PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Development of Aircraft Attack on Locust Swarms in Africa Since 1945 and the Start of Operational Research on Control Systems [and Discussion]

D. L. Gunn and H. D. Brown

Phil. Trans. R. Soc. Lond. B 1979 **287**, 251-263
doi: 10.1098/rstb.1979.0058

Phil. Trans. R. Soc. Lond. B **287**, 251–263 (1979)
Printed in Great Britain

SETTING THE SCENE

The development of aircraft attack on locust swarms in Africa since 1945 and the start of operational research on control systems

By D. L. Gunn
Taylors Hill, Chilham, Canterbury, Kent CT4 8BZ, U.K.

The work described here was essentially a search for innovation, to replace existing, totally inadequate, methods of locust control. It was, from the start, quantitative, not only because the experiments would not otherwise be fully meaningful but also because the huge scale of locust control required forward planning, efficiency and economy. From these premises arose emphasis on devising methods of assessment of locust numbers, alive or dead, on measuring everything relevant, and on analysing causes of mistakes and other failures. What was wanted was not merely good techniques of killing locusts but complete systems that could be used in a variety of circumstances.

Developments after our first moves in 1945 and 1947 are also outlined. They were so successful that less than 30 years later, in spite of wars and other international difficulties, as well of those of the control systems themselves, an exceptionally widespread upsurge of Desert Locusts was checked successfully (Rainey, Betts & Lumley, this symposium). A period of unusual freedom from Desert Locust plagues resulted.

1. Introduction

Locust swarms are often so extensive and so dense that once they settle in a crop, it can be destroyed before any attack on the swarm can begin. Therefore attacks on the locusts must be made outside the crop, if possible in the places of origin of the swarms or on their route. Such a strategy will sometimes destroy locusts that would never have reached any crop, but that is a price to be paid for security.

Two types of locust species can be distinguished according to the extent of the initial breeding areas from which the very large numbers of a plague come. Type B locusts have a few, relatively small, initial breeding areas – outbreak areas – where plagues start; for the Red Locust (*Nomadacris septemfasciata* Serv.), the outbreak areas total not much more than 5500 km^2 and the plague area is one thousand times as large. Type B also includes both the African and the Russian forms of the Migratory Locust (*Locusta migratoria*). Close control of hoppers (nymphs, larval forms) of such species in their outbreak areas seems obviously sound and if successful would avoid any need to attack adults.

The American Rocky Mountain Locust (*Melanoplus spretus* Walsh), on the other hand, probably spread over no more than four to ten times its area of origin (Riley, Packard & Thomas 1878, 1880, 1883). The Brown Locust of South Africa (*Locustana pardalina* Walker) and the Australian Plague Locust (*Choirtoicetes terminifera* Walker) also have extensive areas in which swarms may originate; these swarms spread over areas which are indeed large but not many times larger than the areas of origin. These species are all type A.

The Desert Locust (*Schistocerca gregaria* Forsk.) is perhaps in a special position. The species does not live permanently in any limited areas from which all plagues arise. The habitats are so unstable that favourable conditions may arise in any of many places that the migratory habits of even isolated Desert Locusts make accessible to the species. It is not so much the ratio of any area of actual origin of a particular plague to the extent of the invasion area that matters; it is the wide scatter and large number of places that may become favourable for early swarm breeding that makes their firm control too costly to be guaranteed.

Desert Locusts therefore fall into type A for practical purposes. Some control of hoppers can help in a policy of attrition and indeed has until fairly recently been the main line of control; but methods of killing adult swarms are essential with type A species. Uvarov's idea was that the mobility of locust swarms could be matched only by the mobility of aircraft.

2. Behaviour of locust swarms

John Kennedy had, in 1942–4, collaborated with Russians in Persia, and continued in Kenya, in experimentally dusting swarms from aircraft with 14% dinitro-ortho-cresol dust (DNC) (Kennedy, Ainsworth & Toms 1948). The dust made a fine show but its effects were unpredictable and sometimes slight. The time regarded as available for dusting was very short because a migrant swarm streamed away from its roosts inconveniently early in the day, even if not disturbed by low flying aircraft.

I came on the scene in 1944, apparently as co-author of a rather academic book on potentially relevant analysis of the elementary behaviour of animals (Fraenkel & Gunn 1940, 1961). My initial brief was simply to study the behaviour of swarms and in particular to define the conditions in which there would be a reasonably long time for aircraft operations after dawn and before the migrant swarm streamed away.

Early in 1945, a team including a young physicist, Douglas Yeo, and four Royal Air Force men, three of them tour-expired bomber officers, went to Kenya. By the time we were equipped and provided with a radio truck, drivers, a cook and so on by the R.A.F., the party was large but still mobile. The scientific party was keen and energetic. The support provided by the R.A.F. was everything that could be desired.

We followed one particular swarm for 18 days, from the Kenya Highlands to the egg-laying sites near Lake Rudolf. On 10 of the 17 mornings the roosting site had been located at sunset and we were able to study it as a potential target for air-to-ground spraying from before dawn until it flew away (Gunn *et al.* 1948*c*). Altogether we studied 17 swarm departures from dawn to stream-away.

The locust's behaviour was recorded in relation to the usual meteorological elements, with emphasis on temperature, namely air temperature, locust body temperature and radiation. For radiation, we required an instrument to integrate the radiation falling on a locust's surface from sunrise to swarm departure and for this purpose a special instrument had to be developed: the Gunn–Bellani radiation integrator (Gunn, Kirk & Waterhouse 1945; Gunn & Yeo 1951). In the upshot, the simplest summary of departure conditions did not include measurements of radiation; the instrument did, however, come into use for other purposes, starting with Pereira's analysis of water balance in complete drainage basins (Pereira 1959; Pereira *et al.* 1962).

Spontaneous departure from the night roosts depended mainly on air temperature ± 3 °C. It turned out in later years that although this result applied to our conditions in the Kenya Highlands, it did not necessarily apply to other Desert Locust areas and conditions (Waloff & Rainey 1951). It served our immediate purpose.

An incidental but important result was clear evidence that a Desert Locust swarm is a coherent entity. 'When large numbers of individuals come together and remain together for long periods while moving through a complex and highly variable series of natural situations with no discoverable common factor other than the crowd itself, one is left with the strong impression that the animals are bound together by reactions to one another' (Gunn *et al.* 1948*c*, p. 23). The details of these reactions have since been reviewed by Waloff (1972*b*) following up a hypothesis first put forward by Rainey and Sayer 20 years earlier (Rainey & Sayer 1953). This continued cohesion of mobile populations has since come to be recognized as the most clear-cut manifestation of gregarious behaviour.

Treating a swarm as a unit cleared the way for detailed analysis of reasons for day-to-day directions taken by it. Although we were quite unable to forecast the zig-zag movements of our swarms, as can be done today (Rainey 1963), we concluded that the initial direction taken by a swarm was generally with the wind when its speed was 1.5 m/s or more, but random in direction in more gentle winds.

3. AIR-TO-GROUND SPRAYING

The importance of Desert Locust control in the Middle East during the war had enabled the Chemical Defence Experimental Station at Porton in Wiltshire to bring its expertise to bear on development of locust spraying methods. The contributions of Porton to logical developments, innovation and simulation of operations as well as laboratory testing of insecticides and readiness to help in solving operational problems were very large in the following twenty years and crucial to the successes achieved.

By mid 1945, Kennedy and the staff at Porton had prescribed a solution of DNC in oil, the dosages required and the methods of spraying it from aircraft. In Kenya we were then fortunate in getting help from the Anti-Malaria Flight (F/Lt E. C. Jaques) using a Baltimore aircraft with a 1350 l tank fitted in the bomb bay. Back at Nairobi, we therefore made up insecticide solution from what we could get there, the 14% DNC dust, using a steam-heated de-greasing plant at the R.A.F. airfield and a mixture of light diesel oil and heavy furnace oil in equal proportions. This turned out to contain about 2% DNC.

The spray technique was to discharge the liquid from a pipe 6 cm in diameter so that it was shattered into drops of various sizes on entering the slip-stream. The aircraft was to be flown at right angles to the wind. The big drops would fall almost straight down, while smaller and smaller drops, with their successively lower terminal velocities, would be carried further and further by the wind before reaching ground level, so covering a wide swath on each spray line. We used a repetition interval of 50 m giving overlapping swaths, based on the work at Porton (Kennedy *et al.* 1948). Julius Ward came out from Porton, so we had guidance in all sorts of unfamiliar matters, including assessing drop sizes and distribution in the swath. The dosage could be decided in advance and appropriate allowance made for the wind by deciding on a height/wind product: the stronger the wind, the lower the aircraft would be flown. Some 70% of the emitted liquid – seldom more, sometimes less – could be found by sampling on the ground.

By this technique, the aircraft was flown high enough to avoid disturbing the locusts; but it was always uncertain if there would be time to complete the spraying before the swarm moved off. We carried out five such operations. The time available for the spraying itself was even shorter than that from the end of demarcation of the swarm to its departure; the technique required a wind steady in speed and direction, but the wind settled down, after being light and variable at dawn, only a short time before the swarm left (Gunn *et al.* 1948*a*).

What we learnt in Kenya, however, made possible a valuable success 2 years later in air-to-ground attack on a threatening but rather static population of adult Red Locusts in the Rukwa Valley outbreak area of Tanganyika (now named Tanzania). This was undertaken at short notice, taking advantage of insecticide ten times as concentrated and other developments; and we were able to complete our final report on it for publication within 6 months of the Council's decision to mount the operation (Gunn *et al* 1948*b*).

In that publication, we tried to calculate what the operations would have cost under operational conditions, as distinct from experimental conditions, to show how the cost per unit would depend on the scale of operations and how such calculations could be used to help in choosing systems of control. In later years this led on to thorough operational research on control of Red Locusts, so that within 10 years every method of control had been changed (Lloyd 1959). Not only was the service then capable for the first time of preventing any Red Locust outbreak, it could do so at about half the previous annual cost, a 'non-Parkinsonian' result (Gunn & Symmons, 1959; Gunn 1960).

In our 1947 calculations, we ignored the considerable cost of ground party personnel and vehicles. For the Desert Locust, however, the necessity of having ground parties at all defeated the objective of matching the mobility of swarms with the mobility of aircraft so that, apart from the inadequate time available before swarm departure in the morning, this system simply would not do.

4. AIR-TO-AIR SPRAYING

Accordingly, in Kenya in 1945, we had next tried spraying swarms in flight, using Porton's spray-curtain methods. These had to depend on assumptions to supplement information then available about the structure of swarms, their density and their speed over the ground, and about the airspeed of the locusts. The original idea was to spray repeatedly between two air-positions, marked by smoke puffs. Each spray line would open out into a spray-sheet as the larger drops fell faster than the smaller ones. The resulting curtain of drops was to be flown through by the locusts which could be expected to pick up enough to kill them, under conditions indicated by a long series of laboratory determinations of pick-up and toxicity of insecticide sprays applied to individual flying locusts (Kennedy *et al.* (1948), whose work was later extended by Wootton & Sawyer (1954) and MacCuaig (1962)). Theoretical models of the spraying of flying swarms had also been developed (Ward in Gunn *et al.* 1948*a*) later followed by Sawyer (1950), Rainey & Sayer (1953) and MacCuaig & Yeates (1972). The advantages of this system of spraying would be that (*a*) most of the hours of daylight were available for operations and (*b*) no ground party required, unless for checking.

We now know that various assumptions that had initially been necessary were not applicable. The headings of the individual locusts in a swarm are by no means all the same or even nearly so; the direction of elongation of a swarm does not indicate locust headings, which may in fact be effectively almost random in direction in some swarms (Rainey & Sayer 1953; Waloff 1972). The directions of wind, swarm elongation and most common locust heading may be all different. In fact the airman had an impossible task in trying to decide where to lay the curtain.

Nine air-to-air operations were done. Some failed because of defective radio communications, some because the instructions were (not surprisingly) too difficult for the pilot to carry out, and some because the assumptions made in the theory were inapplicable.

5. 1945

Thus in spite of cordial and massive help from the Chemical Defence Experimental Station at Porton and from the R.A.F. at home and in Kenya, and hard work by an enthusiastic team in the field, we did not kill many locusts. We had, however, made a start on finding out systematically how to attack locusts more effectively and more efficiently. So the methods we used, the theories behind them, the results and the mistakes we made were all described and published. In the event, the techniques that we had most fruitfully found out and used were field methods for the quantitative assessment of locusts in swarms, of reconnaisance, of spray distribution, of numbers of locusts killed, and other necessary procedures. Some of these are outlined in later sections below. They constituted initial contributions to an integrated and logical programme of research and development aimed at better insecticides, spray gear, tactics and strategy. At the same time, laboratory research in universities and elsewhere was stimulated and helped, with a view to providing a better background of knowledge of the physiology and behaviour of locusts; perhaps the best known of these were the physiology and aerodynamics of flight by Weis-Fogh starting in 1947 (Krogh & Weis-Fogh 1951) and the insect detoxication of insecticides by R. T. Williams and others from 1951 (Robinson, Smith & Williams 1953), and there were others too many to mention (Rainey 1961).

Probably our most important innovation was the introduction of Porton-based methods of physical analysis. From the start, we measured, estimated, altered, and measured again, so that any method tried could be properly analysed to indicate how to do better next time.

Perhaps the most important of all was the realization that spray technique, however good, was not enough in itself. A technique less than the best could be the most effective if it fitted best into locust behaviour, wind structure and changes, human limitations, terrain and so forth. In fact what was wanted was a complete system – certainly with a very good technique – which was the best available as a system.

6. LOCUST AIRSPEED

We were able to record the first direct measurement of the airspeed of a free flying locust (Gunn *et al.* 1948*c*). Mr Graham's figure of 4.6 m/s at 29 °C was later confirmed by Rainey & Waloff (1951) by a vector treatment of visual observations, giving 4.9 m/s at 31–32 °C (see also Waloff 1972*a*); improved data subsequently secured photographically by H. J. Sayer (1956) gave a figure of 5.5 m/s (in Rainey 1963). These figures of field data refer to locusts in swarms flying low in 'rolling' swarms (see below), in which the individual locusts are therefore likely to have taken to flight shortly before; these figures are about twice as large as those obtained in sustained tethered flight in a wind-tunnel (3 m/s by Weis-Fogh 1952) and at Porton (2.75 m/s Kennedy *et al* 1948, Wootton & Sawyer 1954). Weis-Fogh calculated that 3 m/s could be sustained for 12 h continuous flight without fuel running out, but 4–5 m/s for only 4–5 h. Since, in the tropics, swarm migration over land may continue for 10 h daily, it is not surprising to find that the locusts do not generally fly continuously but feed to some extent daily.

Airspeeds are thus now available which are probably applicable to both continuous flight and rolling flight, figures that are required for calculating the drops picked up by a flying locust and therefore affecting emission rates and drop sizes required.

7. Swarm structure

Our observations showed much variation in swarm structure. Sometimes the locusts flew very densely up wind, low, in a narrow stream, which would make a vulnerable target; but that was rare. More commonly the swarm was less concentrated. The locusts in front tended to settle and feed, while much of the swarm passed over. But the settled ones would take off and join the main stream soon enough to avoid being left behind. This we called a 'rolling' swarm and was like a huge amoeba. I do not recall ever seeing a swarm that was not in some degree rolling; non-rolling swarms are indeed rare (Rainey 1958*b*). Sayer's photographic techniques, including double or quadruple exposure (1956, 1965), showed clearly that there was no fixed relation between locust heading and swarm track, if only because of the different headings between different groups of locusts in one swarm at one time (Waloff 1972*b*). In such conditions, the swarm would generally progress more slowly than the wind, so that a curtain laid in front of it would be blown away ahead and not kill a single locust. Rainey & Sayer (1953) followed rolling swarms in full migration and found that the track of each swarm was close to directly down wind, but with ground speeds slower than the corresponding wind-speeds.

Finally, in hot sunny weather a swarm could often be seen from afar, towering thousands of feet into the air. We now know that this formation is due to locusts being carried up by air rising in thermals after being heated by the ground (Rainey & Waloff 1951, Rainey 1958*b*).

8. Reconnaisance

With our knowledge of swarm structure and some experience of seeing swarms from the air, a zoologist–navigator posted to the Anti-Locust Flight (F/Lt Graham) embarked on a systematic quantitative study of finding swarms. He described methods of systematic searching by air, visibility of settled swarms in relation to size and angle to the sun's rays and also visibility of flying swarms in relation to size, distance and structure (Gunn *et al.* 1948*a*). His were the first steps in systematic and quantitative planning of air reconnaisance; subsequent results from this approach were reviewed by Rainey (1962).

We knew nothing about forecasting detailed movements of individual swarms. We were told by Mr R. E. T. Hobbs, Agricultural Officer at Kitale, when we followed a swarm through that district, that swarms had gone that same way, between Mt Elgon and the Cherangani Hills, at the same season year after year. This was the direction of the seasonal wind when it set in a little later, but our observations were made between seasons, with wind directions at ground level too variable to show relationships with our erratic swarm tracks.

In later years, once a swarm had been found, its subsequent direction of movement could be predicted according to wind direction at the appropriate height (Rainey & Sayer 1953, Rainey 1963).

9. Population estimation and assessment of results of attacks

Before 1945, little had been attempted on population assessment and that mainly by Ramchandra Rao (1942). Nobody had any idea of how many locusts there were in a plague nor of how to assess control operations effectively.

The classical method of catching and caging locusts before and after control operations is almost useless. First, spray deposit and therefore often mortality are variable in the target area, especially at the edges; second, sprayed locusts tend to contaminate others in the same cage; and third, after spraying, unaffected locusts are difficult to catch and affected ones are not. Leaving aside the third point, with any number of cages reasonable for travel in field conditions cage assessments are not reliable. In any case, the method provides only figures of percentage mortality which is not the main need.

In a policy of attrition, what is needed is the total number of locusts killed to indicate the effect on the plague; we estimated this figure on several occasions in 1945, the largest number being 2.7 ± 0.5 million, which was far exceeded in later years.

The effectiveness of an insecticide can also be estimated by using, in a given system, numbers of locusts killed per unit of actual insecticide; in 1947 we expended $1\frac{1}{2}$ tons of 2% γBHC solution and killed about 3 tons of locusts, a mass ratio of one unit of actual toxicant to 100 of locusts (Gunn *et al.* 1948*b*). Rainey (1958*c*) later achieved a ratio of 34000 in a favourable case but probably about 500 or 1000 in a whole campaign (Rainey 1954). Rainey & Sayer (1953) were able to demonstrate the merits of the, then new, very concentrated solution of γBHC in oil by using only 225 l of it; this solution turned the tide against the Desert Locust in Morocco in later years, in what proved to be the first strategically effective campaign against the Desert Locust. Such figures are essential in planning and costing operations (cf. §3).

We established suitable sampling methods of finding totals of dead locusts (Gunn *et al.* 1948*a*), but populations of live locusts presented more difficult problems. It seemed impossible to count living locusts in swarms, either settled or flying, though radar techniques are contributing such evidence on flying swarms (Ramana Murty *et al.* 1964, Schaefer 1976). We photographed locusts in many situations for subsequent study and a general method did emerge from that.

Our first success took advantage of an air-to-ground spray operation in which the aircraft was inadvertently flown too low for the wind speed. The result was black lines of insecticide (in furnace oil) on the dripping bushes and on the ground, killing all the locusts there probably within minutes, with practically unsprayed strips between. The widths of the sprayed and unsprayed strips were measured and the corpses counted in a series of transects. The whole area of the swarm was also measured. The total area of black lines and the total number of corpses in the measured transects enabled the density of settled locusts to be calculated and from that the total in the original swarm and the total killed (Gunn *et al.* 1948*a*). This soon developed into the drench spraying method of finding locust densities and in turn total numbers in swarms (Gunn *et al.* 1948*b*, Rainey 1958*c*). In this intentional spray-drenching the aircraft is flown not only as low as possible but also against the wind, not across it, so as to make the sprayed strip as narrow and sharp-edged as possible.

Our other general method was photographic. We photographed and counted a local density of 160 locusts per square metre on flat ground, which was of no general value because many were on surrounding bushes. We then used photographs of locusts passing at eye level, and of course began with a moment when there were plenty of locusts to photograph, rather than a representative sample of the whole swarm. We assumed that the locusts were all the same length and used pictures where they were square on to the camera's sight line. From the geometry of this situation, we were able to record an average of 14 locusts per cubic metre. Extending the method to photographing vertically upwards, in 1947 in a Red Locust swarm we found an area-density of 36 locusts per square metre (Gunn *et al.* 1948*b*).

This was the start of developments by Sayer (1956, 1965), who invented a special camera shutter for this and other purposes, by Hemming and finally Waloff (1972). Photographs were taken vertically upwards from the ground with a very high quality (F24) aircraft camera fitted with a telescopic lens, and these could show the locusts clearly enough up to 400 m above. By photographing at regular intervals during swarm passage, not choosing dense parts of it, representative volume densities were found. These were generally much less than our density of 14 locusts per square metre which was generally 100 to 1000 times too large for an average of a swarm in full migration.

Following Gunn *et al.* (1948*a*) swarm areas were estimated by timed aircraft traverses and the total number and sizes of swarms in a plague could be estimated by adequate aircraft reconnaissance. Taking representative values of area-density, Rainey estimated in 1954 the order of magnitude of the total size of a Desert Locust invasion of Kenya and Tanganyika. He also estimated the numbers killed, so providing the most revealing analysis of a control system, especially for comparison with the immediately previous control of hoppers in Ethiopia and Somaliland (Rainey 1955, 1958*a*; Rainey *et al.*, this symposium).

Quite different methods have been developed for static populations of Red Locusts in outbreak areas (Scheepers & Gunn 1958; Symmons, Dean & Stortenbeker 1963).

10. INSECTICIDES AND DROP FORMATION

I shall be saying very little about these subjects. R. D. MacCuaig will cover insecticides in his paper (this symposium) and he will deal with some of his many contributions to locust control in this field. We had to work with the only insecticide available then and there (DNC), a very effective and quick-acting one too, and we recommended that a way be found of making a solution ten times as concentrated; we could then use air as the only diluent that uses no payload, is cost free, harmless and always abundant. Porton did not take long to achieve a 20% solution of DNC, using as solvent what was then a waste product. The new solution was used not only in Africa in 1947 and later, but also in the Argentine. The solvent was further used to make up concentrated γBHC, a toxicant which is roughly as toxic to locusts as DNC, and furthermore cumulative though slow in action, as well as being without the toxic properties of DNC to mammals and plants.

With the more concentrated solution, drops produced by emission from an open pipe through the slip stream would not serve, for one big drop would be an overdose. Moreover the Baltimore aircraft sprayed at 90 m/s compared with 35–50 m/s of the smaller aircraft subsequently used, speeds that would not shatter the liquid so much. At first, spray booms with the usual types of nozzle were used extensively, with the disadvantages of frequent blockages of jets, a drop spectrum not under close control, and a high pressure plumbing system. The spinning disc used in the laboratory gives drops of two sizes, the main drops and small satellites, but this would not serve because it is so easily overloaded, so that rapid emissions with standard drops are impossible. Eventually the spinning cage has become the best method of drop formation, giving a close spectrum under control; it was first used against the Desert Locust in 1957 in West Africa (Mallamaire & Roy 1958).

11. An improved system for controlling flying swarms

It was Rainey & Sayer (1953) who found a solution to the problem of the best tactics for controlling a swarm in full migration. It was charmingly simple. The aircraft was flown across wind through the top of the swarm above its thickest part, which was sprayed. This was arrived at by using a mistaken method in 1952 (trying to spray the settled locusts under a rolling swarm, using the flyers as markers) and then analysing the results fully in the best Porton tradition. The graphical analysis introduced by Sawyer (1950) was used and extended. This indicated that it was the flying locusts and not the settled ones that had supplied most of the corpses (Rainey & Sayer 1953, Rainey 1974). The technique was then adjusted for best attack on the flyers.

The new method was used to try to control a very large invasion of Desert Locusts from Ethiopia and Somaliland into Kenya and then on into Tanganyika from January to March 1954. The campaign extended over nearly 1000 km from the Somali border into central Tanzania and lasted 65 days. On 55 of those days, swarms were attacked, using a series of ten bases, moving back with the advance of the invasion. About one tenth of a tonne of locusts was destroyed per litre of 20 % DNC, to totals of 165 tonnes of insecticide and 1 or 2 × 10^{10} locusts. This could have been no more than a quarter of the invading locusts (Rainey 1954); it was, however, comparable in unit cost with good hopper baiting in Ethiopia and Somaliland, which may perhaps have halved the original potential invaders (Rainey & Sayer 1953, Rainey 1958*c* and especially 1958*a*). The scale of the combination of operations was clearly too small, but one may imagine what an unchecked invasion would have been like.

At the same time, techniques of hopper control were also being analysed and improved, as is discussed in my other paper in this symposium.

In any event, what had been begun in 1945 had reached a useful stage by 1954. By the end of the following decade, there was evidence (see Rainey, Betts & Lumley, this symposium) that even against the Desert Locust, the scale and effectiveness of control operations were beginning to solve the problem of preventing plagues.

In order to summarize how those changes have come about, the following list starts with Kennedy's work at Porton, goes on to the lines of development begun in Kenya in 1945, and then brings the story up to date.

1. Laboratory methods of testing toxicity of insecticides to locusts, not only by topical application but also by pick-up of spray droplets by (tethered) flying locusts.
2. Field studies on locust swarm behaviour, not only at morning departure (§2) but also in swarm formation (§7), and the airspeed of individual locusts (§6), necessary for deciding on the characteristics of the spray required to attack flying locusts.
3. Field methods, devised at Porton, for measuring distribution of spray (§§ 3,5).
4. Field methods of estimating total numbers of locusts killed, to enable kill per unit of insecticide to be calculated (§9).
5. Field methods of estimating numbers of live locusts to facilitate assessments of relative effects of operations and also to enable the magnitude of an invasion and the cost of controlling it to be estimated (§4).
6. Methods of finding swarms and estimating their importance as targets (§8).
7. Methods of producing spray droplets (§10).
8. Methods of choosing aircraft and equipment and organizing operations, to which several groups contributed, especially Mallamaire & Roy (1958).

9. Theoretical and graphical models of spray-curtain behaviour, begun at Porton, in relation to attack on flying swarms, enabling toxicity, emission rate, drop spectrum, height to fly and so forth to be decided and harmonized with one another.

10. Methods of forecasting direction of swarm migration and locust endurance, to which laboratory studies on locust physiology in flight contributed.

11. Biogeographical studies to establish national, regional, and international strategies.

The uses to which these developments were put are outlined in the papers in this symposium, by Adefris, Abdallahi, Roy, Joyce, Rainey *et al.* and the other paper by this author, and they are also woven into other papers.

References (Gunn)

Fraenkel, G. S. & Gunn, D. L. 1940 *The orientation of animals. Kineses, taxes and compass reactions.* Oxford: Clarendon Press. Reprinted 1961 with additional notes. New York: Dover Press.

Gunn, D. L. 1960 Nomad encompassed. *J. ent. Soc. S. Afr.* **23**, 65–125.

Gunn, D. L., Graham, J. F., Jaques, E. C., Perry, F. C., Seymour, W. G., Telford, T. M., Ward, J., Wright, E. N. & Yeo, D. 1948*a* Aircraft spraying against the Desert Locust in Kenya, 1945. *Anti-Locust Bull.* **4**.

Gunn, D. L., Kirk, R. L. & Waterhouse, J. A. H. 1945 An improved radiation integrator for biological use. *J. exp. Biol.* **22**, 1–7.

Gunn, D. L., Lea, H. A. F., Botha, D. H., Callaway, S., Clackson, J. R., Immelman, A., Taljaard, J. J. & Ward, J. 1948*b* *Locust control by aircraft in Tanganyika in 1947.* London: Anti-Locust Research Centre. Pretoria: Locust Control and Research Section, Dept. of Agriculture.

Gunn, D. L., Perry, F. C., Seymour, W. G., Telford, T. M., Wright, E. N. & Yeo, D. 1948*c* Behaviour of the Desert Locust in Kenya in relation to aircraft spraying. *Anti-Locust Bull.* **3**.

Gunn, D. L. & Symmons, P. M. 1959 Forecasting locust outbreaks. *Nature, Lond.* **184**, 1425–1426.

Gunn, D. L. & Yeo, D. 1951 The Bellani spherical pyranometer or radiation integrator: calibration and improvements suggested. *Q. Jl R. met. Soc.* **77**, 293–391.

Kennedy, J. S., Ainsworth, M. & Toms, B. A. 1948 Laboratory studies on the spraying of locusts at rest and in flight. *Anti-Locust Bull.* **2**.

Krogh, A. & Weis-Fogh, T. 1951 The respiratory exchange of the Desert Locust during and after flight. *J. exp. Biol.* **28**, 342–357.

Lloyd, J. H. 1959 Operational research on preventive control of the Red Locust. *Anti-Locust Bull.* **35**.

MacCuaig, R. D. 1962 The collection of spray droplets by flying locusts. *Bull. ent. Res.* **53**, 111–123.

MacCuaig, R. D. & Yeates, M. N. D. B. 1972 Theoretical studies on the efficiency of insecticidal sprays for the control of flying locust swarms. *Anti-Locust Bull.* **49**.

Mallamaire, A. & Roy, J. 1958 La lutte contre le criquet pèlerin en Afrique Occidentale Francaise. *Bull. Prot. vég.* p. 113.

Pereira, H. C. 1959 Practical field instruments for estimation of radiation and evaporation. *Q. Jl. R. met. Soc.* **85**, 1–8.

Pereira, H. C., McCulloch, J. S. G., Dagg, M., Hosegood, P. H. & Pratt, M. A. C. 1962 Assessment of the main components of the hydrological cycle. *E. Afr. agric. For. J.* **27**, 8–15.

Rainey, R. C. 1954 Recent developments in the use of insecticides against locusts. *Rep. 6th Commonwealth ent. Conf. London*, pp. 18–51.

Rainey, R. C. 1958*a* The comparative assessment of control methods. *Proc. 10th Internat. Congr. Ent., Montreal* 1956, **3**, 263–268.

Rainey, R. C. 1958*b* Flying locusts and atmospheric turbulence in eastern Africa. *Q. Jl. R. met. Soc.* **84**, 334–354.

Rainey, R. C. 1958*c* The use of insecticides against the Desert Locust. *J. Sci. Food Agric.* **10**, 667–692.

Rainey, R. C. 1961 The Desert Locust: an international challenge. *New Scient.* **10**, 709–711.

Rainey, R. C. 1962 Aircraft reconnaissance and assessment of locust populations. *Rep. 2nd int. agr. Aviation Congr. September* 1962, *Grignon, France.* pp. 228–233.

Rainey, R. C. 1963 Meteorology and the migration of Desert Locusts. *Anti-Locust Mem.* **7**.

Rainey, R. C. 1974 Flying insects as targets for ultra-low-volume spraying. *Brit. Crop Prot. Monogr.* **11** (or **12**), 20–28.

Rainey, R. C. & Sayer, H. J. 1953 Developments in use of aircraft against flying swarms. *Nature, Lond.* **172**, 224–228.

Rainey, R. C. & Waloff, Z. 1951 Flying locusts and convection currents. *Anti-Locust Bull.* **9**, 51–72.

Ramana Murty, Bh. V., Roy, A. K., Biswas, K. R. & Khemani, L. T. 1964 Observations on flying locusts by radar. *J. scient. ind. Res.* **23**, 1–8.

Ramchandra Rao, Y. 1942 Some results of studies on the Desert Locust in India. *Bull. ent. Res.* **33**, 241–265.

Riley, C. V., Packard, A. S. & Thomas, C. 1878, 1880, 1883 *First, Second and Third Reports of the United States Entomological Commission relating to the Rocky Mountain Locust.* Washington, D.C.

Robinson, D., Smith, J. N. & Williams, R. T. 1953 Studies in detoxication (locusts) 45. *Biochem. J.* **53**, 125–129.

Sawyer, K. F. 1950 Aerial curtain spraying for locust control. *Bull. ent. Res.* **41**, 439–457.

Sayer, H. J. 1956 Photographic method for the study of insect migration. *Nature, Lond.* **177**, 226.

Sayer, H. J. 1965 The determination of flight performance of insects and birds and the associated wind structure of the atmosphere. *Anim. Beh.* **13**, 337–341.

Schaefer, G. W. 1976 Radar observation on insect flight. *Symp. R. ent. Soc. Lond.* **7**, 157–197.

Scheepers, C. C. & Gunn, D. L. 1958 Enumerating populations of adults of the Red Locust (*Nomadacris septemfasciata* Serville) in its outbreak areas. *Bull. ent. Res.* **49**, 273–285.

Symmons, P. M., Dean, G. J. W. & Stortenbeker, C. W. 1963 The assessment of adults of the Red Locust in an outbreak area. *Bull. ent. Res.* **54**, 549–569.

Waloff, Z. 1972*a* Airspeeds of freely flying locusts. *Anim. Beh.* **20**, 366–371.

Waloff, Z. 1972*b* Orientation of flying locusts in migrating swarms. *Bull. ent. Res.* **62**, 1–72.

Waloff, Z. 1976 Characteristics of Desert Locust plagues. *Anti-Locust Mem.* **13**.

Waloff, Z. & Rainey, R. C. 1951 Displacement of Desert Locust swarms. *Anti-Locust Bull.* **9**, 1–50.

Weis-Fogh, T. 1952 Fat combustion and metabolic rate of flying locusts. *Phil. Trans. R. Soc. Lond.* B **237**, 1–36.

Wootton, N. W. & Sawyer, K. F. 1954 The pick-up of spray droplets by flying locusts. *Bull. ent. Res.* **45**, 177–197.

Discussion

H. D. Brown (*RLCS, Pretoria*). Although plague locusts can be conveniently separated into type A and type B species on the relative sizes of their source and invasion areas, the distinction is not always as clear cut as one would like it to be. In the case of the Red Locust, type B species which was originally believed to swarm from only two small permanent breeding areas in central Africa, there have been, for example, an increasing number of upsurges, especially over recent years, from areas that were not previously regarded as outbreak areas. The number of areas favourable for the production of migrant swans has in fact increased now to seven, and in time more will undoubtedly have to be added. Significantly, high flood levels in the two original key areas, the Rukwa Valley and the Mweru wa Ntipa, have virtually eliminated them as important Red Locust breeding areas and the control effort has had to be shifted elsewhere. This has important implications for control strategy for it implies that a number of ecologically similar floodplain grasslands – the preferred habitat of the Red Locust – and there are many of these scattered over central and southern Africa, could at some time or another become active and produce swarms. Although only a small number of swarms may in fact be produced from some of these areas, their importance cannot be overlooked, for it seems that only a few escaping swarms were sufficient to start the last Red Locust plague. Rather than a few fixed outbreak areas for the Red Locust being known, it is beginning to appear that virtually any sufficiently extensive floodplain grassland, i.e. large enough to produce swarms, is a potential swarm-production area. And over the whole range of the species these areas undergo periodic cycles of suitability, because of climatic and/of habitat changes, and function intermittently as locust outbreak areas. These 'shifting outbreak areas' widely scattered over Africa south of the equator therefore cover a much larger proportion of the invasion area than was previously considered possible. This obviously influences control strategy and greatly increases the task of preventive control and supervision of such scattered areas and in effect is one of the operating problems presently facing IRLCOCSA in central Africa which has had to increasingly extend operations to a growing number of distant areas in order to prevent swarm escapes.

D. L. Gunn. I welcome the comments of Dr Dick Brown, whose first contact with Red Locusts was only two years after mine; he is now in charge of Red Locust control in South Africa. I gain the opportunity of expanding some ideas.

When the International Red Locust Control Service was formally set up by treaty in 1949, after 8 years of British–Belgian cooperation in the work, only one area–Mweru wa Ntipa–was *known* to have produced swarms which were *known* to have begun the plague of 1930–44. The Rukwa Valley was also considered important and Michelmore had cast suspicion on the Malagarasi Basin; other possible areas were discussed. It was, however, administratively sound tactics – at which Uvarov was expert – to define clearly the tasks for the proposed IRLCS, namely to control the two main areas.

It was, of course, biologically unlikely that areas would be sharply divided into outbreak and non-outbreak areas and, as Dick Brown has indicated, events have discouraged a sharp division. In my discussion of this (Gunn 1960*b*, pp. 115–117), I also proposed four criteria of a true outbreak area which recent events have not satisfied. In particular the fourth criterion has not been satisfied in that no plague has arisen from escaped swarms. Indeed nothing more has been heard of them or of any progeny.

The Wembere in Central Tanganyika was suspected of being an outbreak area in 1953. It produced a migrant swarm in 1959 when Rukwa was producing only moderate numbers of locusts; in most years since then there has been some control in Wembere and in four years swarms have emigrated and not been controlled. They have not started plagues. Perhaps they were too few – the number of swarm reports is little indication of the number of swarms – and we have no indication of numbers of locusts. Perhaps several seasons of successful breeding in the best breeding areas – the outbreak areas – are necessary to reach numbers of locusts adequate for a plague (Gunn 1960*a*, p. 287). That seems to have happened in Mweru wa Ntipa in 1928–30 (Gunn 1955), when one swarm was reported to be four miles long in 1930. The statement that the plague of 1930–44 was started by only a small number of swarms is often repeated and it encourages control people not to let even one swarm escape; but nobody knows how many there were or how large and the sparsity and sketchiness of reports discourages belief that what was reported was all there was.

During the last 15 years or so, when the Mweru wa Ntipa and Rukwa regions have been too widely and too continuously flooded to produce locusts, it is a pity that the Wembere and its populations were not studied and recorded as intensively as the classical areas have been and that the hopper control methods were not brought up to the standard achieved with Desert Locust hoppers.

The Wembere swarms have not started plagues, possibly because the Wembere is unsuitable, for example in relation to seasonal-wind migrations and secondary breeding areas; on the other hand, in the 5 years of escaped swarms, purely temporary features may have been against them. Perhaps the most likely hypothesis is that control within the Wembere has reduced the numbers too much to allow that enormous increase in numbers that is probably essential. In any case, the activity of the region seems to have risen as that in Mweru wa Ntipa and Rukwa declined to practically nothing because of flooding; during the next drier phase presumably the status of the 1950s will be restored, making Wembere – and presumably the Mozambique breeding area which has released swarms into Rhodesia – not so much additional areas as alternatives.

The operational importance of classifying outbreak areas is this; when I was Director, I was empowered by the treaty to control the two classical outbreak areas and to watch Malagarasi.

If a serious Red Locust situation arose elsewhere, it was to be regarded as a local matter; but only the IRLCS was equipped and experienced in controlling Red Locusts and anything done should be done both quickly and well, in the interests of all. I would have to choose between taking time to seek authority from the contributing governments to go outside the treaty provisions and so lose the chance of success and, on the other hand, adopting a Nelsonian attitude to the treaty and acting at once. After I had been Director for a few years, the Council was sympathetic to my attitude of not waiting. My successors preferred to multiply so-called outbreak areas and be formally correct.

In the same practical way, Dick Brown is absolutely right that any migrating swarms should be destroyed as they were in east Rhodesia in 1972 and 1974, whatever their origin. The task of the control services is to prevent plagues and nobody else is equipped and trained to do this without delay. So whether the swarms come from accepted outbreak areas or not, they should be destroyed. But let us not waste substance on localized increases of population that are of no importance. Expert understanding, methods of assessment and experience are required to avoid both waste and failure.

References

Gunn, D. L. 1955 Mweru wa Ntipa and the Red Locust. *Nth. Rhod. J.* **2** (6), 3–15.
Gunn, D. L. 1960*a* The biological background of locust control. *A. Rev. Ent.* **5**, 279–300.
Gunn, D. L. 1960*b* Nomad encompassed. *J. ent. Soc. S. Afr.* **23**, 65–125.