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Dispersal and redistribution of some Orthoptera and Lepidoptera by flight[1]

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Multidisciplinary research, successively on the Desert Locust, the African armyworm and the spruce budworm in particular, has established for each pest:

(1) flight on scales of regularity, density, duration and distance substantially greater than had previously been envisaged, and resulting in -

(2) dispersal which is not random but is very significantly geographically patterned, in a manner which is dominated by the interaction of wind-systems and the flight-behaviour of the insects, so that -

(3) these geographical patterns of dispersal characteristically include concentration, in convergent wind-systems, to give high population-densities which are of major importance in the population dynamics of the pests and in the incidence of damage.

DESERT LOCUST (*Schistocerca gregaria* FORSK., Acrididae)

The Desert Locust of the Bible remains, in 1978, one of the most serious problems of pest management facing the governments of some forty countries of Africa and south-western Asia; and some of the resources and facilities made available to meet the seriousness of this problem have helped to provide findings of general entomological significance. Thus early aircraft reconnaissance for flying swarms not only located targets for spraying operations (and furthermore made it possible to estimate the extent of the shortfall of particular control campaigns - RAINEY *et al.,* 1979); such air reconnaissance, by providing successive day-to-day and often hour-to-hour fixes of the positions of individual swarms, demonstrated how closely the direction of displacement of each swarm was that of the wind in which it flew (RAINEY, 1963), and changed with the wind-direction (fig. 1). Displacement with the wind means, in general and on balance, movement towards and with zones of wind-convergence (areas into which there is a net excess of inflowing air, and above which air accordingly rises). Examples of such zones are provided by most depressions (and particularly by their frontal systems), and by the intertropical convergence zone (ITCZ), a permanent feature of the global atmospheric circulation at which winds from the northern hemisphere meet winds from the southern hemisphere. Fig. 2 (top) illustrates movements of swarms into the ITCZ, in its early summer position across Africa at about 15°N. and through northern India, both with northerly winds from breeding areas in north-western Africa and the Middle East, and with SW monsoon winds up the Somali peninsula; see also fig. 3. Such movements of airborne insects into zones of wind-convergence can be ecologically highly significant in two respects. The first is

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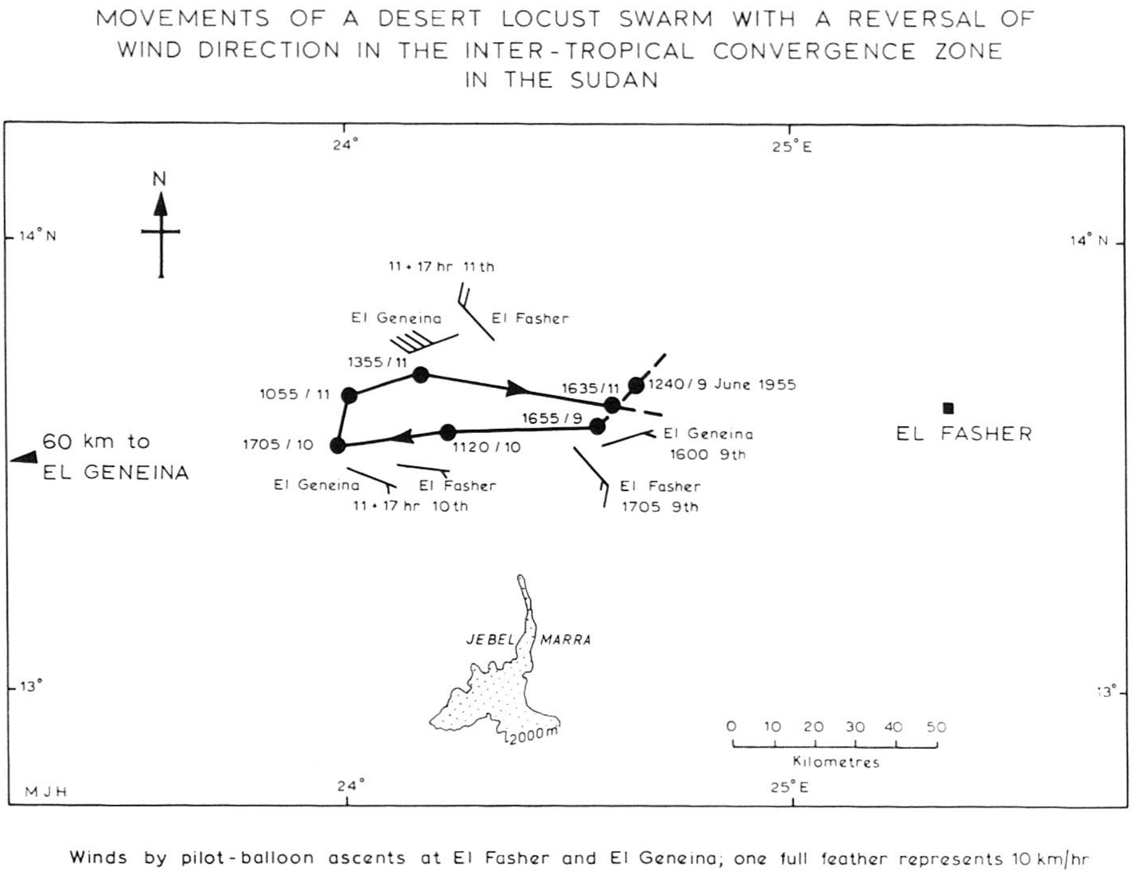

Fig. 1: Successive fixes of a single swarm, at times and dates indicated, showing how direction of displacement of swarm changed with changing winds, and illustrating antithesis of earlier definition of migration as displacement under the control of the animal.

because wind-convergence is essential for the production of rain. Free soil-moisture is essential for the development of the locust egg; and down-wind displacement also enables flying locusts (and Sahel grasshoppers like *Aiolopus* and *Oedaleus)* to utilise the kinetic energy of the wind-systems to locate and exploit the ephemeral but often extensive vegetation which follows the occasional rains in these arid regions. The survival value of such down-wind displacement may indeed be relevant to the evolutionary origin of flight itself. Secondly, airborne insects constrained against continued ascent, e.g. by effects of air temperature in limiting flight activity, are concentrated by wind-convergence, in a manner readily considered quantitatively, and indeed at rates which may double population densities in periods of the order of an hour over areas of hundreds of km^2 (RAINEY, 1976). There is now evidence that other insects besides locusts are from time to time concentrated in flight, by wind-convergence, to densities comparable with those in locust swarms; locusts however differ from these other insects in the extended periods (sometimes of weeks) over which their high densities can be maintained, by gregarious behaviour, in coherent travelling swarms.

AFRICAN ARMYWORM *(Spodoptera exempta* WALK., Noctuidae)

This is another migrant pest, whose attacks on cereals and grazing in southern and eastern Africa and south-western Arabia at times approach the severity of major locust invasions. A typical sequence of heavy attacks began with infestations being reported in Malawi and Rhodesia in October 1976, and in the course of the following nine months (and about nine generations) extended for some 2500 km northwards across Tanzania, Kenya, Ethiopia and the Yemen Arab Republic (RAINEY, 1979). Integrating the information provided by all available field reports of larval infestations with that given by the corresponding nightly

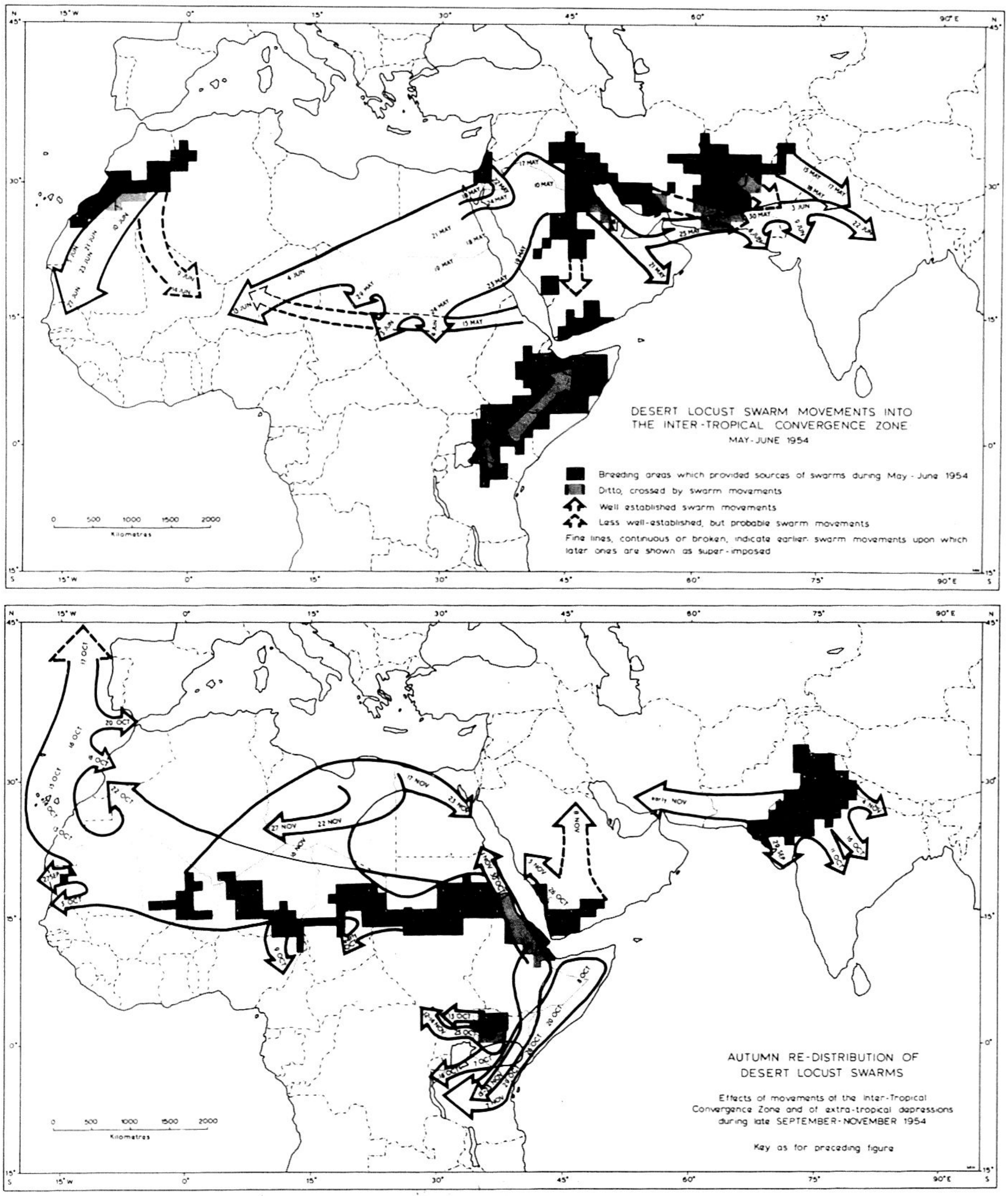

Fig. 2: Major Desert Locust migrations 1954; deductions from day-by-day analysis of locust reports and corresponding meteorological data, illustrating geographically-patterned dispersal. As in most years, there were two main periods of extensive migration, as shown, with the intervening months characterised by extended periods of effectively static locust distribution, attribuable to effects of wind systems and of limiting temperatures.

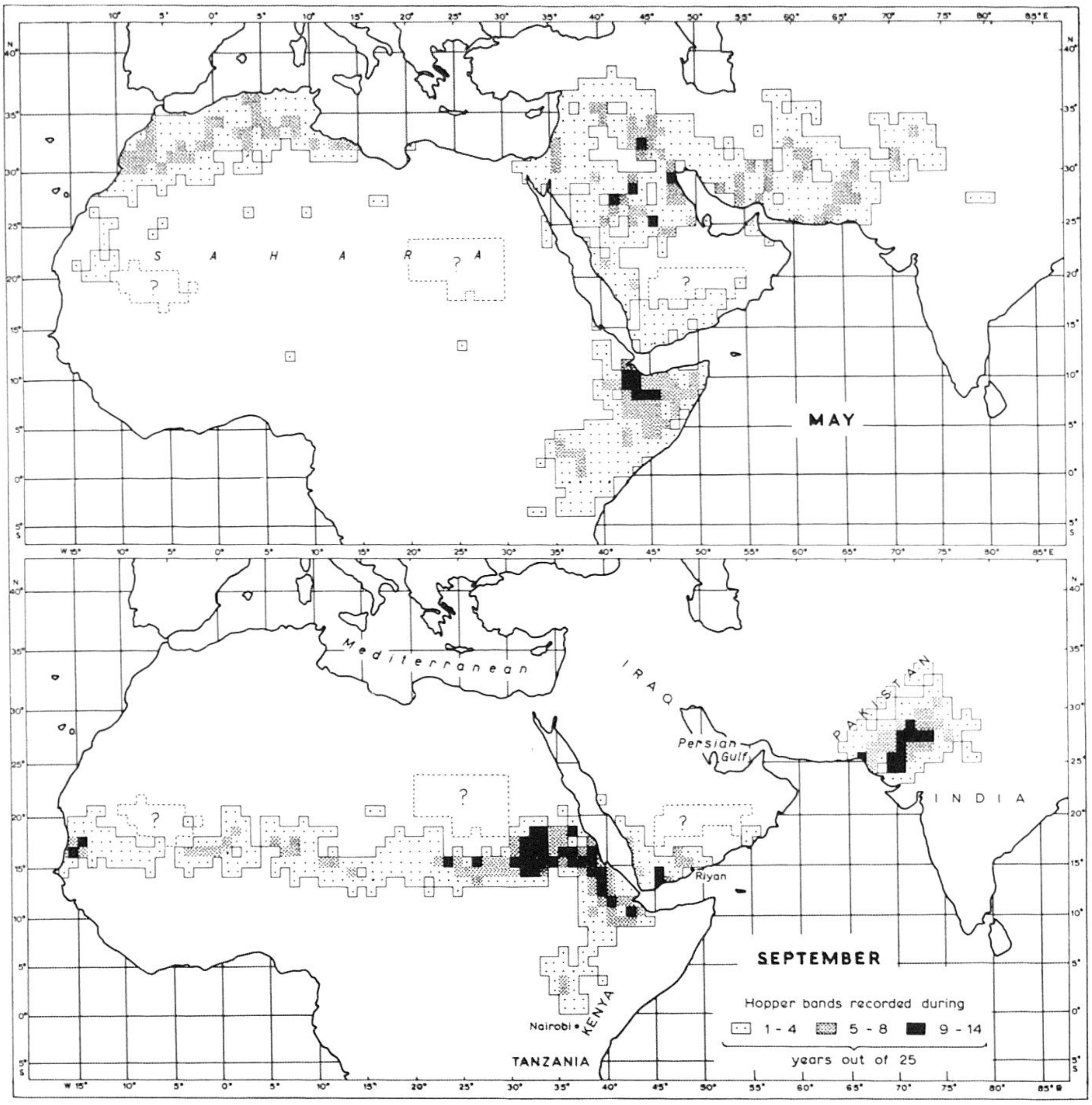

Fig. 3: Contrasted seasonal breeding-areas of the Desert Locust, shown by number of years in which bands of nymphs were reported in each degree-square during two representative months (? = area where reports largely or wholly lacking). Seasonal breeding-areas are areas and seasons of rainfall - e.g. winter-spring in N.W. Africa; summer south of the Sahara. The differing seasonal breeding-areas are connected by quasi-regular patterns of seasonal migration as in fig. 2.

catches of *exempta* moths at an international network of light-traps (and, since 1975, of pheromone traps - CAMPION *et al.,* 1976), by techniques of mapping and analysis based on those developed for Desert Locust forecasting, has likewise provided detailed evidence of seasonal patterns of long-range migration (BROWN *et al.,* 1969) and of comparable effects of wind-systems, illustrated by fig. 4 (HAGGIS, 1971). On this particular occasion the moths had been concentrated by the wind-convergence to a spacing averaging little more than 2 m apart (RAINEY, 1976). Similar concentration by convergence at a wind-shift has been repeatedly observed with other species in the ITCZ in the Sudan, most strikingly by radar, with moths (including *Spodoptera littoralis)* at high densities giving a line-echo a few hundred metres wide and many kilometres long (SCHAEFER, 1976).

SPRUCE BUDWORM *(Choristoneura fumiferana* CLEM., Tortricidae)

Destruction of mature softwood forest by defoliation by the spruce budworm can have major consequences for the economy and employment of regions of North America which are highly dependent on the forest industry. The crucial importance of flight activity in relation to the management of this pest (recognised with the help of the simulation modelling study reported by CLARK (1979) and also by SANDERS (1979), led to four seasons of intensive field research by the Canadian Forestry Service, with the support of the New Brunswick Department of Natural Resources, using radar and specially-instrumented aircraft (GREENBANK *et al.*, in press).

The earlier results of this programme are illustrated in fig. 5, showing how, with a DC-3 aircraft using Doppler navigation and precision wind-finding equipment, it was possible to locate and explore a meteorological front, subsequently

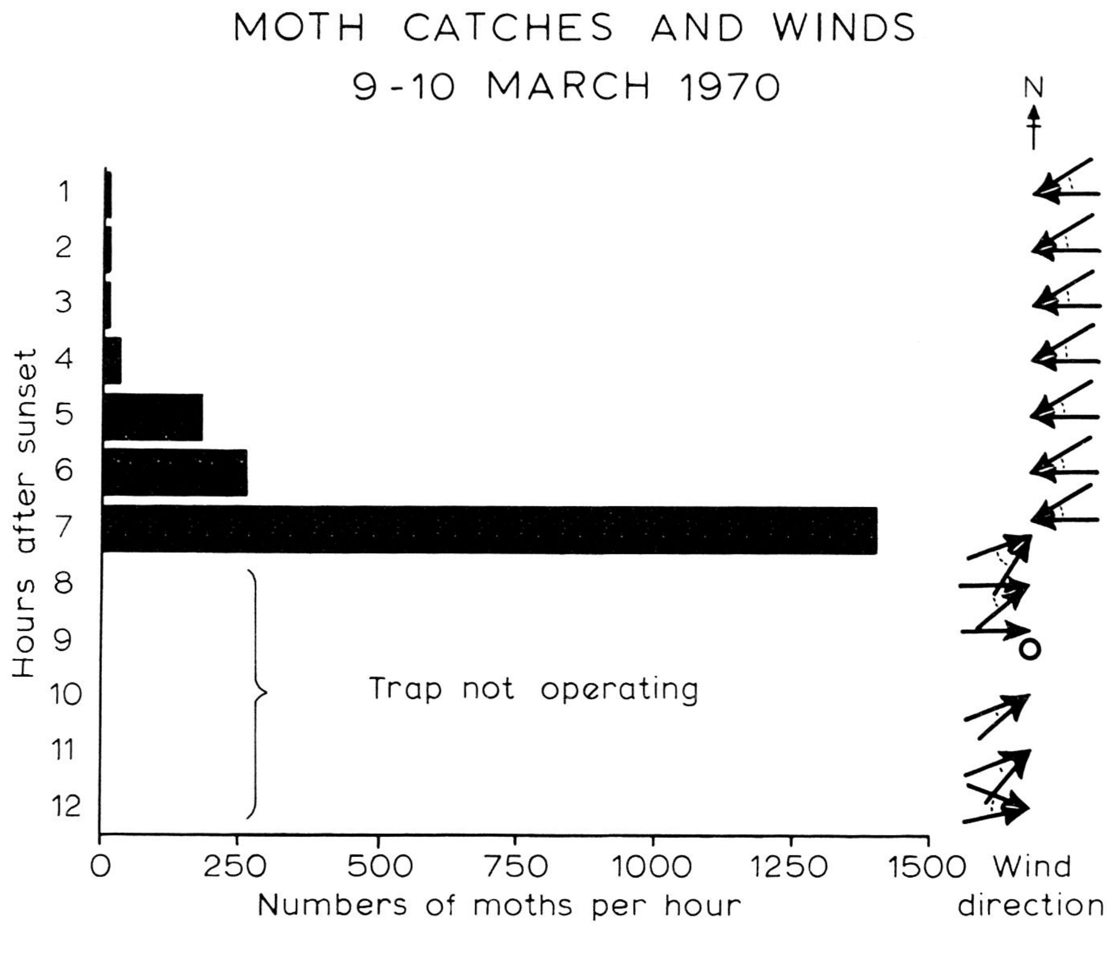

Fig. 4: Hourly catches of *Spodoptera exempta* in an automatic light-trap near Nairobi, Kenya, with a wind-shift representing the passage of the African Rift convergence zone; mechanism failed under overload after 7th hour (HAGGIS, 1971).

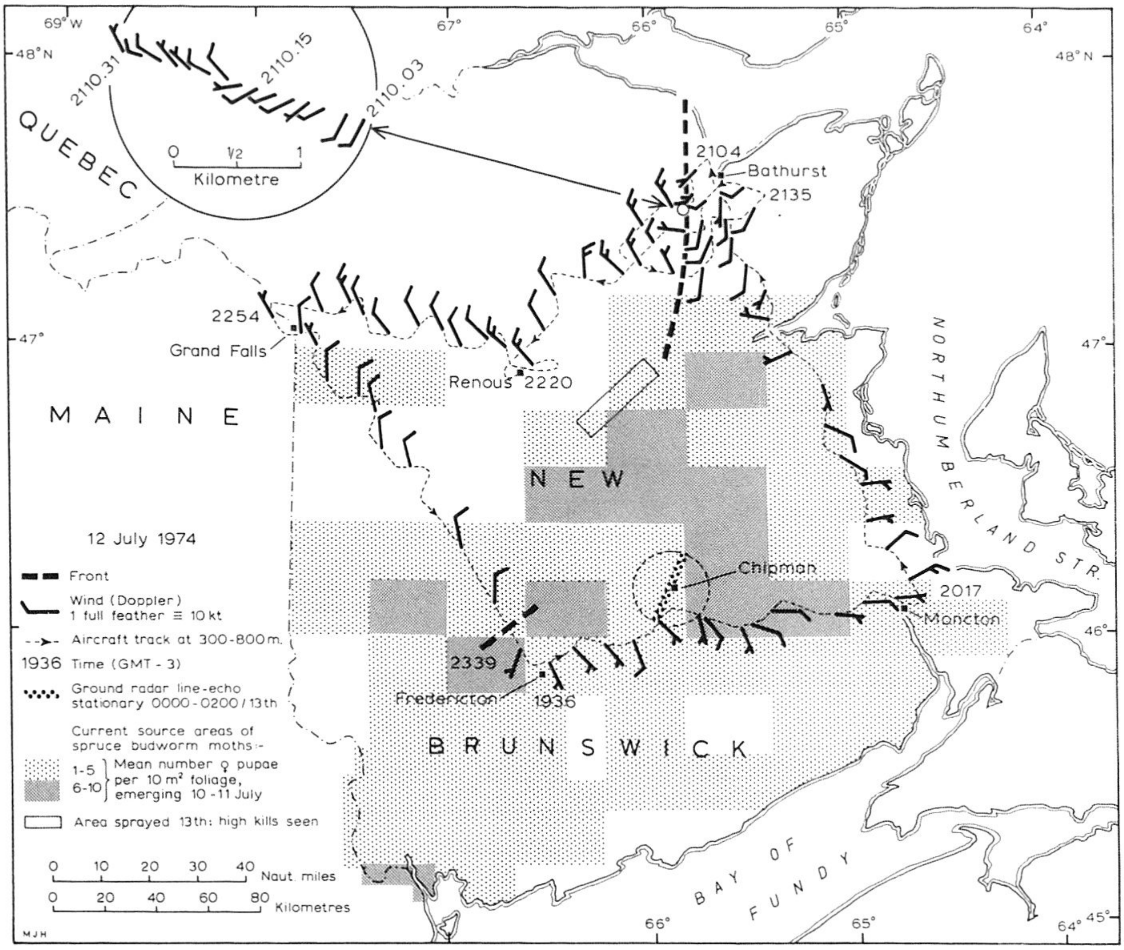

Fig. 5: Spruce budworm moth concentration in zone of wind-convergence; integrated findings from specially instrumented aircraft, ground-based radar, province-wide field survey, and assessment of large-scale spray trials.

elucidated by Professor R.B.B. Dickison, and marked by a very sharply defined wind-shift (see traverse shown enlarged in the inset). This was found to be associated with wind-convergence of an intensity implying, on the simplest of assumptions, concentration at rates giving more than ten-fold hourly increases in the area densities of flying moths. At Chipman a radar line-echo, representing in all probability another part of the same feature, aligned NNE/SSW and visible on the ground radar for a length of 30 km, was recognised independently by Professor G.W. Schaefer, and confirmed as due to spruce budworm moths at high density by aircraft trapping by a Cessna 185 from Chipman at 90–300 m from 2033 to 0025 the same night. This same concentration of moths, envisaged as having settled later in the night not far from the line of the front as found from the DC-3 and seen on the radar, may also be suggested as having accounted for the specially high moth kills (up to 60 moths/m^2) which were recorded in the particular block indicated by the rectangle SE of Renous, following large-scale aircraft spraying operations against settled moths next day. Fig. 5 also summarises the detailed evidence available on the source-areas of the moths in the airborne concentration, provided by the routine pupal survey counts at a thousand sampling points in New Brunswick (weighted by the area of susceptible forest within each 200 km^2 unit),

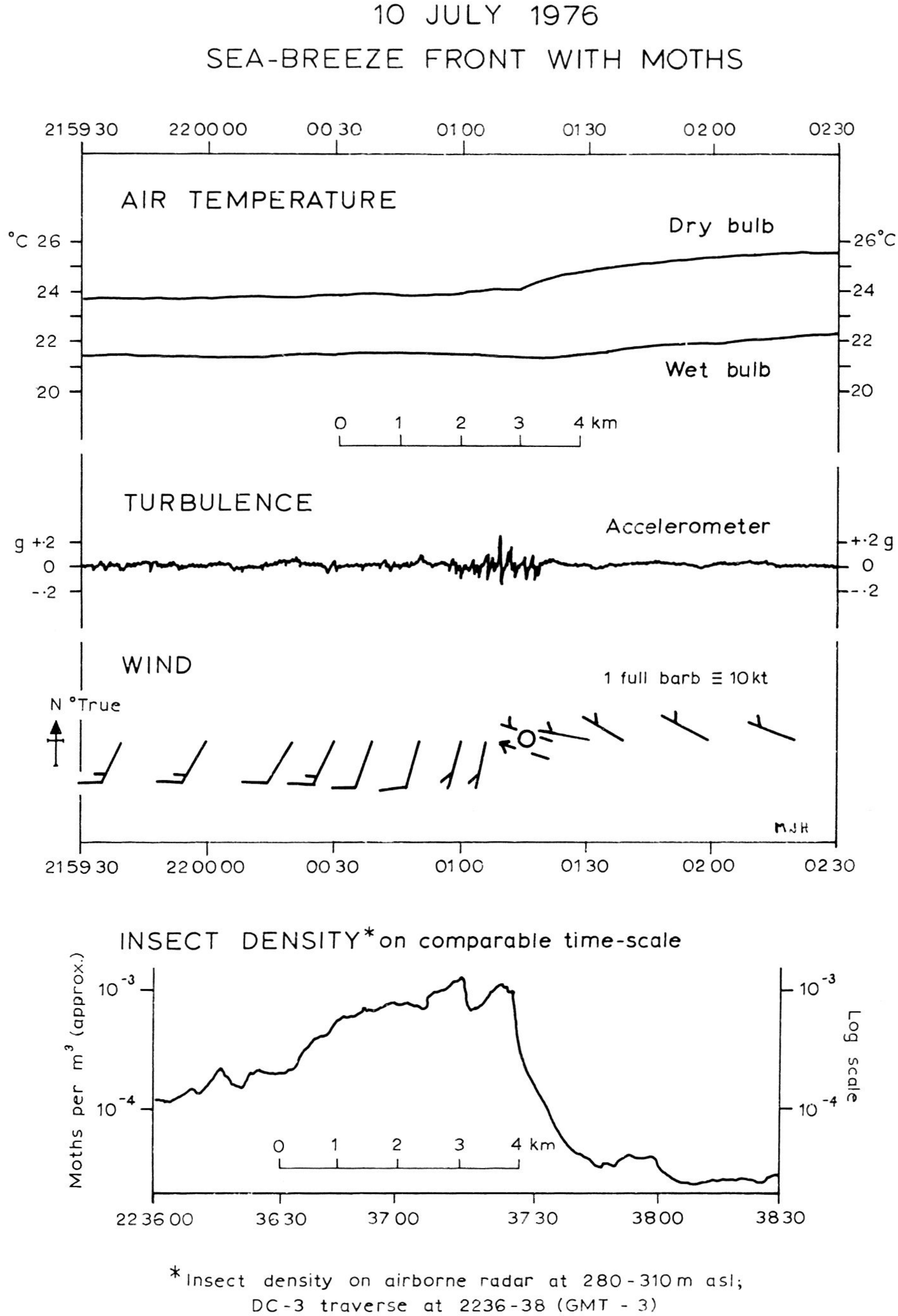

Fig. 6: Air temperature, humidity, turbulence and wind measured from DC-3 while traversing sea-breeze front, together with absolute moth density recorded by airborne radar while subsequently overflying front in same direction.

and by the emergence data of the current season for each of the seven phenological zones covering the province.

The logical next step was the development of a downward-looking airborne insect-detecting radar (SCHAEFER, 1979) and its use in an aircraft equipped for wind-finding and for recording other meteorological factors as well as for insect-sampling, with results illustrated in fig. 6. This shows some of our observations on the concentration of spruce budworm moths by convergence at the wind-shift where a cool sea-breeze from the Bay of Fundy was meeting the warmer and drier inland air. It epitomises the approach which began with locust control, and illustrates the proven techniques now available for systematically seeking, locating, assessing and potentially attacking the wind-formed airborne concentrations of a number of major insect pests.

ACKNOWLEDGEMENTS

I am most grateful to Dr. WERNER BALTENSWEILER, to ETH and to the Royal Society of London for the opportunity of participating in this meeting, which also provides an appropriate occasion for emphasising how much the development of this approach, using specially-instrumented aircraft and radar, has owed to the initiative of Professor R.J.V. JOYCE and to the backing of Ciba-Geigy Ltd., and to the continuing support of Dr. F.E. WEBB, who was indeed primarily responsible for introducing the use of radar into forest entomology.

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