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Nocturnal Grasshopper Migration in West Africa: Transport and Concentration by the Wind, and the Implications for Air-To-Air Control [and Discussion]

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Nocturnal grasshopper migration in West Africa: transport and concentration by the wind, and the implications for air-to-air control

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During radar observations of the migratory flight of *Oedaleus senegalensis* and of other grasshoppers in West Africa, we have observed that nocturnally flying insects are sometimes concentrated by mesoscale zones of wind convergence. The concentrations were typically 1.2–2.0 km wide, often more than 20 km long, and were similar to those observed elsewhere. The convergence zones appeared to be usually caused by atmospheric gravity currents. Some of these currents were cold air outflows from rain storms, and others were possibly of katabatic origin. Occasionally zones may also have been caused by bores and gravity waves set off by these currents.

In this paper, we investigate the practicability of controlling populations of sahelian grasshoppers by the air-to-air spraying of insecticide onto such concentrations of insects. Using our data on concentration in convergence zones and a rudimentary model of zone distribution and behaviour, we estimate that less than 30% of the flying population of grasshoppers would be entrained in convergence zones, and that effective search for the concentrations might require the simultaneous use of at least two aircraft per 500 km square.

These results imply that strategic control by air-to-air spraying is unlikely to be practicable. It is necessary to emphasize, however, that the evidence on which this deduction is based is fragmentary. A much more definitive conclusion could be expected from the results of further research with an aircraft equipped with a wind-finding system and a radar able to measure and delineate insect concentrations.

1. Introduction

Recent studies have shown that *Oedaleus sengalensis* (Krauss) and many other species of grasshoppers of the Sahel and Sudan-savanna zones of West Africa, engage in long-distance, windborne, migratory flights at night. Evidence obtained by monitoring changes in ground populations (Popov 1976; Lecoq 1978*a*, *b*; Duranton *et al.* 1979) and, particularly, the direct observations of migration by radar (Riley 1975; Schaefer 1976; Riley & Reynolds 1979, 1983; Reynolds & Riley 1988) have revealed the magnitude and regularity of these flights, which are best viewed as an essential part of an adaptive strategy for colonizing and exploiting the transient sahelian habitat.

One of the consequences of grasshopper migration at heights above the ‘flight boundary layer’, as defined by Taylor (1974), is that the grasshoppers will inevitably be carried downwind and towards zones of wind convergence (Rainey 1976; Pedgley 1980) where there is a net horizontal inflow of air. Aerial densities will tend to increase if incoming airborne insects are constrained against ascent in the upward divergent air currents which compensate for the horizontal convergence (Rainey 1976). Wind convergence zones occur on various scales, but some of the most active occur at fronts and windshift lines associated with mesoscale (i.e. from tens to hundreds of kilometres) airflows, such as cold outflows from convective storms. Several authors have observed that mesoscale windshift lines are frequently associated with linear accumulations of airborne insects which appear on the radar plan position indicator (P.P.I.) display as a moving 'line-echo' (Schaefer 1976; Reynolds & Riley 1988; Drake 1982 for concentrations of grasshoppers), and it seems clear that these convergent winds can increase the aerial density of flying insects by up to 100 times (Drake & Farrow 1988).

Apart from being of intrinsic meteorological and entomological interest, the concentration of nocturnally migrating insects at windshift lines may have implications for pest control. For example, Joyce (1983) reports that in Sudan, the grasshopper *Aiolopus simulatrix* (Walk.) becomes a pest of economic significance only when concentrated by convergent wind fields. Moreover, he suggests that it is only when the grasshoppers are in these airborne concentrations that control is worthwhile. This has led to proposals for the location of wind convergences by aircraft equipped with doppler navigation systems, followed by the delineation of any associated insect pest concentrations by an insect-detecting radar (Schaefer 1979), and the destruction of the pests by air-to-air spraying (Rainey 1972, 1974*a*, 1976, 1979; Joyce 1976, 1981, 1983). Insecticide droplets are picked up much more effectively by flying insects than by those on the ground (Rainey 1974*a*), so less insecticide would be required with air-to-air ultra low volume (ULV) spraying and reductions in both cost and environmental pollution could be anticipated.

The main purpose of this paper is to interpret available data on grasshopper concentration in a way which may help to assess the practicality of such a control scheme. Most of these data come from radar observations of flying insects made during four seasons' work on grasshopper migration in the sahelian zone of Mali, West Africa. Information is presented on the frequency, extent and aerial density of line-echoes, and we incorporate the data into a simple descriptive model of convergence zone behaviour. We examine the implications of the model for the proposed aerial 'search-and-destroy' control strategy, and discuss other factors which would be of relevance in air-to-air control. The identity of the meteorological mechanisms which may have produced the concentrations is also briefly considered.

2. METHODS

Radar observations were made on larger-sized insects (> 100 mg) by using a modified marine, X-band (3.2 cm wavelength) radar at the following places in Mali: Kara (14° 10′ N, 5° 01′ W) in the flood plains of the middle Niger delta; Alfandé (15° 48′ N, 3° 04′ W) in the northeast of the delta; Tin Aouker (16° 48′ N, 0° 08′ E) in the Tilemsi Valley, north of Gao; and Daoga (15° 53′ N, 0° 14′ E) on the River Niger, south of Gao. The observational periods at each site are shown in table 1. The equipment and observational procedures are described in Riley & Reynolds (1979, 1983). Continuous records of wind velocity, and of air temperature and humidity were made at each site.

3. RESULTS

(*a*) *Take-off and emigration*

Long-distance migratory flight in sahelian grasshoppers commences just after dusk, when mass take-off of flight-ready, largely post-teneral, individuals occurs in response to decreasing illumination (Riley & Reynolds 1979, 1983; Schaefer 1976). This mass take-off has been

Table 1. Frequency of occurrence of line-echoes observed at four sites in Mali, West Africa

month (dates)	site (year)	number of evenings	number of hours of PPI observations	number of line echoes	number of line echoes per evening	number of hours between line echoes
September (19–30)	Daoga (1978)	12	63.9	3	0.25	21.3
October (1–23)	Daoga (1978)	23	138.0	4	0.17	34.5
October (9–21)	Tin Aouker (1978)	13	120.1	16	1.2	7.5
October (24–31)	Kara (1973)	8	41.5	1	0.13	41.5
October (23–24)	Kara (1975)	2	9.4	0	0	—
November (2–11)	Alfandé (1975)	10	38.4	1?	0.1?	38.4?
November (1–9)	Kara (1973)	6	29.8	0	0	—
November (1–23)	Kara (1974)	2	114.9	0	0	—
November (19–27)	Kara (1975)	9	33.3	0	0	—

routinely observed during radar studies; it occurs to a varying degree every night in the rainy and post-rainy seasons in Mali when suitable grasshopper populations are present and temperatures are above a threshold of about 23 °C. Grasshoppers ascend under their own power (Rainey 1974*b*) at climb rates of *ca.* 0.4 m s^{-1} (Riley & Reynolds 1979) to heights of several hundred metres, when they are usually, but not always (see Riley 1975), above their 'flight boundary layer'.

Radar displays during the dusk take-off of grasshoppers at Tin Aouker typically showed dense plumes and concentrations of multi-target echo appearing from areas of clay known to harbour large numbers (1200–3300 ha^{-1}) of *Aiolopus simulatrix*. The plumes were observed to disperse gradually as the insects in them displaced downwind, presumably because of differences in individual insect orientation and air speed, and because of the effects of wind shear and turbulence. Thus the grasshoppers did not undertake nocturnal migration in a cohesive swarm like those of day-flying, gregarious locusts and it appears necessary to postulate mechanisms that could reconcentrate migrants to the densities seen to invade cultivations.

At the peak of the dusk emigration period (about 50 min after sunset), the volume density at 100 m above ground and averaged over all observational evenings at Tin Aouker and Daoga, gave a mean of about one grasshopper-like insect per 10^4 m^3 (range from about one per 10^3 m^3 to about one per 10^5 m^3). The corresponding densities were lower at the Alfandé site (mean of about 5 per 10^6 m^3). Similarly Schaefer (1976), working on grasshoppers in the Gezira province of Sudan, found that emigration densities ranged from about one per 10^3 m^3 to about one per 10^6 m^3.

Schaefer (1976) reported that large numbers of grasshoppers take off on migratory flights under particular weather conditions in the field, and Bergh (1988) discovered in the laboratory that the take-off rate of *Schistocerca* increased with the passage of cold fronts. Other workers have noted that higher numbers of certain acridids often appear at light after storms and other disturbances (Clark 1969, 1971; Farrow (1979) for *Chortoicetes terminifera* (Walk.); L. D. C. Fishpool, personal communication for *O. senegalensis* and other species in Mali), and this may also indicate a relationship between increased flight activity and disturbed weather. In these cases however, it is possible that the observed increase was caused by storm-associated aerial concentration in the vicinity of the light traps, rather than by a stimulation of flight activity *per se*. Any tendency for take-off to be stimulated by disturbed weather would, of course, increase the number of insects available to become concentrated in the mesoscale convergence zones normally present in such weather.

(*b*) *Duration of flight*

Our observations have shown that the aerial density of grasshoppers in flight tends to decline as the night develops (figure 1). It could be argued that this decline occurs because habitats progressively further upwind of the radar support progressively lower grasshopper populations, but this explanation seems unlikely because the decline tends to occur at rather similar rates in winds from a wide variety of directions, and at different sites. An alternative, and much more probable cause is that there is a large spread in the flight endurance of the individuals that make up the grasshopper population. Some will begin to descend after only short flights whilst others continue for longer, with the result that aerial density will fall as time progresses. Sometimes the rate of decline is initially rather dramatic, and then becomes less rapid. On other occasions, a more uniform rate is maintained for most of the night (figure 1). The various rates of decline can be interpreted in terms of mean flight period. For example, the

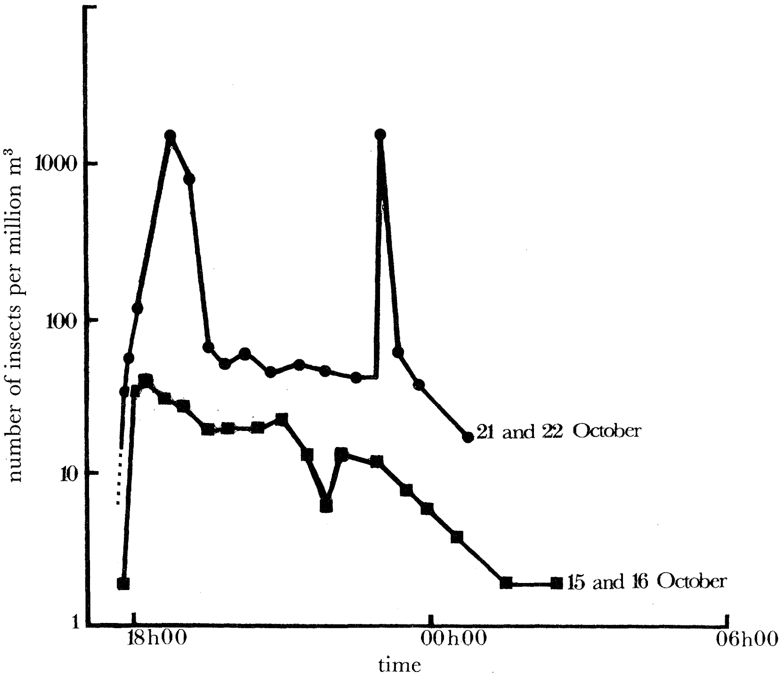

FIGURE 1. The variation in volume density of insects (mainly grasshoppers such as *Oedaleus senegalensis*) flying between 140–170 m above ground at Tin Aouker, during the nights of 15–16 and 21–22 October 1978.

density–time data shown in figure 1 for 15 and 16 October could be explained if it is assumed that the distribution of flight endurance amongst the population was exponential, with a mean flight period of 2.7 h. The more gradual slope found for the 21 and 22 October (after the initial rapid decline) implies a mean period of 6 h for the long-distance fliers. The detection of flying concentrations of grasshoppers 5–7 h after the dusk take-off period (Riley & Reynolds 1983; Reynolds & Riley 1988) provides more direct evidence that a night's migration is usually accomplished in single long flights, rather than in a series of short ones.

(*c*) *Concentration in wind convergence zones*

Observations in the rainy season in the sahelian zone of Mali revealed many occasions when dense or relatively dense (namely, 0.003 to 3×10^{-5} insects per m^3) line concentrations passed over the radar. On all the occasions which we investigated, these concentrations were aligned along, and moved with, a windshift line at altitude. The phenomena were usually accompanied by corresponding changes of windspeed and/or direction at ground level, but these changes were sometimes unremarkable and might have passed unnoticed had not the radar results focused our attention on them. Many minor shifts in wind velocity recorded at ground level were not associated with any radar evidence of convergence, so it appears that conventional anemometry did not provide a reliable indication of convergence aloft.

At the altitudes at which most insects were flying, i.e. within the lowest kilometre of the atmosphere, there was always a net horizontal inflow or convergence of air in the features studied. An example of the phenomenon in which the convergence reached a value of $5 \times 10^{-3}\ s^{-1}$ is described in Reynolds & Riley (1988). Another example with a weaker convergence ($1.4 \times 10^{-3}\ s^{-1}$) is shown in figure 2.

Several authors have observed similar moving linear accumulations of insects and have noted their apparently invariable association with windshift lines (see, for example, Schaefer (1976); Riley & Reynolds (1983); Reynolds & Riley (1988) for sahelian grasshoppers). In some cases the cause of the windshift was self-evident, e.g. sea breeze fronts (Drake 1982), storm outflows (Schaefer 1976; Pedgley *et al.* 1982), or the Inter-Tropical Front in Sudan (Schaefer 1976), but in other cases the mechanism was less certain or unknown (Schaefer 1976; Riley & Reynolds 1983).

The concentrations are usually about 1.2–2 km from front to back, but much greater in lateral extent: Schaefer (1976), for example, observed a length of 60 km of a storm outflow in Sudan, and Drake (1982) over 40 km of a sea breeze front in Australia. In these and other cases the concentrations probably extended laterally well beyond the range to which they could be detected by the radar.

Some figures for the aerial density of insects found within line-echoes are given in table 2; the highest values approach those found in (sparse) locust swarms (1 per $10^3\ m^3$) (Waloff 1972).

(*d*) *Frequency of occurrence of line-echoes*

The frequency at which we observed the passage of line-echoes varied considerably between month and site (table 1). There appeared to be more line-echoes towards the end of the rainy season (September–October) than after the rains (November), but this could have been partly attributable to the fact that different sites were used in the two periods. At only one of our sites (Tin Aouker) were line-echoes as frequent as one per night. Schaefer (1975) working in the Gezira area of Sudan in October, reported that line-echoes occurred on 12 occasions during

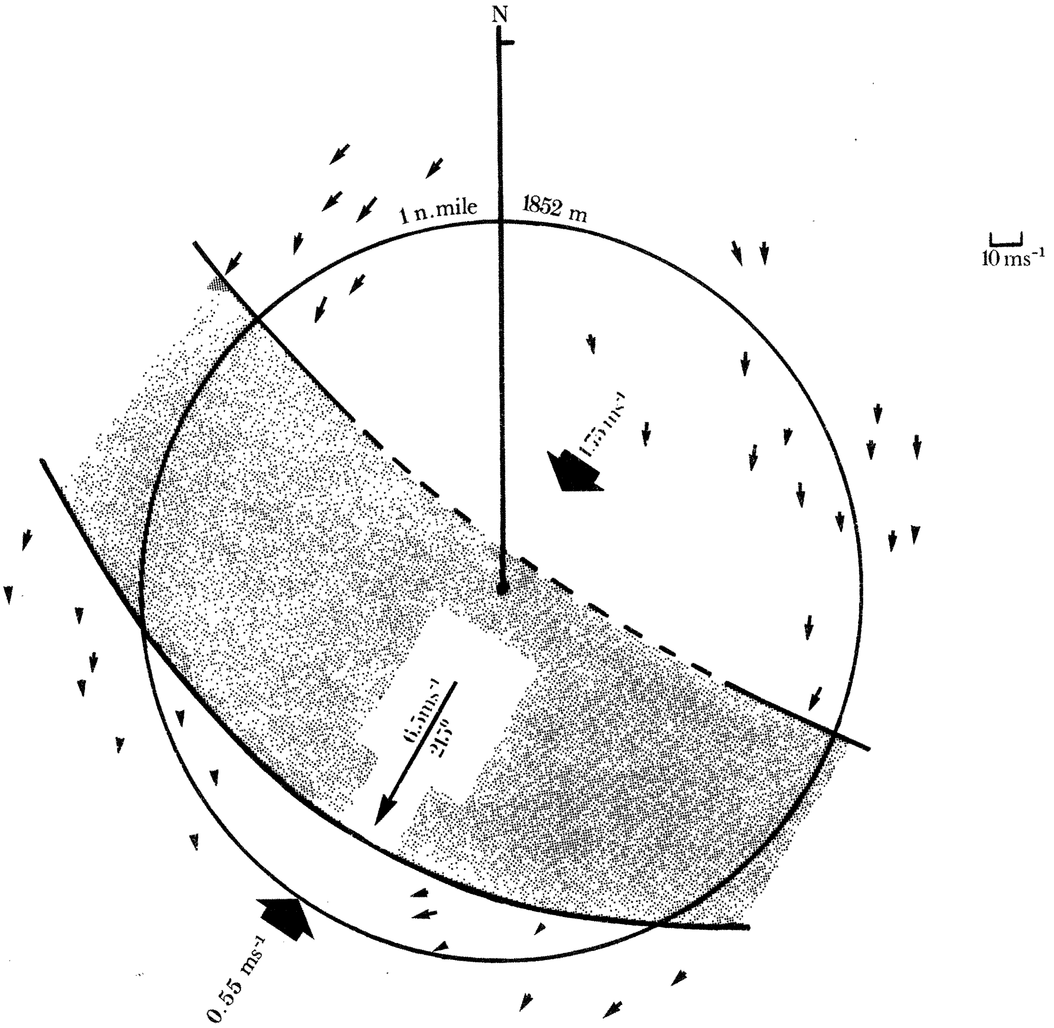

Figure 2. Diagram from the radar PPI display showing a line-echo passing over the Tin Aouker site at about 19h22 on 20 October 1978, moving towards 215° at 6.5 m s^{-1}. The small arrows represent the displacement velocity, relative to ground, of a selection of individual insects. The estimated average ground speed and direction of insects in front of the line-echo was 7.0 ± 1.4 (s.d.) m s^{-1} towards 201° ± 27°, and the corresponding values behind the line-echo 9.0 ± 1.5 m s^{-1} towards 195° ± 17°. The large broad arrows show the mean velocity of the insects *relative* to the line-echo and perpendicular to it. The horizontal convergence (Sc) over the 1.6 km width (Lc) of the zone was 1.4×10^{-3} s^{-1}.

96 h of observation over 22 nights. The average interval between events (8 h) was thus very similar to the value (7.5 h) found by us at the Tin Aouker site. There are apparently no data for the frequency of line-echoes earlier in the rainy season (June–August).

(*e*) *Weather during passage of line-echoes*

Most (18 out of 23) line-echoes studied at Daoga and Tin Aouker were accompanied by an increase in surface wind speed of between 1 and 4 m s^{-1} (except in one case on 20 October 1978 which was clearly attributable to the gust-front of a storm, where the wind speed increased suddenly by 9 m s^{-1}). Increases in wind speed were sustained for periods ranging from 5–10 min up to several hours. In 10 cases there was a well-marked change in direction of insect movement (reflecting a change in wind direction) at the leading edge of the line-echo (see

Table 2. The characteristics of some line-echoes observed accumulating flying grasshoppers in Mali and Sudan

date and time	volume density in line-echo (number per m^3)	increase in volume density at leading edge of line-echo	area density of line-echo (number per hectare)	length (km)	grasshopper species accumulated	place	reference
21-10-78 23h00	Up to 0.0015	*ca.* 50 ×	*ca.* 4000	at least 22 km	mainly *Oedaleus senegalensis*	Tin Aouker, Mali	Riley & Reynolds (1983) and unpublished results
10-11-78 22h15	Up to 0.0001	15 ×	—	at least 8 km	mainly *Oedaleus senegalensis*	Tin Aouker, Mali	Reynolds & Riley (1988) and unpublished results
11-10-78 02h27	Up to 0.003	*ca.* 80 ×	—	at least 16 km	*Diabolocatantops axillaris* & *O. senegalensis*	Tin Aouker, Mali	Reynolds & Riley (1988) and unpublished results
17-11-78 20h28	—	60 ×	*ca.* 1000	60 km	mainly *Aiolopus simulatrix*	Radma, Sudan	Schaefer (1976)

example in Reynolds & Riley 1988); on the other occasions there was an increase in target speed but little change in direction (figure 2). On most occasions there was no change in surface air temperature (14 out of 23 cases) or dew point (13 out of 23 cases) with the passage of the line-echo. In only one case was there a substantial fall in temperature (−8.5 °C) and rise in dew point (+3°), and this was clearly attributable to the above-mentioned storm outflow. On the remaining occasions the temperature showed a small rise (*ca.* 1 °C) (or a small fall followed by a small rise), and the dew point usually fell slightly. The line-echoes with an accompanying change in temperature or dew point were also those with a marked shift in wind direction.

Apart from the line-echoes associated with the storm on 20 October, and the line-echo described in Reynolds & Riley (1988), which was probably an outflow associated with patchy rain from middle-level cloud, there was little evidence of precipitation within radar range (at least 40 km) at the time the line-echoes were observed. It would thus appear that if the concentrations are formed by outflow gravity currents they must propagate far from their parent rain-storms.

(*f*) *Speed and direction of movement of line-echoes*

The line-echoes moved with ground-speeds in the range 4 m s^{-1} to 14 m s^{-1}. At Tin Aouker, line-echoes came from the southeast quadrant (south to east) or from the north quadrant (N.W.

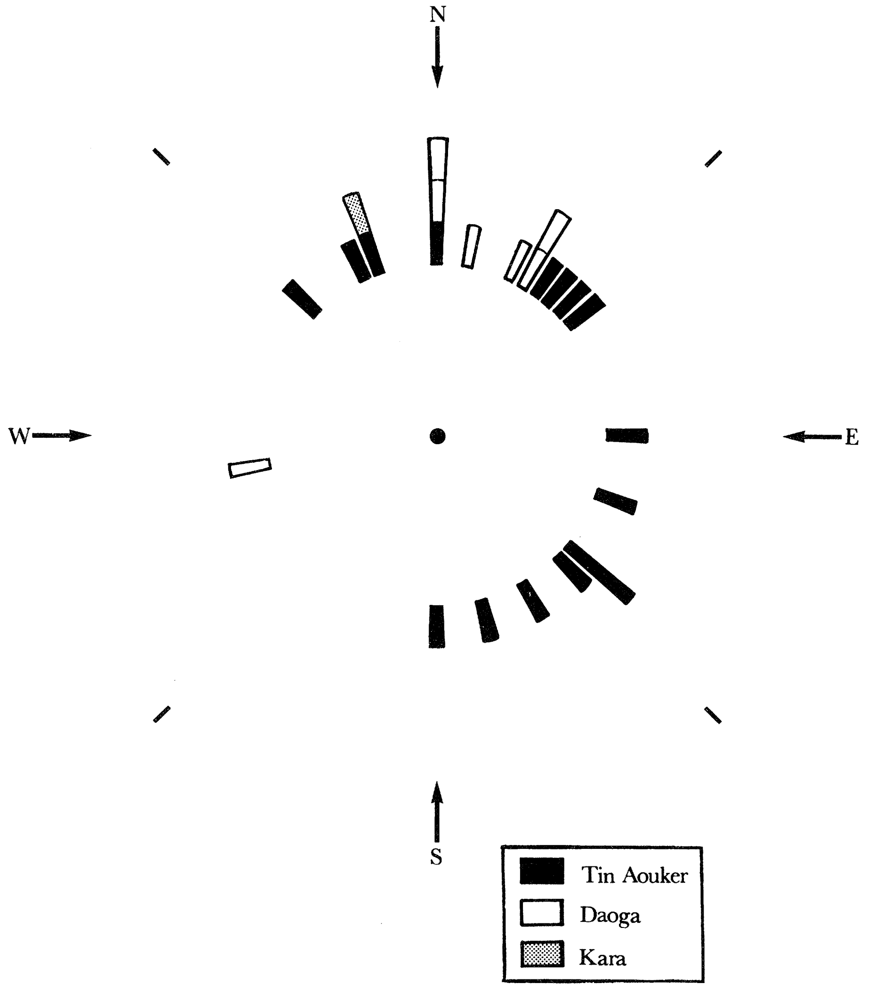

Figure 3. Circular histogram showing directions from which the observed line-echoes came.

to N.E.), while at Daoga, they came (with one exception) from the north or northeast (figure 3). We note that line-echoes hardly ever came from the west or S.W., although winds from this direction occurred during the observational period, and, indeed, line-echoes occurred within southwesterly wind fields. Schaefer (1976) working in Niger stated that line-echoes associated with nocturnal windshift lines arrived 'almost invariably from the S.E.'. He attributed them to gravity currents flowing down a shallow drainage slope. Likewise in our study it seems probable that some of the windshift lines approaching from the north or N.E. were katabatic in origin or that their flow was enhanced by the slight gradient from this direction. The line-echoes approaching Tin Aouker from the S.E. could have originated as gust-fronts from storms or disturbances far to the south.

4. Discussion

(*a*) *Factors to be considered in control schemes*

There are two main approaches to the problem of controlling migrant insect pests with insecticides. One method is to attempt to reduce the population of the pest species as a whole, over large geographical areas (as in the case of Desert Locust control), and the other is to concentrate on the more limited tactical objective of attacking only those parts of the population which constitute an obvious and direct threat to crops. In the case of grasshoppers migrating over long distances, the direct threat to crops is difficult to predict; proposals for air-to-air spraying of insect concentrations thus appear to be directed more towards large area, strategic control than towards limited tactical defence. If this is indeed the case, their success will depend on whether a significant proportion of the target population is likely to become entrained in convergence zones, and therefore vulnerable, at least in principle, to attack by air-to-air spraying.

(*b*) *Proportion of the population liable to concentration*

As we have observed, sahelian grasshoppers such as *O. senegalensis* often spend several hours in migratory flight, usually displacing downwind towards the Inter-Tropical Convergence Zone. During these flights a proportion should be concentrated by mesoscale zones of wind convergence. To compute the size of this proportion we need to have a representative knowledge of the spatial and temporal frequency of the convergence zones and of their strength. Unfortunately, representative data on mesoscale convergence zones in the Sahel are not currently available. This is partly because the density of wind recording stations is so low, but mainly because, in the absence of radar data, conventional anemometry records do not appear to provide a reliable indicator of the presence of zones likely to produce insect concentrations aloft. Data on entomologically significant mesoscale convergence in the Sahel thus appear to be confined to that accrued during the very limited periods of radar operations by Schaefer and by ourselves. Although this information is scarcely adequate to characterize the region as a whole, it does at least provide a basis for a first rudimentary estimate of the proportion of airborne grasshoppers likely to accumulate in convergence zones.

We assume a primitive descriptive model in which linear convergence zones generated from a single source occur randomly but are roughly parallel to each other, and that airborne insects are initially uniformly distributed. It is also assumed that the insects do not change their altitudinal distribution. Then, if the average strength of a zone is Sc, its lifetime Tc, its width

Lc, and the average (perpendicular) distance between zones is L, the percentage, P, of the airborne population likely to be concentrated into a zone (by the end of the zone's life) is:

$$P = (Sc \times Tc \times Lc \times 100)/L\,\%. \tag{1}$$

Sc and Lc were directly observable by radar (figure 2), but L must be estimated from the observed line displacement speed and the interval between the passage of successive lines. Thus, suppose that the convergence zones evolve at an average spatial separation of L, at temporal intervals Tg, and that they move with a speed V. If we assume $Tc < L/V$, i.e. that their lifetime is less than the time taken to traverse their separation distance, then the average interval, Ti, at which zones will be seen to pass over a fixed point is:

$$Ti = (L \times Tg)/(V \times Tc). \tag{2}$$

Substituting for Tc in (1) gives:

$$P = 100 \times ((Sc \times Lc)/V) \times (Tg/Ti)\,\%.$$

Unfortunately, one of the quantities on the right-hand side of this equation, Tg, is not known, so we cannot evaluate P from our data. However, we can estimate its maximum value because the upper limit of (Tg/Ti) is unity (convergence zones cannot arrive at the radar faster than they are generated). Thus

$$P < 100 \times (Sc \times Lc)/V\,\%. \tag{3}$$

Typical values for Sc, Lc and V are, respectively, $10^{-3}\ \mathrm{s^{-1}}$, 1.2×10^{3} m and $5\ \mathrm{m\ s^{-1}}$, which suggests that $P < 30\,\%$, and it may, of course, be much lower. It may be noted that actual values for P, rather than upper limits, could be calculated directly from equation (1) if values for L and Tc could be determined by some other method, for example, by the use of an airborne radar.

It was implicitly assumed in equation (1) that individual grasshoppers remain airborne at least as long as the lifetime of a typical convergence zone, and this assumption merits some scrutiny. Our data suggest that concentrations as high as fifty-fold or more (table 2) occur in the Sahel, and at typical observed convergence rates of the order of 10^{-3}, this implies that zone lifetimes (Tc) are about two to three hours. Our observations of density variation with time, and of discrete overflights imply mean flight lengths are often longer than this in the Sahel, and may be as long as 5–7 h. Schaefer (1976) concluded from time–density data, that in the case of grasshoppers in the Sudan, the average flight duration was probably about 1.5 h during the take-off peak, but about 5 h for individuals which remained in flight after this period. Overall, it seems probable that on many occasions the majority of migrant grasshoppers do indeed remain airborne long enough to be effectively concentrated should they encounter mesoscale convergence phenomena, and so on this count at least, equation (1) should be valid. On some occasions, however, it seems that the bulk of the airborne population lands within an hour or so of take-off (see the data in figure 1 for the night of 21–22 October 1978), and in these cases only a small fraction will remain airborne long enough to be affected by convergence zones.

It must be emphasised that our expression for the maximum value of P was made on the basis of a very rudimentary model of the spatial and temporal distribution of convergence zones. No attempt was made to consider the effect of changing rates of convergence with time, nor that of possible changes in the vertical distribution of insects at the convergence line. Nor was any account taken of the possibility that grasshopper take-off might be preferentially stimulated by disturbed weather conditions. The result should thus at best be taken as a provisional estimate of the maximum fraction of the grasshopper population likely to be concentrated. Much more definitive predictions could be expected if new observations were made with an aircraft equipped with a wind-finding system (to assist in the location, tracking and measurement of convergence zones) and with an appropriate form of radar to monitor insect aerial densities both inside and outside the zones.

(*c*) *Some practical considerations*

Our analysis of current evidence has indicated that the percentage of grasshoppers likely to be entrained in mesoscale convergence zones in the Sahel is too low to make strategic control by air-to-air spraying worthwhile. However, the evidence on which this conclusion is based is far from perfect, and it is conceivable that future investigations will show that enough entrainment occurs to make effective control at least a possibility. It is thus appropriate to briefly consider here some of the practical implications of the proposed control method.

(i) *Finding the concentrations*

Methods of finding insect concentrations in convergence zones, by using an aircraft equipped with a wind-sensing system and an insect-detecting radar, are described elsewhere in this volume (Rainey & Joyce, this symposium). Here, we examine our ground-based radar data in an attempt to assess the practicality of the search task that such an airborne system would face in the Sahel. In the descriptive model proposed in the preceding section, the average separation between convergence lines is given by the equation:

$$L = Ti \times V \times (Tc/Tg).$$

If it is assumed that the lifetime of a zone is less than the interval between the generation of successive zones, i.e. that $Tc/Tg < 1$, and we take $5\ \mathrm{m\ s^{-1}}$ as a typical value for V, then:

$$L < 18 \times Ti\ \mathrm{km}.$$

Our data (table 1) show that Ti varies considerably between October and November. The corresponding average values for L are < 500 km in October, and a larger but undetermined value in November. The lateral extent of the zones we observed was unknown, but we assume (optimistically) that it might approach 100 km. Thus, in a hypothetical search area of 500 × 500 km, on each search leg perpendicular to the alignment of the zones an aircraft might expect to encounter more than 1 zone per leg in October, but perhaps none at all in November. At a flying speed of 350 km per hour, each search leg would take about 1.5 h, and it would require 4 legs or about 7 h to cover the 500 km square. This is more than twice the estimated average lifetime of a zone, so it appears that half the zones might be missed, and that a search using only one aircraft per 500 km square would thus be only partially effective. Much more reliable conclusions than these could be expected from an experimental trial with an airborne system, because the lateral extent, lifetime, and spatial and temporal distribution of zones could then be measured rather than inferred.

(ii) *Insecticide application*

If the estimate of the time required to conduct a systematic search for concentrations is approximately correct, then it is clear that one aircraft would not have time both to look for concentrations and to spray them. The practical implications of a requirement for simultaneous night-time operation of perhaps several aircraft flying co-ordinated and non-routine flight paths, during disturbed weather are considerable. However, given sufficient investment, the logistic and operational problems could probably be overcome, especially now that accurate navigational data are available from the satellite-based global positioning system (GPS), even in very remote areas. Nevertheless, before considering a full-scale control project, it would obviously be prudent to conduct a research program to establish the optimum droplet size distribution for use in the updraft conditions prevailing in convergence zones, and also to evaluate the efficiency of different spray regimes within the zones.

(iii) *Selection of target concentrations*

It is quite possible that the line concentrations to be found over the Sahel will not always consist mostly of target grasshopper species. If this is the case, then indiscriminate spraying of all detected concentrations would be both wasteful and ecologically irresponsible (see general discussion in Rainey (1976)). Unfortunately, the rather small size of sampling nets that can be carried on aircraft means that determination of the species composition of a concentration by aerial trapping is a slow process and would sometimes be impractical. It is thus very desirable that the radar carried by the aircraft should have the capacity at least to distinguish between, say, moths and grasshoppers, and between grasshoppers of substantially differing sizes. There is some prospect that this will be possible in future generations of entomological radars.

(*d*) *Origins of the convergence zones*

Mechanisms that produce wind convergence zones are described in detail elsewhere in this volume (Pedgley, this symposium); we concentrate briefly here on clues that might identify the origins of the zones we detected. The majority of line concentrations observed by us had probably been formed by the head of an advancing gravity (or density) current. Here a flow of cool, dense air displaces or undercuts warmer air and so produces a narrow zone of horizontal convergence. Another type of disturbance of the nocturnal boundary layer which could concentrate flying insects is an internal solitary wave of large amplitude with a closed circulation (these have been observed to form line-echoes in Australia (Drake 1985)). In a circulation, the horizontal components of flow at some level are opposed to the overall wind direction and similarly produce linear zones of (horizontal) convergence.

Two sources of mesoscale cold air flow to be expected in the Sahel are the spreading downdrafts from rainstorms, and the downslope (katabatic) drainage of air which has cooled during the evening. At first sight one might expect that the passage of a convergence zone produced by a gravity current would be clearly revealed by a decrease in air temperature. However, because the arrival of a gravity current usually disturbs the nocturnal temperature inversion, a slight temperature decrease may be masked by mixing within the inversion layer (at least at ground level), and so it may not provide a clue to the origin of the flow. In fact, we almost never detected a substantial fall in surface air temperature during the passage of a line-echo. It thus appears that positive identification of gravity currents is often not possible from surface temperature and humidity data alone.

The scarcity of line-echoes outside the rainy season could indicate that the source of the convergences were gravity currents of the spreading downdraft type. However, as mentioned above, rainfall was seldom detected on the radar behind an advancing convergence zone. The tendency of many of the line-echoes to move in the general direction of the large-scale topographic gradient, i.e. from the north or northeast (figure 3), strongly suggests that some were produced by katabatic flows, or possibly by internal bores or solitary waves set off by these flows (Simpson 1987).

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Discussion

S. E. Hobbs (*Cranfield Institute of Technology, Bedfordshire, U.K.*). Drs Riley and Reynolds have produced a valuable attempt to quantify insect concentrations in mesoscale convergence zones, based on their field work in West Africa. I can add no more to their model, but I agree that it is desirable to have more information about the convergence zones. In particular, it would be useful to have firmer information about the distribution of the zones (how and when they are generated), and the distribution of insects within them.

Our recent experience at Cranfield is concerned with entomological radar systems for both ground-based and airborne work. The airborne entomological radar system is described by Hobbs & Wolf (1989) with examples of the information available from recent field experiments with the United States Department of Agriculture. We have designed and built signal processors to control the radar and data collection, and have developed associated signal analysis techniques. Recent work should allow field radars to measure individual insect radar cross-sections and so provide some degree of target identification (although not as far as species in general). Based on this experience, these comments relate mainly to the radar component of the project.

The most suitable radar for locating insect concentrations would have a wide area coverage, as provided by conventional weather radars for aircraft. The low altitude of some insect concentrations compared with typical cloud heights may limit the useful radar range, but such a tool would be a very powerful way of mapping out the concentrations. Once such concentrations have been found, the Cranfield airborne radar would be suitable for measuring their height and thickness and the number of insects involved, and could provide some indication of species composition (by measuring an insect's mass).

Entomological radars similar to current systems are able to detect individual insects the size of grasshoppers at a range of the order of 1.5 km. The airborne system uses a pencil beam about 40 m wide pointing vertically below the aircraft. With suitable signal analysis techniques, the insect's range is known to a resolution of 15 m or better and its orientation can be measured to within a few degrees. It should also be possible to measure its mass to within a factor of 2–3 by using more recent analysis techniques. In dense concentrations (greater than about 100 per 10^6 m^3) it is difficult to identify signals from individual insects so that individual size and orientation information is lost. However, individuals should be measurable at the fringes. In general, current radar techniques provide all the information required for locating insect concentrations accurately enough for air-to-air control and should be able to distinguish target species from benign species if the insects differ significantly in mass. Entomological radar systems are generally based on standard technology (e.g. marine X-band radars, with standard microcomputers for data collection and analysis) so that implementing such a system does not require inordinate investments in equipment.

Radar, both ground-based and airborne, should help to quantify the importance of insect concentrations at mesoscale convergence zones, and to exploit them if they prove to be significant.

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P. J. Mason (*Meteorological Office, Bracknell, U.K.*). First, I would like to ask what is known about the efficiency of retention of insects within a convergence line. Is there any evidence for varied insect response and turbulence causing significant numbers of insects to leave the region of observed concentration? Might this factor cause your estimates of capture to be optimistic?

Second, I think it is worth noting the interest of air pollution meteorologists in these phenomena. Convergence lines do not of course concentrate passive pollution but they do significantly affect its destination. The convergence lines under stable conditions may be especially relevant as in these conditions pollution hazards are often greatest.

Finally, I must support Drs Riley and Reynolds particular note of the need to formulate a spraying tactic for use in convergence lines. In the case when a free flying swarm is sprayed, I presume that material will tend to move with the swarm and turbulence will mix it through the swarm. In the case of the convergence line the insects are 'trapped' but the spray material will probably not be trapped and will pass through the insects. Spray introduced alongside the insects might only encounter a small fraction of them before being swept away. I think it may require some thought and study to find how to deposit spray in an effective manner so that it is both mixed and encounters the swarm.

J. R. Riley. Very little is known about the efficiency of retention of insects within convergence lines. Large insects with high air speeds ($\sim 4.5\ \mathrm{m\ s^{-1}}$) make progress against the slow winds associated with weak convergence, and hence could presumably fly 'through' a weak convergence zone. Small insects would not be able to do this, but on the other hand, their relatively low falling speeds ($\sim 1\ \mathrm{m\ s^{-1}}$) would make them susceptible to being carried involuntarily out of strong zones by the vigorous updrafts associated with them. Nevertheless, the regular occurrence of 50–100-fold density concentrations suggests that, at least in the early lifetime of a convergence zone, the rate of loss is very much lower than the rate of accumulation. The rate of loss could be established by a systematic study using airborne radar. Such studies might also help to characterize the air flow regime in mesoscale convergence zones occurring under stable conditions and, as Dr Mason suggests, the results might well prove useful in understanding the distribution of airborne pollutants in such conditions.

In an ideal spray regime, the droplet size would be such that their rate of fall more or less matched the average strength of updraft, so that they would remain airborne in a convergence zone for a long time. The insects, by virtue of their (horizontal) air speed, would fly through this 'dynamic suspension' of insecticide and the efficiency of collection could be very high. A fairly detailed knowledge of updraft strength distributions would have to be established before a drop size distribution could be selected, and then there would be the problem that updraft strength tends to increase with height. Thus rising droplets would encounter faster updrafts and hence rise even faster, whilst falling ones would fall faster the lower they got, i.e. the 'suspension' mechanism would be unstable.

R. J. V. Joyce (*Cranfield Institute of Technology, Bedfordshire, U.K.*). Dr Riley has argued that air-to-air spraying of grasshoppers concentrated in zones of wind convergence would be unlikely to make a significant contribution to control. In the sense that 'control', as in the case of the Desert Locust, is the overall regulation of populations, he is surely correct, but it is unlikely that this objective is desirable or economically possible. I think that the most we should aspire to is the regulation of the potentially dangerous populations, i.e., those that are an immediate threat to crops.

My experience with grasshoppers is confined to Sudan, where *Aiolopus simulatrix* (Walker) is of greatest economic importance. In years when this species endangers crops, it has completed two generations of successful breeding, the second generation in the northerly extremity of its distribution where it occurs at densities of the order of 10^3 ha^{-1} over vast areas. To cause crop loss, this density must increase to at least 10^5 ha^{-1} and it is only when airborne in zones of wind-convergence that this increased density has been observed to occur, and it is only when the flight of these insect concentrations terminates in cropped areas that the species is of economic importance. It is also only when the species is present in such zones of wind convergence that they are an economic target for attack. Here they could be destroyed with the minimum amount of insecticide (say, of the order of < 100 ml active ingredient ha^{-1}) with no danger of spray residues on the crop and with no hazard to farmers. Spraying would have to be carried out at night by aircraft instrumented to find the zones of wind convergence and identify the species composition of any insect concentrations. All the elements for such performance are contained in the Airborne Radar System I have described (Rainey & Joyce, this symposium).

J. J. Spillman (*Cranfield Institute of Technology, Bedfordshire, U.K.*). I think that it would be possible to spray within convergence zones, as it is very unlikely that the insects are actually in the continuous updraft. I think you will find they are in the rotary region associated with this, rather than in the updraft itself. Aircraft can cope with the velocities we are talking about. There will be a considerable amount of turbulence, and we would use very small droplets which would diffuse in quite small scale turbulence. I certainly agree that some experiments are needed to demonstrate whether it can be done in practice, but I don't envisage a great deal of difficulty.

K. A. Browning, F.R.S. (*Meteorological Office, Bracknell, U.K.*). Do I understand Professor Spillman to say that he is assuming that the insects would not be in the strong updraft? I would have thought that it's almost inevitable that if they are anywhere, that is where they would be.

J. J. Spillman. They will be there but they will be on the edges as well. They would be falling, so one would have to match the spray conditions to get the relative motion between the droplets and the insects.

V. A. Drake (*Division of Entomology, CSIRO, Canberra, Australia*). This paper represents a welcome first attempt at assessing, for a specific pest and geographic region, the feasibility of controlling populations by air-to-air spraying into mesoscale convergence zones. The authors' simple estimates of the proportion of the airborne population accumulating in wind convergence lines and the search effort required to locate the resulting concentrations, based on observations for a number of localities and years, are generally discouraging, although high variability between sites and seasons (table 1) leaves room for optimism that the technique might be practicable in particular areas, e.g. the Tilemsi Valley in Mali.

Although a comparable series of radar observations exists for the agricultural zone of inland southeastern Australia, I have not yet subjected them to any comprehensive analysis. However, it is my impression that line concentrations in this region arise mainly from storm outflows or from deeply penetrating and katabatically reinforced sea-breezes. In terms of their suitability as targets, the latter have the advantage of being potentially predictable, of probably having a long (hundreds of kilometres) lateral extent, and, in marked contrast to outflows, of being associated with generally settled weather which presents few hazards to aircraft operation. On the other hand, in the more inland areas this type of disturbance does not arrive until around midnight, by which time the intensity of insect migration has often fallen well below its early evening peak. In any case, intense line-echoes with confirmed lateral extents of tens of kilometres occur perhaps only once per week on average in this region. Even when weaker or smaller-scale concentrations are included, the frequency of 'one to three times per night' recorded by Schaefer (1976) in his pioneering Australian observations has rarely been approached in subsequent studies. It therefore appears likely that conditions are no more favourable for routine convergence-zone spraying in southeastern Australia than they are in Mali.

Some more general observations about the practicability of this technique are made in my comments on Pedgley's paper (this symposium).

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M. E. IRWIN (*Agricultural and Economic Entomology*, *University of Illinois and Illinois Natural History Survey*, 607 *E. Peabody*, *Champaign*, *IL* 61820, *U.S.A.*) AND S. A. ISARD (*Department of Geography*, *University of Illinois*, 607 *S. Mathews*, *Urbana*, *IL* 61801, *U.S.A.*). Drs Riley and Reynolds described the use of radar for locating linear echo zones containing large concentrations of grasshoppers within the planetary boundary layer to initiate air-to-air chemical control. That Riley and Reynolds were unable affirm the potential of the technique because their calculations suggested low spatial concentrations and temporal difficulty in locating the zones of convergence, should not dissuade us from investigating this process further.

The inability to locate these zones of convergence and their associated linear echoes, according to Riley and Reynolds, is due to the length of time the zones remain active and their spatial distribution over the Sahel. This points to a considerable knowledge gap concerning the modelling of the planetary boundary layer and to our lack of sufficient instrumentation to detect these zones early during their short-lived existences. One can only wonder if finding these zones might be easier over areas such as the southwestern deserts of North America, a region with a more extensive and intensive meteorological grid.

Riley and Reynolds broached a crucial issue facing our understanding of the dynamics of insect migration. A conceptual model of insect migration often divides the migratory event into three equally important components: take-off and ascent, horizontal translation, and flight termination and descent (Hendrie *et al.* 1986). Riley and Reynolds focus on the horizontal translation components which dictate flight pathways and, consequently, an insect's destination. Several analytical methods have been developed to estimate source regions and pathways of migrating insects in the planetary boundary layer (Scott and Achtemeier 1987). Further improvement of these techniques to forecast the long-distance movement of insects requires the identification of factors that govern the vertical distribution of insects in the planetary boundary layer (Isard *et al.* 1990).

Observations by Riley & Reynolds of grasshopper concentrations in cold air outflows from rain storms, possibly associated with gravity currents, also implicates meteorological factors in the descent component of migration, perhaps the most difficult phase to investigate, and thus understand and predict. In other papers, zones of convergence have been associated with flight termination and descent of insects (Rainey 1976, Schaefer 1976, Pedgley 1982). Other observations suggest that a similar phenomenon is associated with flight termination and descent of weakly flying insects such as aphids (Irwin & Thresh 1988). Thus, an important working hypothesis governing the descent component of migration has been formulated, one that demands rigorous testing. If the hypothesis withstands these tests, the emerging principle will permit a much greater degree of predictability concerning migratory insect descent, something that is sorely lacking in our current abilities to forecast migratory episodes.

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