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The Decline of the Desert Locust Plague in the 1960s: Control Operations or Natural Causes? [and Discussion]

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The decline of the Desert Locust plague in the 1960s: control operations or natural causes?

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The very limited Desert Locust infestations of most years since 1963 have been in striking contrast with the massive attacks experienced up to that time, which were clearly (and often admittedly) beyond the control of the organizations concerned in one or more countries in, for example, every one of the 23 years from 1940 to 1962. Attempting to assess possible effects of control measures on the development of the overall Desert Locust situation, relative to those of natural causes, poses formidable problems. However, new control techniques were deployed on unprecedented scales in particular series of locust campaigns during the early 1960s. Detailed monitoring and mapping of the overall Desert Locust situation provided circumstantial evidence of the probable impact of these campaigns. Further circumstantial evidence of the effects of these developments in methods and organization was provided by the short-lived locust upsurges of 1964 and 1967–8.

1. Introduction

We come now to the crucial question of whether control operations have or have not had any significant effect on the continuing development of the overall Desert Locust situation, apart from any immediate value particular campaigns may have had for the local defence of crops. The same basic question has already been discussed in relation to *Quelea* (Ward, this symposium), and for the Desert Locust opinion is still more sharply divided. Within the past few months, one authoritative viewpoint has reached the text books, implying an answer emphatically in the negative (Uvarov 1977). At the other extreme, the view is sometimes expressed that control methods are now so effective that locusts are no longer a problem. Much of the evidence on this point certainly remains incomplete and circumstantial, and the assessment of the overall results of such control measures presents formidable difficulties.

Thus any assessment of this kind must necessarily involve in the first place some consideration of the natural dynamics of locust populations at times exceeding 10^{11} individuals (and probably rarely totalling as few as 10^8) and, moreover, in almost continuous movement over a total area three times the size of all Europe at speeds up to several thousand kilometres per month. In the second place such an assessment involves corresponding consideration of the mortality to be expected from the scale and nature of control operations, which may be undertaken in more than 40 countries subject to invasion. The magnitude of both these technical problems has at times been considerably underestimated (Bennett & Symmons 1972; Bennett 1976) and the nature of the evidence available (limitations as well as potentialities) is accordingly considered in some detail. Very fortunately, two of the very rare situations in which reasonably valid and comprehensive estimates of the total number and size of the swarms in a particular region have been possible, have proved to be directly relevant to the question of overall adequacy of control. The first provided estimates, even if very approximate, of the shortfall of the control operations undertaken against the swarms which invaded East Africa in early 1954 and against the breeding which had produced them; the second enabled this estimate to be compared and contrasted with the later scales of invasion and of much more intensive control operations in a strategically crucial area of Morocco in 1960–1.

2. Nature of evidence available: scope and limitations

As just indicated, any study of the population dynamics of *S. gregaria* – whether or not concerned with the effects of control – faces problems differing in kind as well as scale from those presented by the populations of almost any other insect so far studied. Even for some other locusts (e.g. *Nomadacris septemfasciata* Serv., the Red Locust of central and southern Africa) it has been shown that the most important populations of the species can remain for many years restricted to the same few thousands of square kilometres of 'outbreak areas'; in addition, most of the locusts within these areas are commonly sufficiently dispersed to allow satisfactory quantitative estimates of the total numbers, by using appropriately standardized procedures of counting the locusts seen to be flushed along linear traverses (Scheepers & Gunn 1958). This is very rarely if ever true of the main populations of the Desert Locust. Not only are these so often (Rainey & Betts, this symposium) in concentrations which are individually both too dense and much too mobile (over areas of tens of millions of square kilometres) to offer any hope of assessment in this manner; even seemingly static, solitary-living populations of this species have been found to show apparently regular flights by night (Waloff 1963*a*), foreshadowing later radar evidence to a similar effect (Schaefer 1976).

It has never yet been possible to establish valid estimates of the total numbers of locusts present at the same stage of two successive generations of any self-contained population of *S. gregaria*, primarily because of the mobility of the adult stage: as well as of its duration, at times exceeding six months in the field and up to 27 months in the laboratory (Rungs 1961).

The mobility characteristic of the populations with which control organizations somewhere or other have been forced to be concerned in every year can be illustrated by records of the breeding of three successive generations during 1951–2, which were first in the Somali Peninsula, next in the Near East, and then on the southern fringes of the Sahara. On a time scale of the order of years (as is necessary for envisaging any overall effect of control measures), nothing less than the entire invasion area can be confidently considered as a completely self contained unit.

(*a*) *Locust numbers in swarms*

Dr Gunn has described in his first paper in this symposium (§§8 and 9) how he and his colleagues took the crucial first steps towards the quantitative assessment both of *Schistocerca* numbers and of the results of control, in Kenya in 1945 (Gunn *et al.* 1948*a*, *c*). Air and ground reconnaissance were used, systematically and critically, to establish and maintain contact with swarms and to assess their area, and objective photographic methods were introduced for the estimation of the densities and, in turn, the numbers of locusts in these swarms. Furthermore, direct counts of the total numbers of locusts killed by the application of a known amount of insecticide in actual control operations in the field were made for the first time.

In following up this earlier work, it was confirmed during the 1950s that the continued cohesion of individual swarms could make it possible to distinguish and follow them by aircraft for periods of a week or more, as Gunn and his colleagues had first done in 1945. Moreover, these subsequent observations provided unexpected evidence (e.g. in fig. 1) of the maintenance

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of approximately constant plan area, not only from day to day (such as one swarm which maintained an area of some 60 km² over a period of 9 days during a displacement of 370 km across south Kenya), but also with swarms both settled and in flight – even travelling with the speed of the wind and with the topmost locusts more than 1000 m above the ground (Rainey 1958*a*, 1963*a*), incidentally posing some challenging questions of behaviour. Furthermore, direct determinations of the area density of locusts in settled swarms, by Gunn's drench-spraying method (§ 9), provided figures which were roughly similar for several different swarms (one in Kenya in 1955 and others in northern Somalia in 1957: McDonald 1955; MacCuaig 1958; Rainey 1958*b*), with averages of about 50 locusts per square metre. This figure was moreover broadly comparable with more extensive, mainly photographic data on volume density and heights of flight (Waloff 1972) in flying swarms, which as usual also included temporarily-settled locusts. Thus particular aspects of the same gregarious flight behaviour which renders most of the usual techniques for enumerating insect populations so patently inappropriate, can in fact operate to make the overall assessment of *Schistocerca* numbers less intractable, by suggesting a useful relation between swarm size and locust numbers.

The degree of constancy thus suggested for area density as well as for plan area led to the convenient approximation that, for order of magnitude considerations, equal areas of swarm may be envisaged as containing equal numbers of locusts, over a range of conditions which is usefully wide. However, these conditions exclude high winds (exceeding the air speeds of which locusts are capable), in which swarm cohesion has been observed to break down, for example during June–August in northern Somalia, and perhaps also the special conditions (intense mesoscale convergence?) in which locusts have been observed in particularly high densities in settled swarms in rugged topography in the Kenya highlands (Gunn *et al.* 1948*c*; Stephenson 1947).

The problem of assessing the total locust numbers in a swarm invasion can thus be resolved into that of estimating the number and size of the swarms present. Valid estimates of swarm numbers and size have however been found to demand a combination not only of exceptional facilities, such as reconnaissance aircraft in sufficient numbers, but also of particular conditions, of swarm behaviour, winds and weather.

The first such occasion followed the very heavy 'short rains' breeding in the Somali peninsula in October–November 1953. This had been sufficiently synchronous (Carlisle, Ellis & Betts 1965) and (although extending over some 850000 km²) sufficiently limited in its distribution relative to the 3½ million km² of the whole eastern African region subject to Desert Locust invasion, to enable an air reconnaissance programme to be planned some weeks ahead, on a biogeographical basis (see § 2*e*), to intercept almost all the resulting swarms in the course of their quasi-regular seasonal migration out of this breeding area down the northeast monsoon, into Kenya and some of them into Tanzania. The leading locusts were intercepted during air reconnaissance flights between Mandera, Bardera and Dugiuma (figure 1), as the locusts approached the Juba river in Somalia, on 24 December 1953, the day after the reconnaissance programme was begun; and during the period 1–18 January 1954, for example, swarms were sighted from 11 aircraft on a total of 326 occasions within the area 3° N to 1° S, 38° to 42° E.

Detailed analysis was begun by large-scale plotting of the tracks of those swarms with which contact had been maintained sufficiently continuously to obviate any risk of confusion with other swarms. This analysis showed swarm displacements, e.g. in figure 1, towards directions which were consistently between northwesterly and southwesterly, in winds respectively between southeasterly and northeasterly. Then use was made of the manner in which, in the quasi-uniform windfields characteristic of the fair weather experienced during these and earlier observations, neighbouring swarms had been found to follow closely parallel tracks as, e.g. in figs 8 and 9 in Rainey (1963*a*) and fig. 5.1 in Rainey (1971). In this way sightings of other swarms made over longer time intervals could be connected; this was done in such a way as to infer the minimum number of swarms needed to account for the total number of sightings,

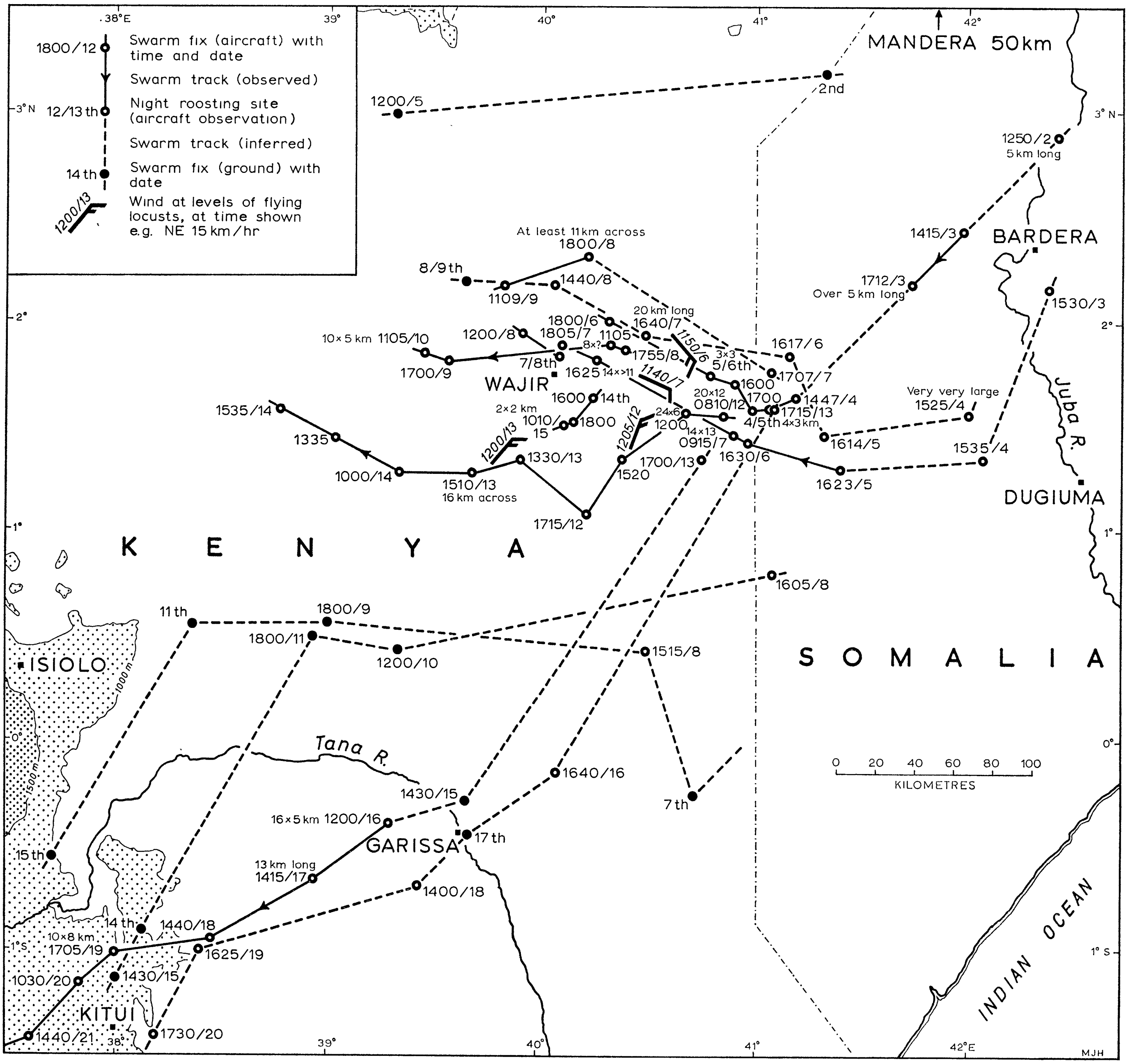

FIGURE 1. Towards the assessment of a locust invasion: some swarm tracks observed and inferred for 2–21 January 1954. Winds from pilot balloon observations at Wajir, averaged vectorially up to the height of the topmost locusts. Further details from Rainey (1963*a*, 1971).

from ground as well as air. This procedure demonstrated the passage across this particular area during this period of at least 28 individual swarms, travelling at 30 to 100 km per day; figure 1, for clarity, shows the tracks of only twelve of these swarms.

A further coincidence of favourable circumstances, in addition to those already mentioned, enabled this analysis to be extended to an assessment of the complete invasion of Kenya during January and early February 1954, found to total some fifty swarms. These circumstances included the fair weather, and the flat and featureless terrain over which the large, high-flying swarms comprising the greater part of the locust population of the region were seen on the regular afternoon reconnaissance flights, at a median sighting distance of 32 km, corresponding to an effective rate of search of 9600 km^2/h. Such observations contrast strikingly with the effective rates of search of the order of a few hundred km^2/h given by subsequent experience of air, reconnaissance for small, low-flying swarms in broken terrain and unsettled weather elsewhere in eastern Africa (Rainey 1963*b* and unpublished). Furthermore, in eastern Africa in early 1954, air reconnaissance was undertaken on a scale (largely made possible by four additional aircraft provided by FAO through the good offices of the late O. B. Lean) previously quite unprecedented and rarely if ever approached subsequently.

The inherent limitations of the more usual ground reports are illustrated by the fact that for the same area and period (1–18 January 1954), the administration, local population and ground locust control staff (which still represent the only sources of swarm reports in many areas), provided in this case a total of 18 reports of swarms. Sixteen or seventeen of these reports were found to relate to 9 or 10 of the swarms followed by the aircraft; one ground report could not be related to any swarm seen from the air. It is possible that some ground witnesses may have regarded further reports as unnecessary in the presence of the aircraft; and eight additional ground reports, relating to a further six of these swarms, were provided by mobile research parties directed from the aircraft. There remained however 12 swarms shown by the aircraft reports to have traversed this area (which was some 440 × 450 km in extent) without having been reported from the ground at all. As H. J. Sayer had noted during the first air searches for swarms in northern Somalia, in 1953, no refinement of processing of the ground reports alone could have established how many different swarms even these sightings related to – nor, of course, could these reports have provided evidence on the swarms which were not seen at all from the ground.

Even the much more densely inhabited area around Delhi (headquarters moreover of a large and particularly experienced locust control organization) has provided striking evidence to the same effect; Venkatesh (1976) has pointed out, from radar evidence which was available on one particular occasion (see also § 3*b*), how the combined corresponding swarm reports from all the usual sources, though numerous, missed at least half the total area of the swarms seen on the radar.

In addition to establishing, as already indicated, the total number of swarms entering Kenya in early 1954, the air reconnaissance observations provided direct determinations of the area of most of the individual swarms, from timed traverses and the groundspeed of the aircraft (reducing the product of length and breadth by a factor of $\frac{1}{4}\pi$ to allow approximately for a roughly elliptical plan-form). Different individual swarms recorded in this way have been found to vary in size by four orders of magnitude, ranging from a few hectares to several hundred square kilometres, so that mere number of swarms, even if known, provides in itself no useful index of the scale of an invasion. As already illustrated, individual swarms measured in this way showed a marked consistency of plan area; and, on occasion, confirmatory evidence of the area of a swarm was provided by the distribution of dead locusts on a roosting site given by the overnight kills resulting from delayed action of limited quantities of insecticide applied to the swarm in flight the previous day. Thus, for example, one swarm near Mtito Andei in Kenya which covered 24 km^2 in flight on 10 February 1955 was found, by further air traverses combined with subsequent ground assessments of dead locusts, to cover 20 km^2 when settled overnight near Maktau on 12–13th (MacDonald 1955; Rainey 1958*b*, 1976 fig. 5.3).

The 50 swarms which invaded Kenya in early 1954 were estimated in this way from the air reconnaissance observations and probably to within about 10%, to cover a total area of approximately 1000 km^2 (initially estimated as 1300 km^2 (Rainey 1954)), with the biggest single swarm covering 200 km^2, and the five largest, which all probably passed into southern Ethiopia, totalling 700 km^2. Experience has demonstrated on the other hand the very great difficulty of obtaining from ground observations, however carefully made, any useful estimate of the size of a flying swarm. Thus for example even to ground parties of experienced observers the 20–24 km^2 swarm of 10–13 February 1955 (see above) was not noticeably larger than several others of about one-tenth its area, mainly because the larger swarm was travelling at a ground speed several times faster than those of the smaller ones, so that there was relatively little difference in the times the swarms took to pass. On another occasion, near Wajir on 14 January 1954, a flying swarm was measured by a mobile ground party as extending for 11 km along a straight road, while aircraft observations at the same time showed that the swarm was in fact about 3 km long, but also that it was travelling at the time in a direction and at a speed sufficiently comparable with those of the ground party to account for the latter's inadvertent overestimate of the length of the swarm. Such are the difficulties encountered even by specialist field parties in estimating swarm size from the ground. Clearly the records of the chance observers who provide the majority of routine swarm reports are still less likely to provide useful evidence on swarm size; the virtual impossibility of deriving swarm numbers from ground reports has already been indicated; and these difficulties must invalidate attempts at quantitative treatment in which they have been overlooked.

Finally, the figure of 1000 km^2 obtained as an estimate of the total area of the swarms which entered Kenya and Tanzania in early 1954 – representing certainly most if not all of the Desert Locust population in the eastern African region south of 5° N (an area of 1.8×10^6 km^2) corresponds, at the density of 50 locusts per square metre of swarm indicated as a probably representative figure by the various lines of evidence (spray-assessment, photography and radar) already mentioned, to total numbers of some 5×10^{10} locusts, about 10^5 tonnes. This approach made it possible to attempt, for the first time, some assessment (Rainey 1954) of the extent to which the control measures undertaken against these locusts, from ground and air, are likely to have fallen short of complete control. A fuller treatment of this crucial point is undertaken below (§ 2*d*), but consideration will first be given to the nature of the evidence so far available on other aspects of the natural population dynamics of the species.

(*b*) *Other evidence on Desert Locust numbers*

For Desert Locust numbers in populations other than adult swarms, data have never been sufficiently extensive and representative to provide any corresponding order-of-magnitude figure for total locust numbers in such populations for the whole of a particular country

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or region, comparable with the figure just given for the swarms in eastern Africa in early 1954.

Thus for the egg stage systematic sampling for egg-pods has provided figures for the number of eggs in parts of egg-fields, up to 0.15 km² on one occasion (Stower, Popov & Greathead 1958). Tentative estimates of the number of layings per female have been made by Popov (1958).

Again, for the nymphal stage data are available (Ashall & Ellis 1962) on the number of locusts in individual hooper bands, ranging from 8000 to 500000, at different instars and for a range of band sizes, but it has never been practicable to mount searches sufficiently exhaustive to provide valid estimates of the total number and sizes of all the bands comprising even a single contemporaneous infestation.

For low-density populations, not in swarms or bands, marking/recapture provided valid estimates of total locust numbers in one area of 3 km² on the Eritrean coast (Waloff 1963*a*), together with striking evidence of the degree of night-to-night mobility of these populations. Counts of flushed locusts seen on linear sampling traverses have been very widely recorded since the pioneer work of Rao (1942), though only very rarely (Waloff 1963*b*) with any calibration of such counts in terms of absolute area-densities. Such counts have nevertheless been used as a basis for estimates of total numbers in such Desert Locust populations, moreover without taking account either of the degree of mobility and hence of nightly redistribution to be expected of this species, or of the intensity of sampling (1 km of meticulous counts of Red Locusts per 5 km²) found necessary even in the much less heterogenous habitats of the Rukwa flood plains. (Scheepers & Gunn 1958; Symmons, Dean & Stortenbeker 1963).

(*c*) *Effects of natural enemies*

Extended specialist field investigations of the effects of natural enemies were first undertaken during the 1950s, in five different countries (Greathead 1962, 1966*a*, 1966*b*). While percentage of infestation is of course not the whole story, the most important insect natural enemy of the Desert Locust in eastern Africa, the Muscid egg-predator *Stomorhina*, was for example found to exceed the 50% level of infestation only in one out of the 57 egg-fields studied (Greathead 1962).

Several quantitative estimates of field mortality in the egg stage have been made (Stower, Popov & Greathead 1958) and estimates of nymphal mortality have occasionally been attempted (Stower & Greathead 1969). Stevenson (1959) undertook field trials of pathogenic bacteria against the nymphs.

Natural enemies subsequently received particular attention during the energetic field work of the well equipped FAO Desert Locust Ecological Survey between 1958 and 1964, in 15 different countries from Senegal in the west to India in the east. Reporting on this work, and after reviewing all other evidence available on this point, it was concluded that in general 'the overall effect of natural enemies as regulators of locust populations is probably rather small in comparison with meteorological and other factors' (Popov 1965).

Biogeographical studies also have directed attention to the movement of groups of swarms from time to time into a series of areas, such as south-eastern India, the Congo, Burundi, Uganda, the southern Sudan, and eastern Nigeria, in which invading swarms can appear to die off without issue (Rainey 1963*a*). All these areas are characterized by rainfall substantially higher than that experienced in the more usual habitats of the species, providing conditions

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under which locusts might be expected to be more vulnerable to a number of natural enemies, including pathogenic fungi such as *Entomopthora* and *Metarrhizium*.

(*d*) *The scale of control efforts and assessment of locusts killed*

The need for assessments of numbers of locusts killed by control operations arose in the 1950s with the development of newer methods of locust control, some complementary and some potentially alternative to methods already in use on a large scale. This posed serious problems of comparative assessment of old and new methods, on a common quantitative basis which could provide an objective criterion for the allocation of resources between the different methods currently available (Rainey 1958*c*). With much of the control effort against the Desert Locust since the early 1940s deliberately undertaken hundreds of kilometres outside the crop areas threatened, on locust populations ranging in density from several thousands to less than one per square metre, the number of locusts killed was clearly a more appropriate measure of achievement than was, e.g. extent of infested area cleared. The comparative assessment of different methods and materials accordingly required estimates of the numbers of locusts killed per unit of insecticide, for which the first field figures can be derived from the data of Gunn *et al.* (1948*a*). This criterion led in turn to estimates of overall expenditure per unit kill, making possible for the first time objective comparisons of the economics of different control methods in the field; it also enabled field and laboratory results to be compared, showing the extent to which the potentialities of particular materials and methods were not realized under field conditions; and, finally, in conjunction with the evidence on locust numbers provided by the methods considered in the preceding section, it made possible a salutary comparison between the most that could be hoped from the scale and nature of the control measures then being undertaken and the scale of the infestations being attacked.

Thus in 1954 such quantitative field assessments were first made for poison-baiting, which was at that time the most widely used method of Desert Locust control. A stomach insecticide, usually γBHC or occasionally aldrin, was used at about 0.1% in a suitably attractive carrier such as wheat bran, crushed millet or rice husks, latterly applied dry (Gunn 1952) mainly against the nymphs, but also when opportunity offered against adults in settled swarms. Under favourable conditions, the efficiency of utilization of the insecticide in such baits was at times found to be remarkably high, in small-scale field tests in which the whole of the bait applied was seen to be consumed by the hoppers in a passing band; a kill of 34 kg third instar hoppers per gram of γBHC was observed in one of the first of these trials (Rainey 1958*c*), and kills of up to 20 kg fourth instar hoppers and up to 17 kg fifth instar hoppers per gram of γBHC have since been recorded (Ashall 1958). These kills correspond to field efficiencies as high as 30–40% of those obtained by the administration of the median lethal dosage in the laboratory (Goodhue 1962). Baiting was also well suited for use by unskilled local labour, and indeed provided temporary employment on a scale which in some important breeding areas such as the Ogaden, semi-arid and pastoral, was a major factor in securing and maintaining the co-operation of the local population.

Baiting has however two major shortcomings, and as a result has declined to a minor role in recent campaigns. Its first shortcoming was the very high cost of application, per unit of active ingredient (found for example to be as much as twenty times the corresponding cost of aircraft spraying in comparable campaigns), because of the cost of the bulky carrier (usually a valuable animal feed) and in particular of its transport, which could together account for more than half the overall costs of a typical campaign of this period. Furthermore, even apart from questions of cost, such transport problems often limited control campaigns in major breeding areas to a scale which as indicated below can now be recognized as inadequate.

The second major shortcoming of baiting was unreliability of action. Locusts at all stages refuse at times to feed on bait, both regularly, for a day or more, at each of their five moults, and also on other occasions, such as when the temperature of the soil surface appears to be too high for them. Furthermore, complete failures of baiting (i.e. no kill at all observed) have also been recorded on a number of occasions even when all the bait had been eaten, presumably in individually sub-lethal doses (Ashall 1958). Again, apart from these complete failures, the rates of kill, per unit of insecticide, found in these bait trials in the field varied by a factor of over 10000, even after allowing for differences in hopper size. A further cause of unreliability was loss of toxicity on exposure in the field, noted with γBHC 3 days after application.

The swarms which invaded Kenya in early 1954, and which probably comprised as already indicated some 5×10^{10} locusts, were in fact escapes from one of the largest-scale baiting campaigns undertaken in what is probably the most important breeding area in eastern Africa, in the Ogaden area of Ethiopia and neighbouring parts of the Somali peninsula in late 1953, on a scale which was considered at the time to have been not far short of the limits imposed by the communications and general administration of these areas. In order to have killed a further 5×10^{10} of the surviving hoppers in the fifth instar, assuming a rate of kill corresponding to the average result of the field tests undertaken on this instar (Ashall 1958), a further 5000 tons of bait would have been required, representing a threefold larger campaign, for a total of 2500 tons was actually applied. Furthermore, this 5000 ton estimate of shortfall assumes that the whole of this additional amount would have been applied without waste and completely consumed by the hoppers; in practice, rates of application of bait are always heavier than this, by a factor which may be anything between two or ten or more.

Consideration of baiting and its shortcomings, together with those of the conventional spraying machines of this period (particularly their lack of effective mobility), led to the development by H. J. Sayer and his colleagues of a new method for the direct application, to the sparse vegetation on which the hoppers are about to feed, of concentrated spray formulations of persistent stomach poisons at dosages in the vicinity of 300 ml per hectare. A gallon by Sayer's exhaust-nozzle sprayer has been found to give a kill comparable with that given by a ton of bait, while retaining some important advantages of baiting. This exhaust-nozzle spraying was the most widely used method of ground control employed in the 1967–8 upsurge, when it was used in ten countries (FAO 1968*a*), and it was again the main method in use against serious Desert Locust infestations e.g. on the Yemen Tihamah in February 1978 (Rainey 1979).

We turn now from the inadequacies of the most widely used of the locust control methods of the 1950s, baiting, on the ground, to the corresponding inadequacies of aerial methods of control at this period; in order to deal with the Ogaden/Somali escapes of late 1953, the scale of the experimental air operations which had been planned against them in Kenya was doubled at short notice by the charter of additional aircraft, raising the cost of air operations to something like 10% of the budget of the Desert Locust Control Organization. The pioneer work of Gunn and his colleagues some nine years earlier had led to solid progress. Thus in 1945 that first quantitative assessment of a control operation against the Desert Locust had recorded a kill of 2000 locusts per litre of $2\frac{1}{2}$% DNC in oil, sprayed from a Baltimore aircraft. That had been an improvized spray-formulation, prepared as described by Donald Gunn in his first paper (§ 3) from a stock of 14% DNC dust in response to evidence of the unreliability of action of the latter formulation (Kennedy, Playford & Beck 1944); and further work was done on toxicity and formulation, and on methods of applying more concentrated formulations. Of these, 20% DNC had given encouraging results, first against threatening concentrations of Red Locusts in the Rukwa valley outbreak area in 1948 (Gunn *et al.* 1948*b*) and later against small flying Desert Locust swarms in Kenya in 1952, and had been followed by 11% γBHC in oil, of which Sayer had encouragingly assessed a fifty gallon sample applied to a flying swarm in early 1953 (Rainey & Sayer 1953). But the assessments of 1954, while substantiating the evidence of progress provided by these earlier findings, also made it very clear that the scale of the aircraft spraying operations of that season, in which some 162 tons of these two formulations were applied, had been quite inadequate. Thus these 1954 assessments, together with further subsequent data on this same point (Rainey 1958*b*), showed that 1–2 tons of these formulations per square kilometre of swarm were needed under these conditions for complete control. Clearly only something like 10% of the thousand square kilometre invasion can have been killed and no more than some local protection of crops could be claimed.

(*e*) *Biogeographical evidence and historical analogues*

Other important evidence on possible effects of particular control operations on the development of the overall Desert Locust situation has been provided by biogeographical analysis. The type of basic biogeographical data available is illustrated by one particular study period of 13 months (May 1954 to May 1955), for which a total of more than 1400 separate reports, some of them comprising up to 580 individual records of swarms, egg-fields and hopper-bands, were received at the Anti-Locust Research Centre, London, from 46 different countries, mainly through governmental channels, but also from ships, travellers, press and other sources.

The geographical distribution of such reporting of locusts is inevitably and strikingly biased by the distribution of human populations and particularly of cultivation; thus for example, a single small swarm among cultivations is commonly reported several times daily (e.g. in the Kitui area of Kenya, January 1954) in contrast with a large swarm which in early February 1955 was followed by aircraft for eight days over the uninhabited hinterland of Mombasa without ever being reported from the ground at all (fig. 5.15 in Rainey 1976).

Nevertheless such records have been found capable of providing, by the use of appropriate methods of mapping and analysis, a picture of the overall distribution of the Desert Locust, and of its changes from day to day, from season to season, and from year to year, which is probably better established than that available for any other species of animal.

The systematic mapping and analysis of such material began some 50 years ago. Notable early findings included the basic seasonal patterns of long-range migration, connecting successive areas and seasons of breeding, which were found to be areas and seasons of rainfall (see for example Waloff 1946, Uvarov 1957). Objective methods of mapping and analysis, integrating information on the spatial and temporal distribution of the adults with that from the egg and nymphal stages, were later developed (Rainey 1963*a*), initially for establishing and studying day-to-day changes in distribution in relation to the corresponding synoptic meteorology, and incidentally found necessary in elucidating the locust history in 1962 in India and Pakistan (§ 3*b*). Together with the findings from aircraft observations on the tracks of individual swarms, these methods led to the recognition and interpretation not only of complex and sometimes unexpected swarm-movements (e.g. fig. 5.5 in Rainey 1976 and fig. 6.2 in Betts 1976) but also of extended periods of almost static population distribution. A similarly objective mapping procedure to summarize the overall Desert Locust situation for each individual month since 1942 has similarly systematized the study of year to year changes in locust distribution and the recognition of analogues for particular movements and situations.

For the present purposes, the most important findings from this biogeographical work have been:

(i) the degree of regularity of the seasonal changes in geographical distribution (illustrated by the striking contrasts between the different monthly hopper frequency maps, such as those shown in fig. 6.1 in Betts 1976; and again by the Desert Locust invasions of 1960–6, when 48 different countries were invaded, many of them repeatedly, but without a single case of swarms arriving without recorded precedent in the area and at the time of year concerned);

(ii) the extent to which these locust movements can be elucidated in detail from data already available and from what is now known of the relevant aspects of locust behaviour and of the effects of the weather systems concerned (illustrated by the particularly complex locust situation in eastern Africa during September–November 1954, for which it was subsequently found possible to assign each of hundreds of separate swarm-reports to one most probable source-area, up to 1700 km away and 6 weeks earlier, out of the four distinct source-areas which were involved in this situation (Rainey 1963*a*, 1976 fig. 5.5); as a result of (i) and (ii):

(iii) the reliability with which the changing distribution of the young swarms, moving out from the new source provided by a particular infestation of hoppers, can be forecast (Betts 1976), recognized and interpreted; and, conversely:

(iv) the significance which can accordingly be attached to any failure of such swarms to reappear as expected in new areas after the usual disappearance from their source-area by emigration (commonly initially as inconspicuously scattered fledglings which are liable, as was strikingly seen from the air in Somalia and Kenya in early 1955, to 'snowball', in Sayer's term, to form the coherent swarms which may first appear several hundred kilometres away downwind from the areas of earliest fledging.

An illustration of the last point – and one which is particularly relevant to the present subject – is that for successful forecasting of Desert Locust invasions it was (until the early 1960s) not only possible but necessary to disregard potential effects of control operations on subsequent developments in the overall Desert Locust situation.

3. Salient features of the Desert Locust situation of the early 1960s

Previous speakers have illustrated how the major locust upsurge of the middle 1950s stimulated improvements in control methods in many countries. However, Desert Locust attacks were clearly (and often admittedly) beyond the control of the organizations concerned in one or more countries in every one of the 23 years from 1940 to 1962. Against this background, the 1960s subsequently proved to cover one of the most dramatic changes so far recorded in the history of Desert Locust plagues. Thus the widespread infestations of 1960, 1961 and 1962, heavy enough to be a matter of national concern in a number of countries, were in striking contrast with the next 3 years, with infestations so light and restricted as to present major difficulties in the field work which had been internationally planned for those years under the

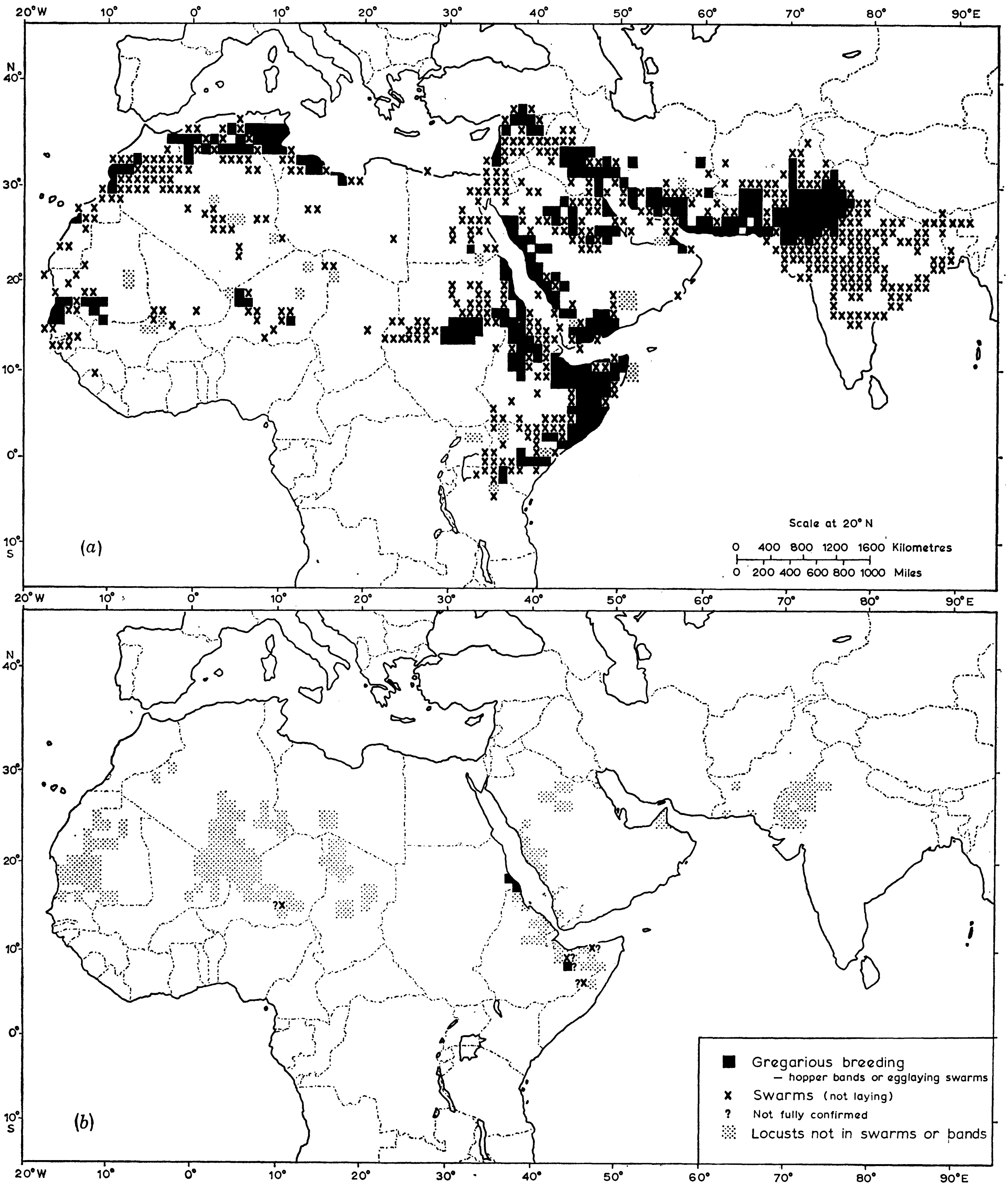

FIGURE 2. Decline of the Desert Locust plague. (a) 1960, (b) 1966.

42 nation UN Special Fund Desert Locust Project (FAO 1968*b*). This contrast is illustrated by figure 2, summarizing the situation in 1960, when swarms were reported in 36 different countries and hopper bands in 28 of them, and that of 1966, with swarms reported in three countries and seen by locust control staff in only one of them, while hopper bands were reported in only three countries.

During 1965–6, Desert Locust infestations appear indeed to have been at their lowest level for at least the preceding 27 years, and probably for the subsequent 12 years also. However, as was emphasized at the time (FAO 1966), locust populations have declined in the past to low levels, apparently like those of 1966, in circumstances in which it is now clear that the effects of control measures can be expected to have been quite negligible, and it is therefore essential to study fully the circumstances of the decline of the early 1960s, in the detail which was made possible by the Project.

(*a*) *Collapse in the west*, 1960

In western Africa in the summer of 1960, exceptionally heavy rains were experienced in southern Mauritania and in neighbouring areas of Senegal and Mali; a number of stations, including Timbuktu, recorded July rainfall totals higher than at any time during the preceding 30 year reference period. Now the same convergent wind flow which is necessary to produce such rains must be expected to bring into the same area airborne locusts from distances commonly hundreds and sometimes thousands of kilometres away. Breeding at this season is to be expected in an average year along most of the length of the Inter-Tropical Convergence Zone between western Africa and India; in 1960 summer breeding in the western region showed a marked concentration into the area of Mauritania and Senegal which had experienced these exceptional rains (figure 3).

Within this same region, following substantial crop-losses to locusts in 1957, the strategy and tactics of locust control had been effectively revolutionized, as Jean Roy has described (this symposium, § 1) by the establishment of the regional Organisation Commune de Lutte Anti-acridienne (OCLA), forerunner of OCLALAV (Roy, § 2), with a series of progressive change-overs from small-scale ground-dusting and baiting operations to lattice-spraying aircraft operations using dieldrin in oil solution (Mallamaire & Roy 1958). These methods were not only more reliable, in terms of kill, but were also applied on a scale larger than that of earlier campaigns, by more than an order of magnitude, with 8000 km² treated in this manner in 1959. Against the much lighter infestations of 1960, some 2170 km² were so treated (Besnault 1963); and it is suggested that the total potential production of swarms in western Africa may well have been considerably reduced because of the exceptionally large proportion of the summer breeding which in 1960 took place within the area covered by such operations.

Even so, not all known areas of the 1960 summer breeding in western Africa were so covered (e.g. some 400 km² in Mauritania), and escaping swarms, moving northwards as is usual at this season, reached Morocco and accumulated from November onwards in the Souss valley; swarms are regularly 'trapped' in this valley for months at a time during autumn and winter under the combined effects of topographical and meteorological factors, reviewed for example by Rainey & Aspliden (in Rainey 1963*a*). Here, again, following devastating crop losses in 1954, the Moroccan Service de la Défense des Végétaux had developed an organization for aircraft attack on the invading swarms, using materials and methods based on those developed in eastern Africa a few years previously (Perret 1956), and applied, probably for the first

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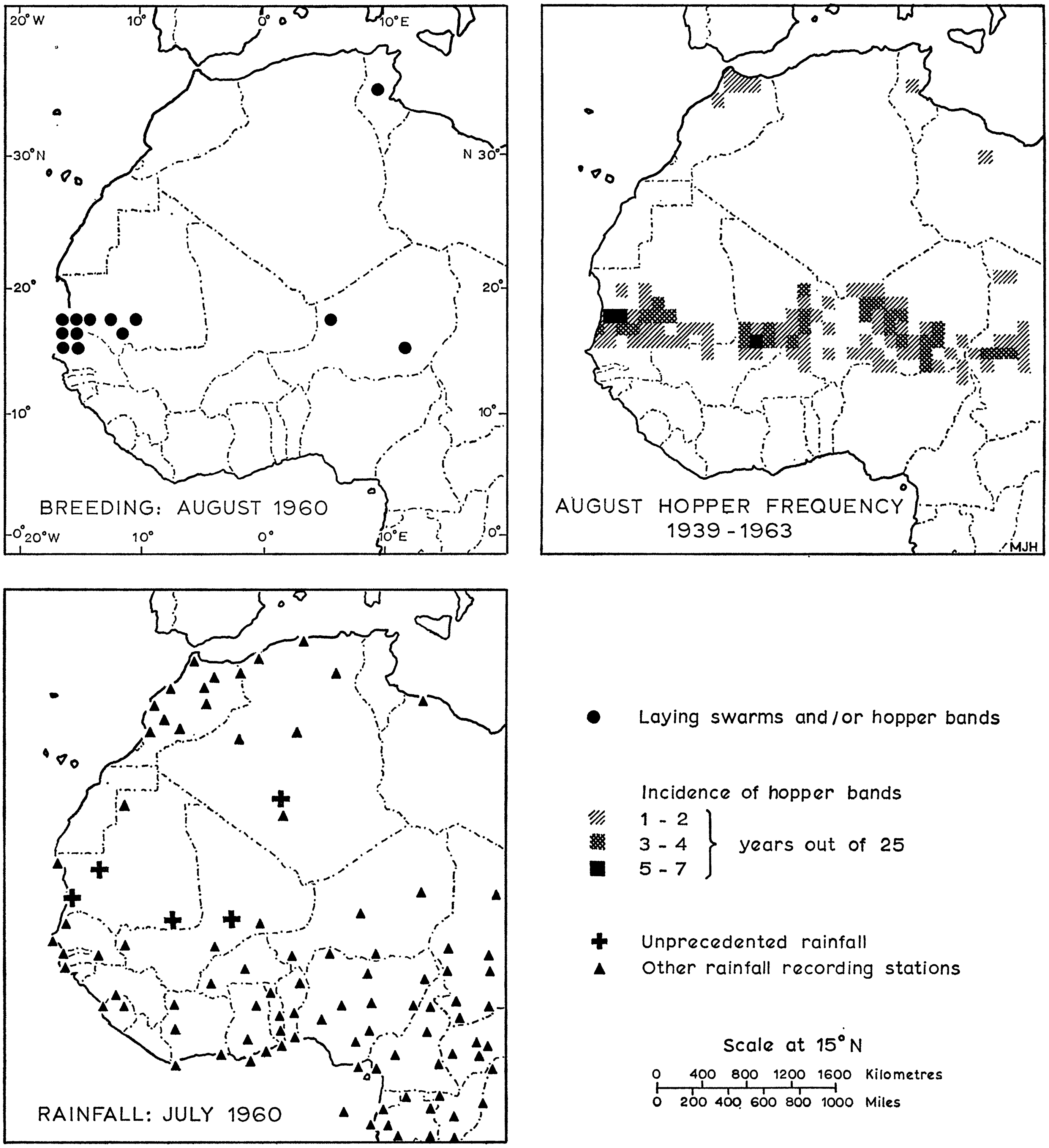

Figure 3. Main summer breeding of Desert Locusts in the western region, 1960.

time in the history of any method of Desert Locust control, on a scale which measured up to the magnitude of the problem. These developments had followed particularly fruitful exchange visits, arranged by Lean at FAO, with J. S. Hewitt of the East African Desert Locust Survey visiting Morocco in late 1954, and a Moroccan mission under M. Hudault visiting the Desert Locust Survey Airspray Unit in operation in Tanzania in early 1955.

The scale of successive annual campaigns in the Souss had increased, with financial help initially from France and later from the United States, to a maximum effort in the 1959–60 season, when 3400 tons of concentrated insecticide (active ingredients 270 tons γBHC and

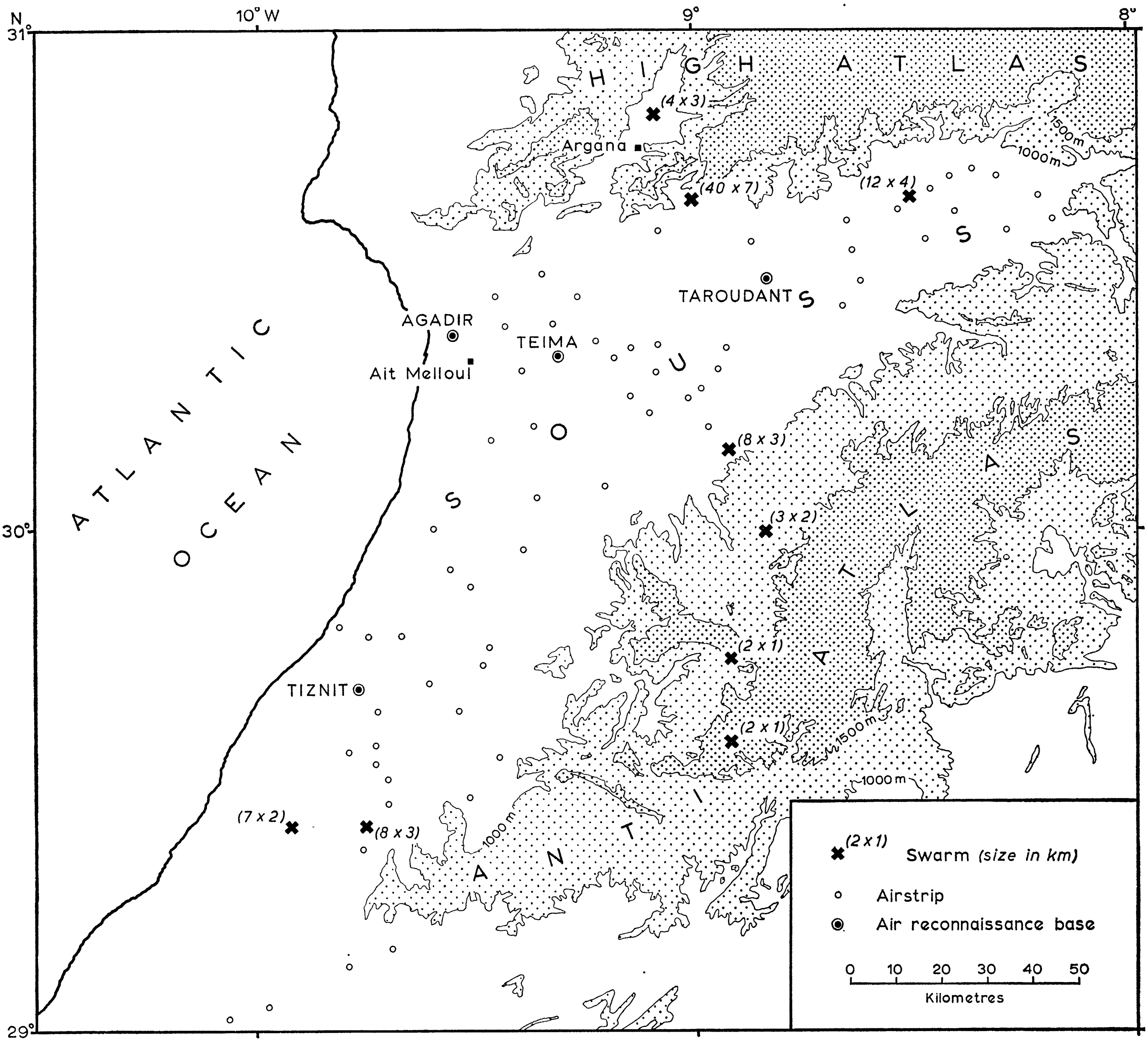

FIGURE 4. Towards the assessment of a locust invasion: settled swarms in the Souss valley, Morocco, 1 December 1960.

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100 tons malathion) were applied by 25 aircraft during a period of 4 months. In 1957 W. F. Mabee of the U.S. Department of Agriculture, with six years experience of Desert Locust Control in 13 countries, had visited the Souss and reported locust kills from air spraying as 'exceptionally good'. Following his visit, U.S. loan funds were approved for locust control support in Morocco previously provided by France. By 1961 this U.S. support for locust control in Morocco had totalled more than $11 million (Cavin 1961), utilized with ruthless logic and outstanding organizational expertise (Sayer & MacCuaig 1961; Gilot 1965) by the Moroccan Locust control organization and its French experts.

In 1960 the invading swarms duly reached the Souss in November, probably already depleted as indicated by the OCLA operations, but still shown, by very significant air reconnaissance (§ 1), to amount to rather more than 500 km². Thus an early air reconnaissance on 16 November recorded 11 swarms estimated to total 295 km², most of them still in the Anti-Atlas, and on 1 December (figure 4), when most of the swarms had reached the Souss and neighbouring valleys, intensive air reconnaissance of this area (in which one of us, R.C.R., was privileged to participate, from Taroudant) showed 9 swarms totalling 412 km²; in addition there were reports, on the same date, of three swarms to the east, outside the valley. Complete and effective air reconnaissance cover of the Souss valley and neighbouring areas, without duplication of reporting, was attained, almost daily, by a procedure which had been developed to suit local conditions (particularly of locust behaviour), independently and differently from the system which had been used for assessing the swarms invading Kenya. In the Souss the reconnaissance was carried out in the late afternoon by a number of light aircraft, operating simultaneously from different bases, with each aircraft undertaking a complete search of a limited separate sector, for settled swarms, and making traverses of each swarm found. The swarms in the Souss valley were attacked by the Moroccan locust control organization, from mid November 1960 until February 1961, by which time some 1500 tons of concentrated insecticides, again mainly 10% γBHC in oil, had been applied to the swarms, equivalent to nearly 3 tonnes per km² of swarm: a quantity which could conservatively be regarded as adequate in terms of the East African assessments.

Not only the Souss, but the whole of northwest and west Africa then became completely clear of reported swarms, in an entirely unprecedented manner. Thus swarms have been recorded invading the Souss valley in the autumn, as they did in November 1960, during 29 out of the 55 years up to 1968, but the 1960 invasion was the only one of the 29 which was not followed by known spring breeding in Morocco, Algeria and/or Libya. Moreover, this was in spite of suitable rainfall conditions in early 1961, in some of the areas appropriate for such breeding by any hypothetical swarms which might be suspected to have escaped unnoticed from the Souss (figure 5). Thus in January 1961 there were some 40 mm of rain at Biskra, in an area of frequent spring breeding in Algeria, and where in 1955 for example there had been egg-laying in mid-February following only 14–23 mm rain in late January. Furthermore, the next few swarms to appear anywhere in western Africa, in Niger 6 months later in August–September 1961 and some 2500 km away from Morocco, are much more likely to have represented an extension of the known infestations in the Sudan (some 1250 km away and less than a month previously) than to have been derived from undetected spring breeding in northwest Africa. There had been no other campaign anywhere on record, against a major Desert Locust infestation in a frequently infested area, for which there was evidence of such complete clearance as for those Souss operations of 1960–1.

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The Souss campaigns were undertaken purely in defence of Moroccan crops; but the report of an exchange visit to Morocco undertaken during these crucial operations of late 1960, by Sayer & MacCuaig (1960), makes what may fairly be regarded as prophetic reference to the strategic significance of such operations in relation to the Desert Locust situation as a whole '...what seems to us even more important from a wider view, is the possibility that the unique situation

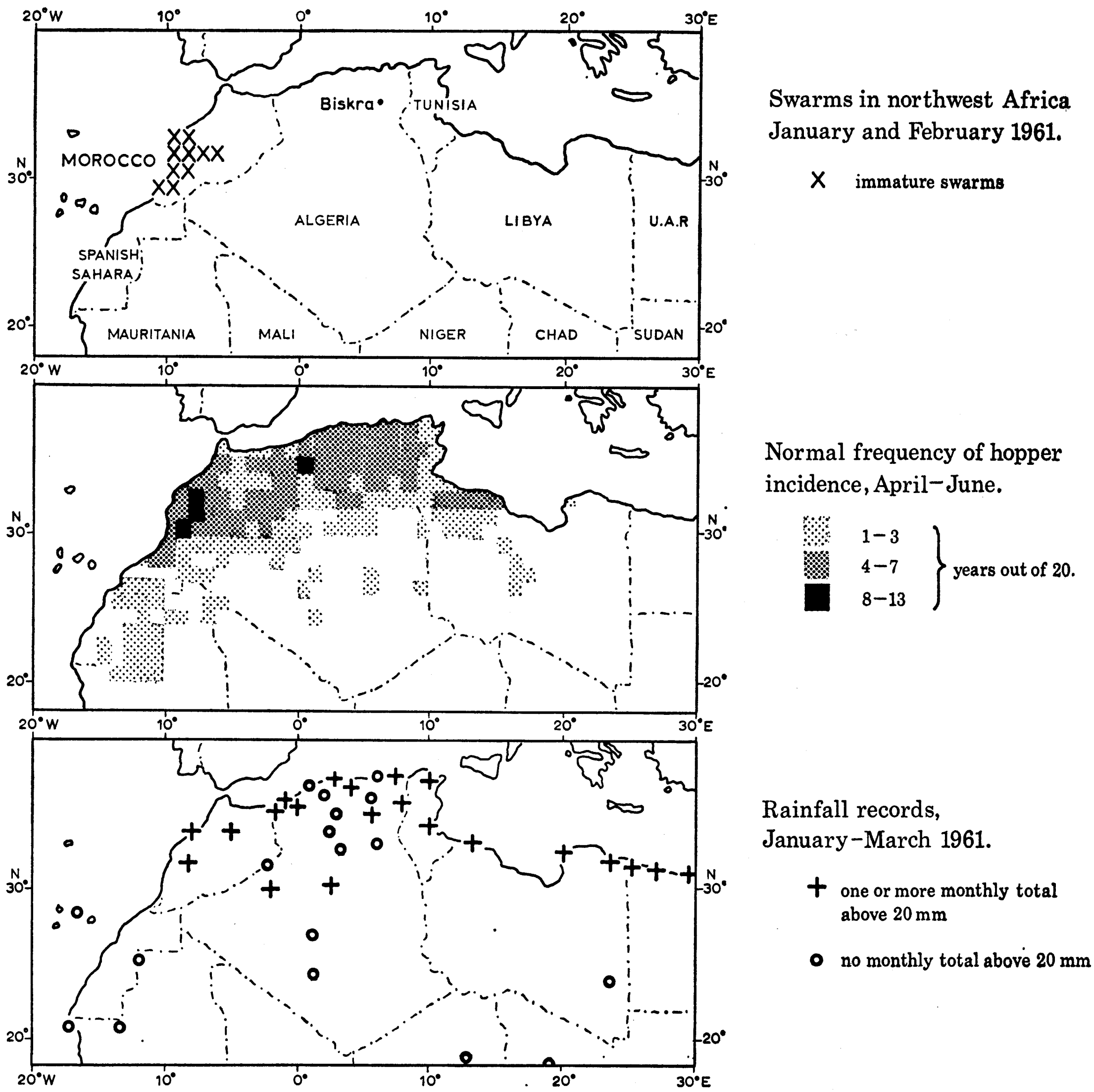

FIGURE 5. The last of the swarms of Desert Locusts in northwest Africa, 1961.

in Morocco, where swarms are relatively static in a limited area and therefore available for attack for a long time, may eventually affect the Desert Locust situation much further away. In our opinions the Souss valley may well be one of those areas of strategic importance in the global approach to Desert Locust control envisaged in the UNSF Desert Locust Project'. Subsequent evidence to this same effect was provided by the manner in which for west and northwest Africa the 1967–8 upsurge likewise terminated with similar aircraft operations in the Souss valley (Bennett 1975, 1976).

(*b*) *Decline in the east*, 1962

In the central and eastern regions of the Desert Locust invasion area, the scale of infestations remained a matter of grave concern until late 1962. Concerning eastern Africa, where aircraft spraying had been undertaken 'on a scale adequate to cause important reductions in locust populations only since 1959' (Desert Locust Survey 1962) there was an unusually severe infestation of swarms, concentrated by convergent winds across the Northern Region of the Somali Republic and neighbouring areas of Ethiopia during June–September 1960, which was treated with some 175 tons of concentrated insecticide from the air, in the largest-scale campaign ever undertaken in this area. The results were illustrated by detailed assessments of dead locusts following the application of 38 tons of concentrated insecticide against a single swarm over a period of six days, which demonstrated a corresponding kill of some 20000 tons of locusts; it was cautiously concluded that 'this campaign seems to have caused a considerable set-back to the development of the locust plague in the Somali Peninsula'. (DLS 1962).

In the Near East and the eastern region the plague culminated in early 1962, when breeding took place over areas extending from Jordan and Turkey to India, and from Ethiopia and the Northern Region of the Somali Republic to the Turkmenyan SSR (reached by swarms for the first time in 32 years). This was the most extensive spring breeding in the Near East for 17 years. It was particularly heavy in Iran (Rainey 1962), with serious crop-loss in the north-east and west; in Afghanistan (described as the most severe for more than 20 years); and in Pakistan (where it was officially stated that 'the locust situation, which took the shape of a national emergency in December 1961, continued its intensity during the first half of 1962'). Moreover, there was no evidence of a subsequent movement of locusts from Arabia into Africa in the early summer of 1962, such as occurred at this season in a majority of earlier years, so that all the escapes from the Near East spring breeding in 1962 are likely to have moved into Pakistan and India. Although natural enemies were noted as active in some areas, such as in the interior of Arabia in spring 1962 (with destruction reaching nearly 90% at one egg-field, by a predator, the Histerid beetle *Saprinus ornatus* Erichson, not previously recorded from this country (Popov 1965)), these areas were not the most important centres of locust infestation at the time.

Control operations were undertaken in spring 1962 in all infested countries, with aircraft used in many cases; but, although there may have been local successes, swarms of the next generation were produced in Ethiopia, Somali Republic, Syria, Iraq, Saudi Arabia, Iran, Afghanistan, West Pakistan and India. Subsequent developments indeed made it clear that over the area as a whole infestations must collectively have swamped the control resources which were employed, and escaping swarms resulting from the Near East spring breeding began to reach the summer breeding areas of Pakistan and India from May onwards.

Objective evidence of the scale of these escapes from the spring breeding areas was provided by a unique series of radar observations made by the Indian National Physical Laboratory in late July 1962 (Ramana Murty *et al.* 1964).

Analysis of these radar photographs, at the Delhi Rain and Cloud Physics Research Centre, demonstrated the presence of flying locusts, within 100 km of Delhi, over a total area of some 900 km^2 on 27 July and 1400 km^2 on the 28th. Moreover, approximate estimates of the volume density or spacing of the flying locusts were computed, assuming a value of 1 cm^2 as a reasonable value for the echoing cross section of a locust; this value is in fact consistent with the results

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of subsequent direct experiments on this point (Schaefer 1976). The volume densities so found were 0.07 and 0.13 locust per cubic metre, on 26 and 27 July respectively; values of the same order have been given by limited photographic evidence on the denser parts of the tops of high-flying swarms in East Africa. The Delhi radar observations show the locusts in these swarms to have been flying from ground level up to heights which often reached 1500 m above it. Taking the Delhi figures quoted for volume-density and height of flight as representative of the whole area of flying locusts shown by the radar photographs (which must moreover have missed any low-flying locusts in the more distant parts of the field of view of the set), the number of locusts within 100 km of Delhi on 27 and 28 July 1962 would have been of the order of a hundred thousand million (10^{11}), with a weight of the order of hundreds of thousands of tonnes. This was moreover at a time when swarms were also present in a number of other areas, up to 600 km south of Delhi.

Within the next 5 months this very serious situation was transformed to one no longer causing serious concern to the governments involved; and the events of this period are accordingly of crucial importance in the history of the decline of the plague. Evidence of notable mortality from natural causes during this period has been sought, without success apart from indirect and somewhat slight evidence (see below). During this part of 1962 there was for example no evidence of losses by abortive long-range swarm movements of the kind which are known to have occurred in this region in a number of other years, such as those into Madhya Pradesh and Orissa during October – December 1954, or into East Pakistan and Assam during November and December 1960. Nor were there records of losses of locusts at sea, such as those swept out over the Arabian Sea from Kathiawar and Kutch in October 1952. Nor was there any indication of failure of breeding following inadequate rains, as occurred for example in India and Pakistan following shortage of monsoon rains in 1968 and 1973.

On the contrary, this 1962 monsoon breeding in India and Pakistan was in fact unusually widespread, occurring over a total of 88 one-degree squares, the highest total so recorded in the last 30 years. It was also protracted, with evidence of three successive waves of egg-laying, beginning respectively in the second week of July, the first week of August and the second week of September. The only suggestion of possibly adverse conditions encountered by the locusts was the unusually eastward extension across western Uttar Pradesh of the first wave of laying in late July, so that relatively little of this first wave of laying took place in the more usual 'scheduled desert areas' of western Rajasthan and Bahawalpur. As has previously been pointed out (e.g. by Pradhan 1962), the breeding in these easternmost areas is often relatively unsuccessful; and in 1962 the appearance of young swarms of the new generation was subsequently reported only in four of the 35 degree-squares in which the first wave of laying had occurred east of 73° E, as compared with nine out of the 13 degree-squares with laying west of 73° E. Against this initial setback, there was a substantial further invasion from the west (especially Afghanistan), of swarms which moved across northeast Pakistan during the first week of August, and a second wave of laying followed.

Furthermore, over much of the high-frequency monsoon breeding areas, there were heavy September rains, known from previous experience as liable to be associated with a second generation of monsoon breeding, such as played an important part in the resurgence of the plague in 1940 and in 1949 (Waloff 1966). Figure 6 illustrates a particularly important depression which gave very heavy rains during the second week of September, including 251 mm in one day, the 12th, at Hyderabad (Pakistan). Under the influence of the convergent winds of this depression, a large proportion of the still considerable swarming populations then remaining in India and Pakistan were concentrated into topographically difficult areas of Tharparkar to the north of the Rann of Kutch. Here the third wave of breeding began, on the rains brought by this depression as it travelled northwestwards, and on a scale not discovered until a month later, when the nymphs were already in the fourth and fifth instars and it was too late for any hope of effective control by ground methods. This infestation was attacked by the Pakistan

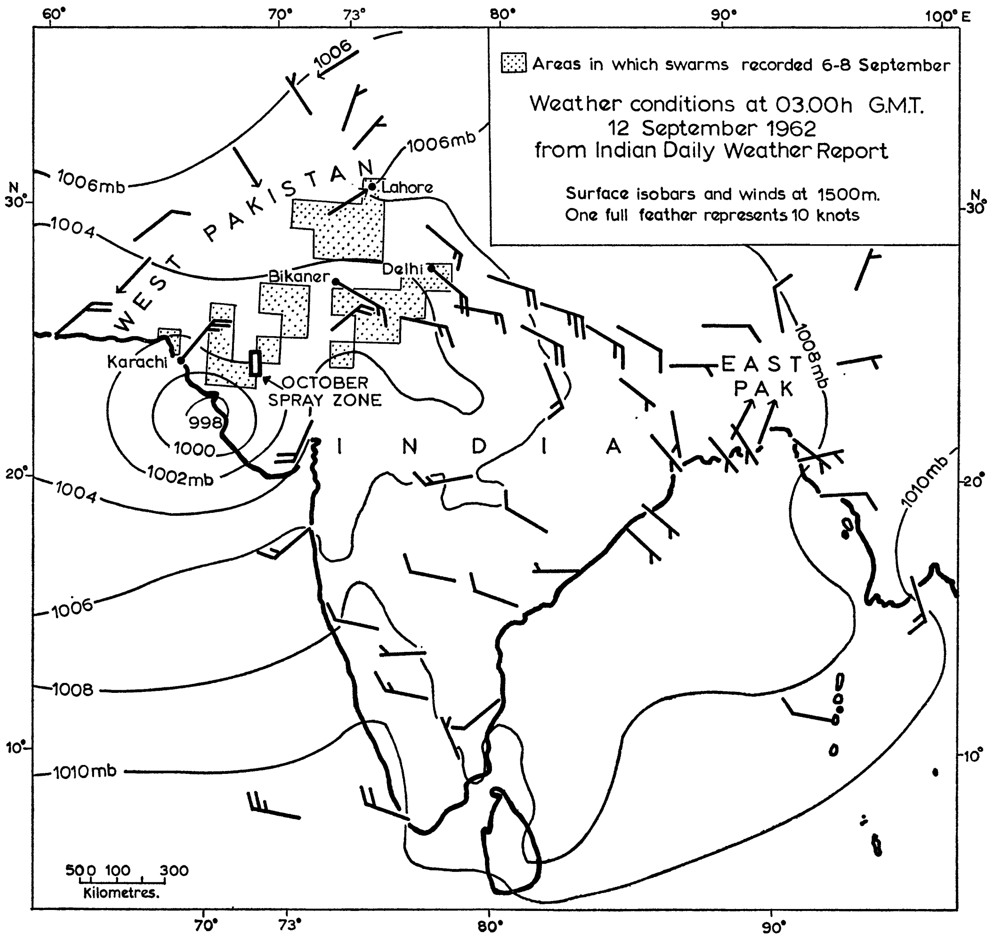

FIGURE 6. Desert Locusts, 1962: the depression which led to the Tharparkar campaign.

Aerial Wing in the largest-scale application yet of ultra-low-volume drift-spraying. This technique, developed (Gunn, second paper § 2*c*) from earlier work in western and eastern Africa, had been demonstrated in Pakistan and meticulously assessed by the FAO Operational Research Air Unit under Jean Roy in operations on a limited scale in India two months previously (Courshee & McDonald 1963). Dieldrin was applied at a rate of only 8 gm/ha by the Pakistan aircraft flying at a height of about 20 m along cross-wind spray lines 1 km apart. An area of 6000 km² was so treated by the Aerial Wing; an 'otherwise impossible situation' was reported to have been brought under control within a week; and there was indeed the first evidence of a radical improvement in the overall situation.

The third wave of laying, which had begun in this way in Tharparkar, subsequently appeared to involve all the progeny of the first wave (which had begun fledging in late August), and

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extended southwards into Kutch, where laying began in mid September and continued until early October. Young swarms of the next generation began to appear in mid November, and these swarms remained until mid December still in Kutch, probably detained by wind convergence at a coastal front between the sea-breeze and an off-shore general wind, as had previously occurred in this area in, e.g. December–February 1954–5 (Rainey & Aspliden, in Rainey 1963*a*). Here they were energetically attacked by aircraft of the Indian Plant Protection Department, and particularly impressive kills were recorded following the use of the special dieldrin-in-oil formulations made available through the FAO/UNDP Project.

A few swarms from India and Pakistan, at least the earliest of them representing progeny of the second wave of laying, had moved westwards across Iran during late October and November, as is usual at this season, and were reported as far west as northeastern Saudi Arabia in December. Unlike all previous westward movements across Iran at this season in 14 of the previous 21 years, there were no confirmed reports of subsequent breeding anywhere in Iran or Arabia. This absence of breeding does not appear to have been attributable to any complete failure of rains, for, although in some of these areas the 1962–3 winter rains were below average, significant quantities of rain were recorded at a number of points within the general area reached by these last few swarms (e.g. 19 mm at Bushehr and 36 mm at Abadan in November 1962, followed by 19 mm at Dhahran and a further 17 mm at Abadan during December).

A few more swarms, representing the surviving progeny of the third wave of breeding, overwintered in Pakistan and bred on a limited scale in northern districts particularly in Sargodha and Rawalpindi Divisions, remaining in and around cultivated areas; and the subsequent hopper infestations were reported as largely eliminated in the early instars by ground-dusting operations by the West Pakistan Department of Plant Protection.

In the hope of throwing some light on this dramatic reduction in the scale of infestation recorded in October 1962, laboratory experiments were undertaken at the Anti-Locust Research Centre on the effects of starvation and prolonged flight on length of life and reproduction of locust previously subjected to sublethal doses of dieldrin. It was found (Watts 1969) that the application of sub-lethal doses of dieldrin to female locusts before laying could transmit sufficient dieldrin to the progeny to kill the first-instar hoppers on hatching. In individual aircraft spraying operations against swarms many locusts necessarily receive sub-lethal doses of insecticide, and it was suggested that a delayed effect of sub-lethal doses of dieldrin may have been involved in this unexpected, virtual absence of recorded breeding by swarms escaping from India and Pakistan in 1962 and perhaps also in 1964 (see below) when concentrated oil solutions of dieldrin were again used. A similar effect may also have been involved in the somewhat unexpected disappearance of swarms from the Somali peninsula in early 1969, following spraying operations with dieldrin in which, on the recommendation of H. J. Sayer (1972), deliberate attempts were made to exploit this effect of sub-lethal doses.

(*c*) *Upsurges of* 1964 *and* 1967–8

In each of five successive breeding seasons in the eastern region between spring 1964 and spring 1966 the locust populations of the region suffered at least some losses to control operations (see Rainey & Betts, fig. 2 this symposium). Attention has already been directed (Waloff 1966) to a number of similarities between the threatening locust situation in India and Pakistan during the summer of 1964 and the upsurge of the plague in the same area and season of 1949, and the possible role of differences between these two years in the nature and scale of the

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control operations undertaken appears also to merit study. Thus in 1964 (following a D.L.I.S. early warning based on effects envisaged from an advancing cyclone to which attention had been specially directed by Mazumdar at the Bombay Meteorological Office) in India alone some 3 tons of 20% dieldrin and 40% aldrin together with 16 tons of 10% BHC dust were applied between August and October. In the campaigns of 1949, on the other hand, more than 90% of the known infested area had only been treated by trenching, with insecticidal treatment confined to the use of 12 tons of 10% BHC dust in the remaining 8% of the area (Venkatesh 1976), and with combined effects likely to have been very much less than in 1964.

A more widespread upsurge of Desert Locust infestations developed, in a manner on which opinions differ (Rainey & Betts and Hemming *et al.*, this symposium) during 1967–8. At this time, some who had been reluctant to concede that control operations appeared to have played a significant part in the locust decline of the early 1960s, expressed the view that this might be the start of another plague comparable in length with that of 1949–62. In the event, the scale of the new infestations had ceased to cause concern by early 1969. From a detailed study of these developments, Bennett (1975, 1976), using an approach differing in a number of respects from our own, concluded that 'in 1968 control was a major factor causing reduction in [locust] numbers'. For present purposes we comment only on two points in the 1968–9 story, which merits more comprehensive study.

The first is the analogy with 1960 in respect of Morocco, which was again invaded, from late October 1968 onwards, by young swarms, this time largely from the Sudan (Betts 1976). Once again the invading swarms became relatively static, in and around the Souss valley, where they were attacked by sustained aircraft-spraying. The scale of the control operations in Morocco was much less than in 1960, with 136 tons of 15% γBHC in oil and 17 tons of other materials (4% DDVP, malathion and 10% γBHC) sprayed.

The resulting control in 1968–9 appears to have been somewhat less complete than in 1960–1, with breeding by a few survivors subsequently detected, though on a very small scale. Nevertheless by the spring of 1969 Desert Locust infestations throughout northwest and west Africa were indeed trivial compared with those of the previous year.

The second point for comment concerning 1968 was the aircraft spraying in Eritrea and the Ethiopian highlands, on a scale unprecedented in these areas. One of us (R.C.R.) had the satisfaction of seeing, in this campaign, the work of Ethiopian pilots of DLCOEA and of the Ethiopian Ministry of Agriculture (impressively recorded by Anthony Isaacs in the B.B.C. documentary film 'The year of the locust'): these operations continued and extended the work of their expatriate predecessors of the Desert Locust Survey, in a manner which justified the cautious optimism engendered earlier by the development of civil aviation in Ethiopia (Rainey 1964).

This was followed by an unusual though perhaps not unprecedented (1948?) disappearance of significant infestations from eastern Africa (see Discussion on Alternative Hypotheses, Adefris). These 1968 operations provided an impressive demonstration of the manner in which the drastic reorganization of DLCOEA undertaken by Vernon Joyce a few years earlier (Joyce, this symposium) with the basic change from operations mainly on the ground to mainly from the air, had indeed improved the effectiveness of the Organization at the same time as reducing the budget – developments strikingly parallel in each of these respects with the changes for which Gunn had been responsible in the Red Locust control of the previous decade (Rainey 1960). In Ethiopia, the Desert Locust story of 1968 may be suggested as a possibly instructive contrast with that of 1958 (Adefris, this symposium).

4. Conclusions

On the question of possible general and long-term effects of control measures on the overall Desert Locust situation, it is necessary to take account of a point made by Hugh Sansom, a meteorologist with many years of service with the East African Meteorological Department. He noted that the last year in which no Desert Locust swarms had been recorded anywhere was 1887, and that the decline in the locusts in the early 1960s had been at the time of a marked change in the global wind-circulation, which had reverted sharply to a type of regime which had prevailed before the 1890s. Sansom therefore suggested a possible connection between these changes in the global wind-systems and in the locust situation in a letter to H. H. Lamb, then in charge of research on climatic variation at the Meteorological Office and now head of the Climatic Research Unit at the University of East Anglia; Lamb (1967) had quoted Sansom's suggestion in a review of recent climatic changes presented 12 years ago at the Royal Geographical Society, and was accordingly asked to up-date and comment on this particular point, before a more general discussion was invited on the Desert Locust decline of the 1960s.

Reverting to the story of the 1960s, it must first be emphasized that the total area which has experienced invasion by Desert Locust swarms covers some 30 million km^2, over at least a million km^2 of which breeding by swarms has been recorded in at least 50% of years. In contrast, the history of the decline of the Desert Locust plague during the 1960s includes several successive occasions on which an important proportion of the overall locust population was concentrated by meteorological factors into restricted areas of the order of a few tens of thousands of square kilometres, and moreover in which recent developments in control methods and materials had made possible control operations which, in scale and in nature, must be expected to have been many times more effective than any control operations undertaken in these same areas up to a few years previously, and in one case with evidence of probable quantitative adequacy. Furthermore, on two of these occasions the evidence of near-completeness of control within the area of the operations was powerfully reinforced by an unprecedented absence of any subsequent appearance of swarms in areas into which there was good reason, from analogues provided by earlier years, for expecting any escaping locusts to migrate. Such unprecedented absence of escapes, following particular control campaigns which on entirely independent grounds are likely to have been of unprecedented effectiveness, can in our view hardly be coincidental.

The most clear cut evidence of effectiveness of control thus relates to individual campaigns, rather than to control measures in general. As late as spring of 1962 there were clearly massive escapes from control campaigns using the previously conventional materials and methods (air as well as ground). Now each of the campaigns discussed above as having possibly contributed to the overall decline was not only undertaken largely or wholly by aircraft, but also used insecticide formulations and spraying methods which had been developed within the previous decade specifically for use against the Desert Locust. These have also been the main methods and materials used in dealing with the subsequent upsurges of 1967–8 and 1978.

We wish to record our thanks to all those who have helped to make this work possible: the late Sir Boris Uvarov, K.C.M.G., F.R.S., and Miss Zena Waloff, O.B.E., who laid the foundations of the dynamic biogeography of the Desert Locust half a century ago, and to the colleagues on whose locust reports, both in the ground and in the air, we have been privileged to work. Our particular appreciation is due to Miss M. J. Haggis, both for her work on the illustrations, and as a member of the D.L.I.S. forecasting team of the 1960s.

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Discussion

H. H. Lamb (*Climatic Research Unit, University of East Anglia*). My purpose is to outline briefly for you what we are beginning to know of the large-scale and longer-term variations of climate, in so far as these probably affect the distribution of conditions permitting the breeding of insects, or where they become concentrated, and of conditions congenial to birds.

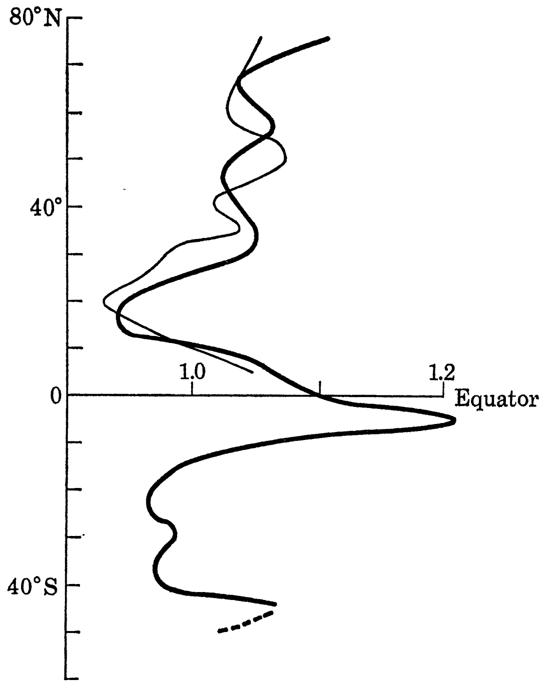

Figure 7. Rainfall anomalies from the Arctic to the Sub-Antarctic, expressed as a proportion of the 1931–60 average. Thin line, 1960–9; broad line, 1970–2.

The Climatic Research Unit is engaged in largely empirical studies of climatic fluctuations and changes, assembling the observations past and present and analysing them in whatever ways seem most apt to reveal the processes going on.

When one makes world maps of the rainfall of the 1960s and 1970s, expressed as percentage of the average yearly rainfall over some longer period such as the 1931–60 average, the pattern over all the lower latitudes between about 40° N and 35° S (essentially the latitudes spanned by Africa) is a simple one of zonally extended belts, giving the appearance of a shift of the desert zones towards the equator, whilst the equatorial rains have been more concentrated than before quite close to the equator, and the northern and southern fringes of Africa have experienced rather more than before of the temperate-zone winter rains.

Over middle and higher latitudes the pattern is quite different, consisting of nearly north–south ('meridional') stripes of conditions alternately wetter and drier than in the first half of this century. These stripes correspond to changed positions (and length) of the waves in the upper westerly wind flow around either hemisphere. As the positions even change from year to year when the middle latitudes westerlies are blocked, or not well formed, as in recent years, these changes have been associated with some great variations of weather from year to year, or from one group of a few years to the next, in middle latitudes.

Figure 7 shows the profile of rainfall anomalies from the Arctic to the Sub-Antarctic: the thin line for 1960–9, the thick line for 1970–2 approximately. The 1970s had so far been much like the 1960s, especially in the lower latitudes. Figure 8 shows the history of rainfall year by year from the beginning of the century near the southern border of the Sahel, at 12–14° N: the smooth sine-curve trend perhaps suggests something like a 200-year fluctuation with the maximum rainfall about the 1930s. Figure 9 is the equatorial counterpart of this, showing the changes in the level of Lake Victoria produced by changed behaviour of the equatorial rains; there the changes are sudden, as if some critical threshold were passed, and the rains switched in 1961 and since, to a regime which yields much more over the catchment near the equator and presumably allows only a much restricted seasonal movement of the intertropical frontal system north and south of the equator. Now this seems to be a reversion to the late nineteenth century regime represented by the level of the lake shown in 1876–80.

A longer perspective can only be presented by reference to the significant correlations with indexes established from data for other latitudes, e.g. the best available assessments of the

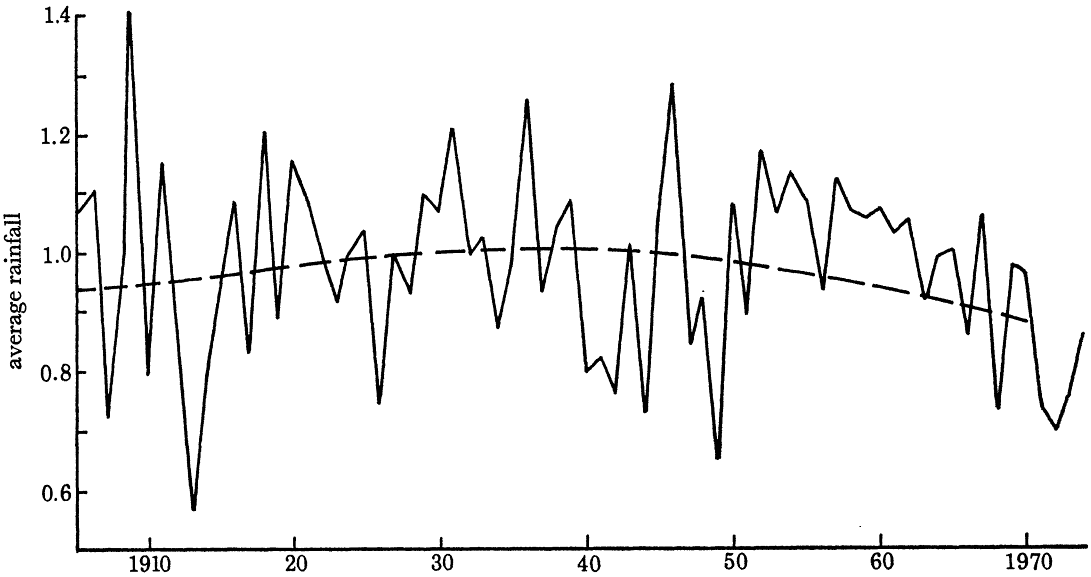

FIGURE 8. Average of rainfall at five stations (Zinder, Niamey, Sokoto, Kano and Maiduguri) bordering the southern Sahel for each year from 1905 to 1974, expressed as a proportion of the 1931–60 average. (Adapted by permission of the Royal Meteorological Society from Bunting *et al.* 1976.)

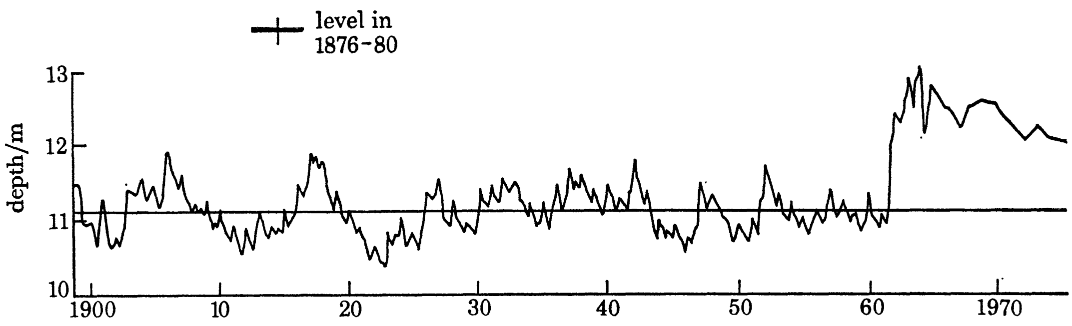

FIGURE 9. Variations in the level of Lake Victoria. Jinja gauge measurements from 1899: monthly averages until 1964, annual averages thereafter. Also showing an early report of lake level in 1876–80 by missionaries in the area.

changes of global temperature, the prevailing temperatures over the northern polar cap and the frequency of westerly wind situations over the British Isles. The last-named seems to confirm the existence of a basic 200-year fluctuation, and all these items had a maximum about 1930–40.

It may be worth reporting that in the great cold extreme of the Little Ice Age climate in the seventeenth century, when glaciers all over the world and the Arctic sea ice were exceptionally extended, the meridional pattern of anomalies seen in recent years in middle and higher latitudes extended south into Africa with the result that at that time there were opposite rainfall anomalies in east and west Africa north of the equator.

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D. L. Gunn. Professor Lamb's figure 9 is specially interesting in showing a sudden rise in the level of Lake Victoria, since sustained, corresponding closely to a simultaneous rise and sustained high level in Lake Rukwa, far to the south. Lake Tanganyika rose greatly about the same time. Professor Lamb also mentions a high level of Lake Victoria in 1876–80; Lake Rukwa was extensively dried up in 1873 and full in 1880, and so remained until at least 1883 and probably 1890 or so, being dry again by 1897. These correspondences are not, however, carried through into the 1934–7 flooding of Lake Rukwa, of which no indication is given in the Lake Victoria records (Gunn 1956). These periods of very high water are important, for they prevent breeding of Red Locusts in the Rukwa Valley (and Mweru wa Ntipa; Gunn 1955) and presumably render other places like the Wembere more suitable for successful breeding than they are in drier periods of years. These facts are important in planning the administration of outbreak suppression of the Red Locust.

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C. F. Hemming. Natural control, such as by drought, has dramatic effects. Control by chemicals *can* have big effects when everything is going in favour of the control organization, but perhaps very little on other occasions. But *we must believe* it is doing some good, to undertake control at all.

Zena Waloff. I would like to add a few words to what Mr Hemming has just said. Without minimizing in any way the effectiveness of control operations which contributed to the end of the last major plague, I would like to point out that when we look at earlier Desert Locust plagues, analysed on a regional basis since 1860 to give durations of plagues within regions (Waloff 1976), there are some 40 regional sequences of which only the termination of the four last, between 1960 and 1962, could possibly be ascribed to partial effects of control. In all other cases, control was either non-existent or completely inadequate, yet plagues came to an end.

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D. L. Gunn. I would like to say another word first about Red Locust and then come back to the Desert Locust. The Red Locust outbreak areas were flooded so completely from about 1961 onwards – and still are – that it would have taken submarine locusts to lay eggs in them, below the tree line. That might have meant that there would be no swarms of Red Locusts until that situation ceased. But, in point of fact, what has Red Locust done? This species exists, in very small populations, in many other places, one of which is the Wembere flats of central Tanzania; and *because* there have been these changes in climate (in which the classical outbreak areas have become unsuitable), the Wembere has now become suitable, and produces a few Red Locust swarms. Now consider the Desert Locust, and its very wide geographical range; if the climate has become unsuitable in the usual places, surely other places will have become suitable, and there should still be plenty of places where very heavy breeding could occur and plagues could start. Are we not in danger of conceding too much to the change in climate of which Professor Lamb has spoken? In the Rukwa valley, we had in 1954–60 a great upsurge of Red Locusts; as time-passes and our perspective improves, I become increasingly impressed with the success of what were then our new methods of control. It looks as if we did then prevent a plague.

R. J. V. Joyce. I think the significant feature of the decline of the Desert Locust plague in the 1960s was indeed that there were successive occasions, in west Africa, north Africa, and India and Pakistan, where the bulk of the world's populations of this pest happened to be temporarily concentrated, and where it was possible for toxic doses to be applied in numbers commensurate with the numbers of locusts present.

But I would like to change the subject a little. At this meeting we are speaking about migrant pests in the sense of pests which everyone recognizes as requiring control before they enter the areas which are at risk. Now, in normal crop protection against other pests, the area at risk is the farmer's fields; but the pest population exists outside his fields as well as inside them, and emigrants from these areas outside immigrate into the farmer's fields: just as at some other stage emigrants from his fields can immigrate into his neighbours' fields. I think the term 'migration' is often an emotive expression; we are concerned with emigration and immigration, and before we can start contemplating any coherent system of pest management the first requirement is to determine the range of distribution of that population to which a regulator needs to be applied. How many pest species breed on the plant on which they were born, or in the field in which they were born? To apply a regulator to a population we must know the extent of dispersal of that population, which is normally a function of its flight activity. To my mind a knowledge of flight activity is therefore an essential requirement for the development of a coherent pest management system.

D. Yeo (chairman). Perhaps Dr Rainey might now help to put what Professor Lamb has said into context.

R. C. Rainey. We did not know just what Professor Lamb was going to say today, and I think that his talk has been particularly useful for stimulating our discussions, because before it the optimists – the protagonists of control – might have had pretty well a walk-over, whereas what he has said perhaps helps to bring the natural causes people back into business. But, for myself, taking into account the evidence we presented on the scale and nature of those particular campaigns of the early 1960s, I would find it very difficult to attribute the speed and extent of the collapse of the Desert Locust populations in Morocco between November 1960 and January 1961, and of those in India and Pakistan between September and November 1962, to a change in climatic regime; and indeed in both cases there are reasons, already mentioned, for considering rainfall in these particular regions and seasons to have been favourable for continued breeding by the locusts. Miss Waloff's comments, indicating her recognition of some difference between the regional declines of the early 1960s and those of earlier years, are significant because her previous work (Waloff 1966) has very recently been cited (Uvarov 1977) as evidence of the absence of such a difference and accordingly in support of attributing the decline of the 1960s primarily to natural causes.

On the other hand, it would in my view be dangerous, in the present state of very limited knowledge, to dismiss as mere coincidence the evidence of major changes both in the tropical atmospheric circulation (as illustrated by the Lake Victoria levels) and in the overall Desert Locust situation around 1890 (which had been preceded by something like a decade of apparent recession) and in the opposite sense around 1960. An extreme view which is sometimes expressed is that control is now so good that locusts are no longer really a problem; and what Professor Lamb has had to say strikes a very useful note of warning in that respect. It may be that in due course the atmospheric circulation will click back in such a way as suddenly to make conditions much more suitable for Desert Locusts than they have been for some time past. Even apart from such a possibility, something which is special about Desert Locusts, as contrasted for example with *Locusta* and *Nomadacris* in their less arid habitats, is the way in which the Desert Locust, like the nomads of M. Abdallahi, can use the exceptional desert rains, occurring over areas sometimes of hundreds of thousands of square kilometres, normally uninhabited, where the response of the immigrant locust populations can be dramatic and without warning. For both these reasons I think we can rule out the view that locusts are no longer a problem.

To me, the events of the early 1960s provide convincing evidence that in some places Desert Locust control had then become good enough to measure up to the size of the job; before then it wasn't ever good enough to do so anywhere. It had therefore become possible, for the first time, for individual control campaigns to be sufficiently effective to suppress major regional infestations, and for a sequence of such campaigns to make a major contribution to the onset of the recession – but subject to the warning that at any time a change of climatic regime may bring back conditions more favourable to the locusts than have occurred since the 1950s.