficiently mild, however, for windborne migrations in other directions (24, 38, 39, 132); movements that lead to the colonization of patches of ephemerally favorable habitat within the interior or that take the migrants northward into the summer-rainfall regions of the subtropics may have more long-term significance for species survival than the long-distance mass flights to the south.

FUTURE DEVELOPMENTS

The material reviewed here demonstrates that migrating insects are affected by a variety of atmospheric processes. For a few species, most notably the desert locust, the behavioral responses to these processes are now known and the advantages of these responses for the species' survival are understood. For several other species the importance of long-distance wind-assisted migration for recolonization of regions affected by severe cold or drought, and perhaps for initiation of outbreaks of economic importance to agriculture, is now clearly recognized. Nevertheless, for most species the ecological significance, if any, of the observed interactions with atmospheric processes is unknown. This is especially true for small-scale processes, which have often been observed in only a very few case studies in which the identity of the migrants has sometimes been uncertain. To observe how individual migrant species respond to the various features of their atmospheric environment, and to establish the extent to which their responses are adaptive, is an obvious objective for future research.

In many cases, existing entomological and meteorological techniques appear to be adequate for the required studies, but they will need to be used more intensively than in the past. For investigations of long-distance movements of individual species, the conventional approaches of trapping and survey of surface populations, mark-recapture studies, and analysis of synoptic-scale trajectories may need to be supplemented by direct observations of migration in progress, using radar and aerial sampling. Layering behavior in the stable PBL and LLJs, and the interactions of migrants with waves, small-scale circulations, and synoptic-scale fronts, are obvious candidates for more detailed radar investigations. These studies will require more intensive aerial sampling and measurement of temperature and wind profiles than have usually been attempted so far. Species that have so far been studied mainly as immigrants should also be observed in their source regions, to determine whether they migrate in other directions in different synoptic conditions.

Observation will be easiest in outbreak situations where the species to be studied is predominant, as significant trap catches are then readily obtained and the identification of radar targets becomes straightforward. Intensive investigations along these lines directed at the spruce budworm moth, *Choristoneura fumiferana* (28, 28a, 29, 64, 91, 120), have successfully demonstrated how dispersal in this species is influenced by several different features of the atmospheric environment.

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