

2002-08
C. W. Stortenbeker

Institute for Biological Field Research ITBON, Arnhem

Observations on the Population Dynamics
of the Red Locust, *Nomadacris septemfasciata* (Serville),
in its Outbreak Areas



1967 *Centre for Agricultural Publications and Documentation*
Wageningen

v

2002-08

The author was awarded the degree of Doctor in Mathematics and Natural Science, State University, Leyden, the Netherlands, on a thesis with the same title and contents.

© Centre for Agricultural Publications and Documentation, Wageningen, 1967.

No part of this book may be reproduced and / or published in any form by print, photoprint, microfilm or by any other means, without written permission of the publisher.

Acknowledgements

I wish to express my gratitude to Dr D. L. GUNN, who as a Director of the International Red Locust Control Service initiated the research programme on the population dynamics of *Nomadacris* and who critically read the manuscript of this paper. I also wish to thank his successor Mr C. DU PLESSIS for his support and interest in the work. I am very grateful to Dr P. M. SYMMONS for allowing me to make use of several of his unpublished results and also for his valuable criticism of the successive stages of the writing up. The same applies to Mr G. J. W. DEAN, whom I want to thank in particular for the many hours on safari and in the office, spent on discussing *Nomadacris* and its habits, discussions that helped much in seeing the problems more clearly.

I am most grateful to the staff of the I.R.L.C.S., several members of which I want to mention in particular: Mr D. F. VESEY FITZGERALD for his inspiring enthusiasm, Dr A. R. W. CROSSE UPCOTT and Mr T. MALUJO for being so research minded, Mr R. R. FORRESTER and Mr B. J. EYSSEL for inspiration derived from their great field experience and Mr E. M. REEKS and his mechanical staff for patiently repairing and maintaining the vehicles.

Most of all I am grateful to the many African staff members and in particular to the African Locust Officer LAZARUS THOMAS MBAO, the Field assistant LUI JOSEPH MSATO and the research scouts Lui, Meriano, Fungulia, Geuza, Oskar, Daudi, Fideli, Modesti, Matthias and Jim, without whom I could have carried out only one-tenth of the work.

I greatly acknowledge the help I received from Dr E. PINHEY, National Museum of Rhodesia, Bulawayo, who classified Odonata for me, and from Dr I. M. NEWELL, University of California, who identified the various mites I found.

I wish to thank Dr P. T. HASKELL and his staff for their great hospitality and helpfulness during my stay at the Anti Locust Research Centre, London.

I want to express my sincere gratitude to Professor Dr D. J. KUENEN for his stimulating interest in the work and for his valuable suggestions for improvements in the manuscript.

I want to thank Dr A. D. VOÛTE for his support, the 'Bureau van de Hoofdingenieur' of the Ministry of Agriculture for drawing the figures and PUDOC for publishing this paper.

Finally I wish to thank my wife for her great help and support from start to finish.

Contents

| | | |
|-------|--|----|
| 1 | INTRODUCTION | 3 |
| 1.1 | The Problem of the Red Locust | 3 |
| 1.2 | Life Cycle and Habitat | 5 |
| 1.3 | Literature | 9 |
| 1.4 | The Problems | 10 |
| 2 | METHODS AND MATERIALS | 12 |
| 2.1 | Population Assessments using a Land Rover or a Swamp Skipper | 12 |
| 2.2 | Catching of Adult Locusts | 12 |
| 2.3 | The Experimental Plots in Burnt-off Grassland | 13 |
| 2.4 | Egg-pod Assessments | 16 |
| 2.5 | Estimating the Incubation Success of Eggs and Egg-pods | 16 |
| 2.6 | Hopper Mortality Estimates | 17 |
| 2.7 | Predator Assessments | 19 |
| 2.8 | Phase Status of Populations Studied | 19 |
| 3 | FECUNDITY OF THE POPULATIONS | 20 |
| 3.1 | Sex ratio | 20 |
| 3.2 | Mean Number of Egg-pods per Female | 22 |
| 3.3 | Mean Number of Eggs per Egg-pod | 27 |
| 3.4 | Factors Influencing the Fecundity | 28 |
| 3.5 | Viability of the Eggs | 30 |
| 3.6 | Mean Number of Viable Eggs per Parent | 31 |
| 4 | INCUBATION SUCCESS | 32 |
| 4.1 | Numerical Data | 32 |
| 4.2 | Predators and Parasites on Egg-pods | 35 |
| 4.2.1 | Rats | 35 |
| 4.2.2 | Mites | 37 |
| 4.2.3 | Scelio howardi | 37 |
| 4.3 | The Effect of Drought | 39 |
| 4.4 | The Effect of Waterlogging of the Soil | 40 |
| 4.5 | Discussion | 42 |

| | | |
|-------|--|-----|
| 5 | NATURAL MORTALITY IN HOPPERS IN THE FIRST AND SECOND INSTARS | 48 |
| 5.1 | Mortality Assessments | 48 |
| 5.2 | Predators on First and Second-Instar Hoppers | 53 |
| 5.2.1 | Asilidae (Diptera) | 53 |
| 5.2.2 | Odonata | 60 |
| 5.2.3 | Other Predators | 75 |
| 5.3 | Other Causes of Mortality | 77 |
| 5.4 | Hopper Mortalities and Predator Densities | 78 |
| 6 | NATURAL MORTALITY IN LATER-INSTAR HOPPERS | 83 |
| 6.1 | Numerical Data | 83 |
| 6.2 | Birds | 84 |
| 6.3 | Other Causes of Mortality | 84 |
| 7 | NATURAL MORTALITY IN IMMATURE ADULTS DURING THE DRY SEASON | 86 |
| 7.1 | I.R.L.C.S. Records 1953-1963 | 86 |
| 7.2 | Birds | 89 |
| 7.3 | Other Causes of Mortality | 90 |
| 7.4 | Discussion. The Correlation between Multiplication Rate and Rainfall | 92 |
| 8 | DIFFERENCES IN IMPORTANCE OF THE OUTBREAK AREAS | 100 |
| 8.1 | Introduction | 100 |
| 8.2 | Outbreak Centres in Central Rukwa | 102 |
| 8.3 | Vegetation Zones in Central Rukwa | 104 |
| 8.4 | Soil Profiles in Central Rukwa | 105 |
| 8.5 | Discussion | 107 |
| | SUMMARY | 110 |
| | SAMENVATTING | 112 |
| | REFERENCES | 114 |

1 Introduction

1.1 The Problem of the Red Locust

The Red Locust, *Nomadacris septemfasciata* (SERVILLE), has been a serious plague during three periods within the last hundred years. From 1847 to 1854 a plague occurred in Zululand and Natal and in about 1892 Red Locust swarms invaded Southern Rhodesia (now Rhodesia) and South Africa from the north (FAURE, 1935). Origin and extent of these plagues are unknown. Again in 1930 swarms began to spread out over Africa, eventually covering most of the continent to the south of the equator. One swarm moved north into the Sudan and some swarms, almost certainly of local origin, were seen in the flood plains of the Niger, the outbreak area of the Migratory Locust, and around Lake Chad (Fig. 1.). The Red Locust is also known in Madagascar.

The origin of the initial swarms that started these plagues remained a mystery, until during the last outbreak the first swarms could be traced back to the marshy grasslands of the Mweru wa Ntupa in Northern Rhodesia (now Zambia), where they were first seen in 1927 and in 1928, and to swarms seen in 1930 in the grasslands of the Rukwa Valley in western Tanganyika (now Tanzania) (MORANT, 1947; SYM-

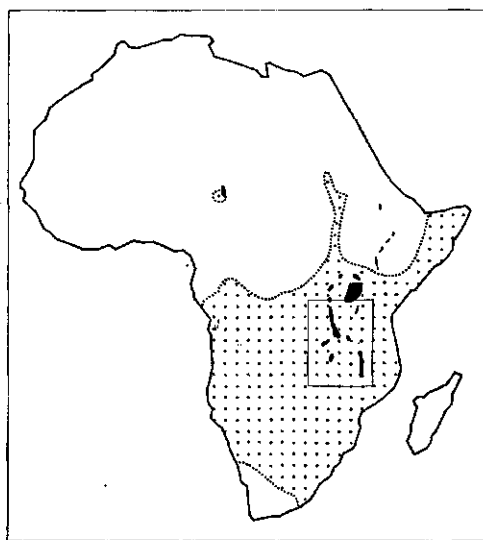


Fig. 1. Part of Africa covered by swarms during the most recent plague of the Red Locust from 1930 to 1945. All recognised outbreak areas are in the area enclosed by the rectangle

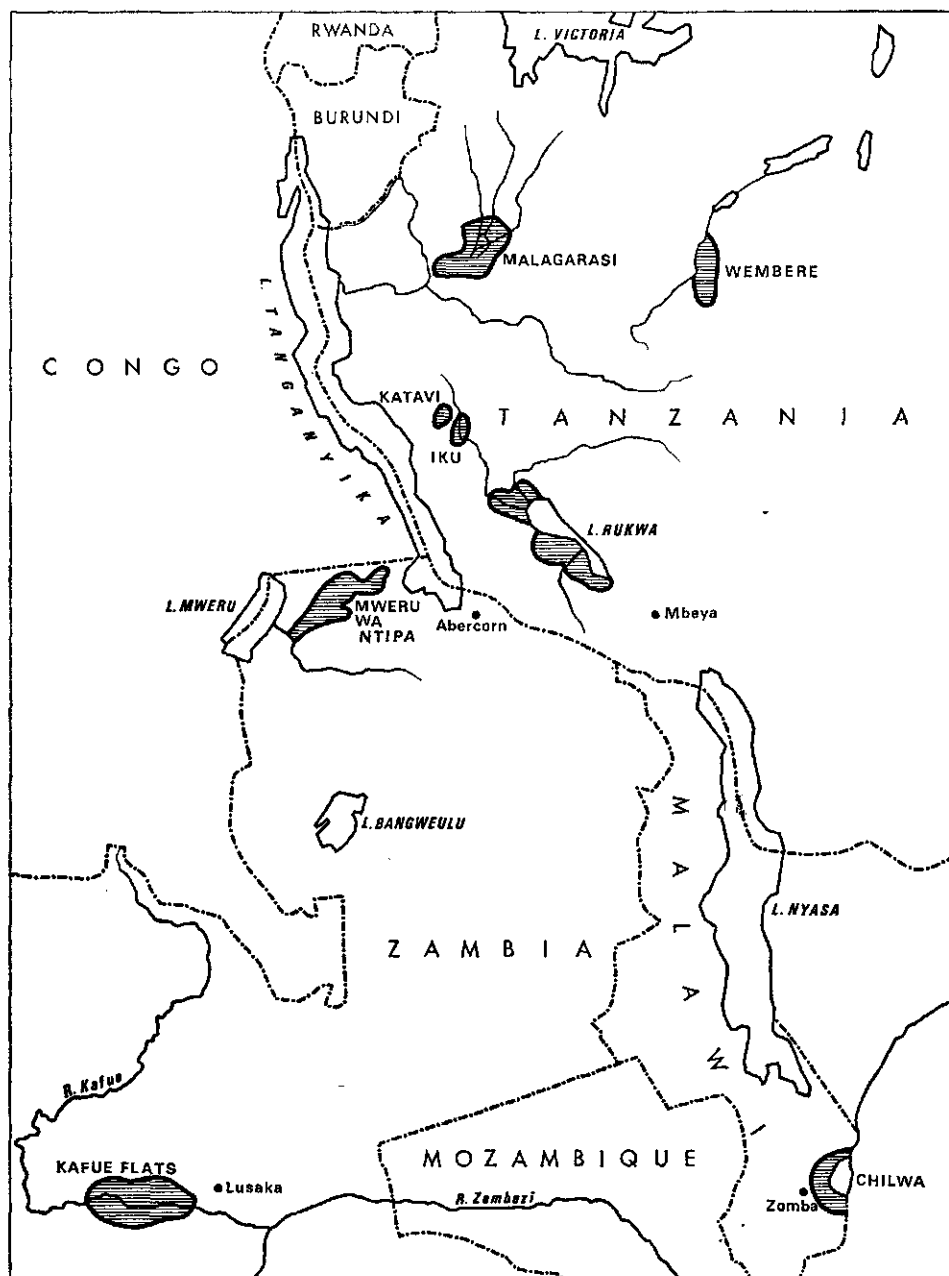


Fig. 2. The recognised outbreak areas of the Red Locust

MONS, 1964). It was concluded that upsurges of the Red Locust start from well defined and relatively small breeding areas, which were called outbreak areas. In 1941 the first control service was set up and in 1949 the present organisation, the International Red Locust Control Service, was established in order to prevent the formation of any further plagues at their source (GUNN, 1957, 1960). Besides the Mweru wa Ntipa and the Rukwa Valley some more of these outbreak areas have been recognised: the Iku plains, the flood plains in the Malagarasi drainage and the flood plain in the southern part of the Wembere depression (Fig. 2). In 1962 minor upsurges occurred in the Kafue flats in Zambia and in the flood plains round Lake Chilwa in Nyassaland (now Malawi), and these areas are now included in the list of recognised outbreak areas, which are under regular supervision and where occasionally chemical control is required.

The most recent plague died down in the years 1940-45, leaving behind small and scattered locust populations (MOSSOP 1951; BACKLUND 1955a; VESEY FITZGERALD, 1954, 1961), and solitary locusts can still be found in grasslands all over the invasion area. It is only in the outbreak areas, however, that numbers fluctuate excessively and that the Red Locust can breed up to swarm density. Several research workers have studied the outbreak areas and in particular their vegetation. They found that the areas have certain features in common, the ecological significance of which remained obscure.

In 1953 the I.R.L.C.S. started a research project on the population dynamics of the Red Locust and it was hoped that this research would ultimately lead to some form of ecological control. At first, time was devoted to the development of a technique of assessing adult-locust populations, using a Land Rover (SCHEEPERS and GUNN, 1958). This technique was examined more closely by SYMMONS, DEAN and STORTENBEKER (1963). In 1959 research into the population dynamics of *Nomadacris* began, in which P. M. Symmons concentrated on enumeration techniques and assessments, with some assistance from G. J. W. Dean and me. In addition Dean worked on predators, and I concentrated on parasites and diseases. In 1960 Dean, and in 1961 Symmons, took up work on different lines and until 1963, when the research project had to be abandoned, the work was conducted by me. Both Symmons and Dean kindly gave me permission to make use of some of their unpublished data. Where this is the case, it is clearly indicated.

1.2 Life Cycle and Habitat

The Red Locust lives in a region with one wet and one dry season per year, the wet season usually lasting from the beginning of November until May. The adults live through the dry season in an immature state and maturation starts only with the first rains. Oviposition follows in about two weeks and a few more egg-pods may be laid at about two week intervals, until the parental population has died out completely. Incubation of the eggs usually lasts between 30 and 35 days and the nymphs

(called hoppers) of one egg-pod hatch simultaneously. Then the hoppers go through six or seven instars, until in February or March the imagines appear.

The recognised outbreak areas have been described in detail by VESEY FITZGERALD (1955 a), BACKLUND (1955 b, 1956) and GUNN (1955 a, 1956, 1960) and the following descriptions can be brief. All outbreak areas are extensive natural grasslands, lying in depressions, and serving as basins for large catchment areas. Since the drainage of each basin is either impeded or closed, the grasslands are subject to prolonged flooding, which can last for several months into the dry season. On the other hand, in the latter part of the dry season conditions usually become extremely arid.

The *Rukwa Valley*, about 200 miles (320 km) long, is part of the African Rift Valley system, lying to the east of, and running roughly parallel to Lake Tanganyika. The deepest part of the valley is occupied by Lake Rukwa which forms the basin of the large inland Rukwa-drainage system with a catchment area of 31.000 sq. miles (80.000 km²). The lake has no outlet, losing water entirely by evaporation. It is, therefore, not surprising that the water is brackish; a high content of sodium carbonate makes it strongly alkaline. The lake is divided into two parts which are separated by a ridge, formed by the delta of the Momba river (fig. 3). The southern part of the lake is deep. The northern part is shallow and has no clear shore line; in periods of years with high rainfall it spreads out over the surrounding grass plains, turning them into semi-permanent swamps, as has been the case since 1962. On the other hand, in series of dry years the northern lake may dry out completely, like it happened in 1953/54 and probably in 1949/50. Normally large parts of the grass plains, which border the north lake mainly to the northwest and southwest, are flooded every year for several months, largely as a result of local rainfall and overflow of the rivers that drain the catchment area, and partly also by the spreading lake. During the dry season the plains gradually dry up again and towards the end of the season water is scarce.

The Mweru marsh, or *Mweru wa Ntipa* is a depression in the N.N.W. of Zambia (formerly Northern Rhodesia), lying to the east of Lake Mweru. Like the Rukwa, the Mweru wa Ntipa is the basin of a closed drainage system, but its waters are less alkaline. There is an area of open water surrounded by grass plains, mainly to the north and west. The *Malagarasi* outbreak area is formed by a number of grass plains in the eastern part of the drainage basin of the Malagarasi river, an area with strongly impeded drainage. The *Iku* plains form a relatively small area about halfway between the Rukwa plains and the Malagarasi. It is an outbreak area of uncertain importance, as in the past it may have been stocked regularly by swarms escaping from the Rukwa plains. The *Wembere* depression, to the East of the Malagarasi and North of Tabora in Central Tanzania, is an area with a more arid climate. The northern part is a steppe. The southern part, the actual outbreak area, is a grass plain, which usually becomes flooded in the wet season. It loses its water

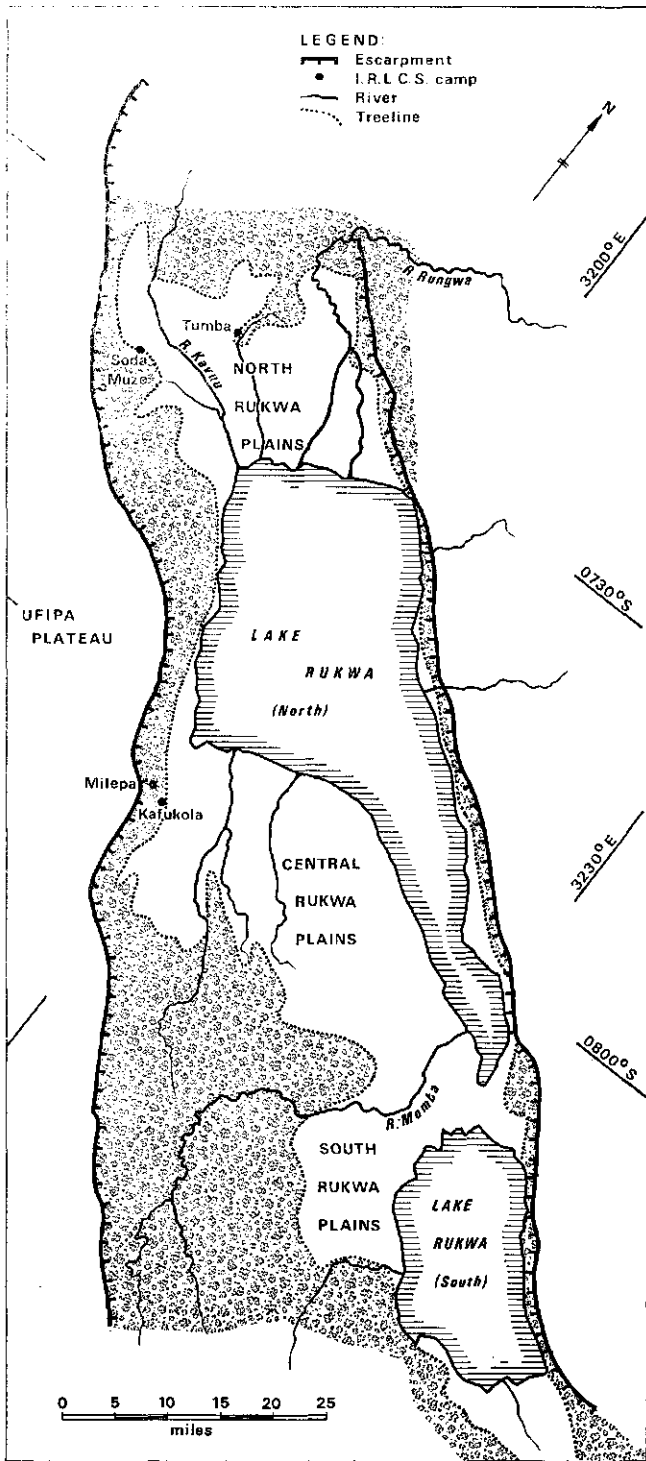


Fig. 3. Lake Rukwa and the surrounding grass plains. The North and Central Rukwa areas are productive outbreak areas. The South Rukwa plains have in the past produced dense concentrations, but in the years under discussion in this paper they harboured virtually no locusts

partly by drainage in northerly direction to Lake Kitangiri, via a channel which is clogged up by vegetation, and partly by evaporation. *Lake Chilwa* is the basin of a closed drainage system on the border of Malawi (formerly Nyassaland) and Portuguese East Africa. In many aspects this area resembles the Rukwa. On the other hand the *Kafue flats*, to the north of Mazabuka in Zambia, resemble the plains in the Malagarasi drainage. The Kafue flats are the most extensive of the many grasslands along the course of the Kafue river.

The vegetation in all these areas is largely dependant on the type of drainage and on the alkalinity of the water. The composition of the vegetation varies from outbreak area to outbreak area, but three types of grassland can be recognised. (VESEY FITZGERALD, 1955 a, 1963 b). In the flood-plain grasslands, where rain water accumulates for lengthy periods every year, usually *Echinochloa pyramidalis* is the dominant grass, frequently in mosaics, mainly with *Cynodon dactylon*. In places where the water is more permanent and fresh, such as in water courses, *Vossia cuspidata* is characteristic; in the Mweru wa Ntipa there are also large beds of *Cyperus papyrus*. On higher ground one finds the rain grasslands, where taller grasses like *Hypparrhenia rufa* and *Chloris gayana* form mosaics with the shorter *Cynodon dactylon* and *Cyperus longus*. Finally in grasslands that are almost annually flooded with alkaline water of the spreading lake (the lake-shore grasslands around Lakes Rukwa and Chilwa), *Sporobolus robustus* and *Diplachne fusca* are the main grasses, with *Sporobolus spicatus* colonising the lake bed when it falls dry.

The adult locusts seem to favour the mosaics, where they roost in the tall grass, but feed mainly in the shorter grasses which in the dry season remain green much longer (DEAN, 1963). The locusts share their habitat with a great variety of game, sometimes in big herds, and with large numbers of birds, among which are obligatory and facultative migrants.

The research on the population dynamics of *Nomadacris* was carried out mainly in the plains that border Lake Rukwa to the north-west, the North Rukwa. These North Rukwa grasslands cover an area of about 250 sq. miles (650 km²). They are enclosed by open woodland. The vegetation consists largely of flood-plain grasslands with fringes of lake-shore grassland along the brackish lake and of rain grassland along the tree line (VESEY FITZGERALD, 1955 a; BACKLUND, 1956; DEAN, 1967 a). The area is traversed by a number of riverlets and channels for local drainage and by the Kavuu and Rungwa rivers, which bring in water from the Rukwa catchment area. North Rukwa was chosen because it is a relatively small area, with reasonably uniform conditions over large parts of it. It usually has an appreciable locust population and regularly requires control. In the experience of the I.R.L.C.S. it is the most variable and productive of all outbreak areas and the multiplication rate of its locust populations (as taken from the parental population at the beginning of the rains to the emergence of the filial population in February/March) is known to have been as low as one, and probably as high as fifty times or more.

Observations were also made in the Central Rukwa plains, an area of between 500 and 600 sq. miles (1300-1550 km²) bordering Lake Rukwa to the south-west and lying roughly 50 miles south-east of North Rukwa. Its vegetation, which will be described in detail in Chapter 8, is far less uniform than that of North Rukwa.

In addition to the work in the Rukwa Valley some observations were made in the Kabwe plain in the Mweru wa Ntipa area and round the Uninji pans near Abercorn (Zambia). The Kabwe plain covers about 7.5 square miles (19 km²) and lies in the first of a number of small tectonic folds, to the north-west of the Mweru wa Ntipa proper. The main Mweru wa Ntipa plains were almost completely under water at the time of observation and could not be used for research, but the Kabwe plain was dry. It used to produce dense concentrations in the years when regular control campaigns in the Mweru wa Ntipa area were required, but in October 1960 the Kabwe population numbered only a few thousand locusts. The main grass is *Hyparrhenia rufa* and there is *Echinochloa pyramidalis* along the drainage line, the Chiwia river, which is no more than an indistinct depression along the southern edge of the plain. The Uninji pans are two small depressions with swamp vegetation, roughly 6 miles to the south of Abercorn. They are good examples of the type of depression called 'dambo' or 'mbuga'; these can be found all over the central part of Africa and they usually harbour a very small population of solitary *Nomadacris*.

1.3 Literature

In the past a number of authors have worked on problems connected to some degree with the population dynamics of the Red Locust, both in the field and in the laboratory. ALBRECHT (1956 a) and CHAPMAN (1959 a) gave some data on sex ratio, WALOFF (1954) counted the numbers of ovarioles, ROBERTSON (1954) compared his own data on mean number of eggs per pod with those of other authors and later (1958 a) gave some more data on fecundity in the field. NORRIS (1959) published data on numbers of eggs per pod and pods per female in laboratory populations and ALBRECHT (1959) studied the influence of crowding on the fertility of female Red Locusts.

SYMMONS and CARNEGIE (1959) demonstrated experimentally that locusts prefer burnt grassland for oviposition and WOODROW (1965 a, b) worked both in the laboratory and in the field on egg laying behaviour and selection of laying sites. ALBRECHT (1956 a) made some valuable observations on the effect of a drought on incubation of eggs, which were followed by laboratory work on this subject by SHULOV and PENER (in preparation).

MICHELMORE (1936) mentioned the larva of a Tachinid fly parasitising hoppers and BREDO (1947) recorded an Asilid species preying on young hoppers. VESEY FITZ-GERALD (1955 b) produced a check list of birds preying on hoppers and adults and DEAN (1964) supplemented this work by estimates of numbers and daily consumption of some of these birds. CHAPMAN (1962) described *Ceracia nomadacridis* as a parasite on immature adults and reported their sterilising effect on females at time of maturation.

GUNN (1955 a, 1956) suggested from historical surveys that a high lake level, greatly extending the area flooded, results in poor breeding in the outbreak areas and that low lake levels favoured the initiation of plagues. SYMMONS (1959) followed this up with a detailed analysis of the infestation level of the locusts in relation to lake level and rainfall. Comparison of eye witness accounts of lake level and of locust incidence in the years 1936-1957 indeed confirmed Gunn's suggestion that a high lake level coincides with a low population level of the locusts. For the period 1942-1956, in which the lake level has fluctuated around a low mean, Symmons was able to correlate the size of the infestation independently: (1) inversely with the mean of the rainfall totals over the Rukwa valley and over the entire Rukwa catchment area in the last but one wet season (highly significant negative regression); (2) with the infestation level of the parent population (significant, positive regression) and (3) with the total rainfall over the Rukwa Valley in the preceding months of October, November and December (positive regression, approaching significance).

Analysis of less detailed data for the Malagarasi outbreak area confirmed that the first two correlations were also valid there (GUNN and SYMMONS, 1959). Finally SYMMONS (1962) analysed multiplication rates in relation to climate, using more detailed data for the North Rukwa area in the period 1953-1962. He found a highly significant inverse correlation between the multiplication rate (from the parents to the fledging of the next generation) in one wet season and the mean of the rain totals of the Rukwa Valley and of the whole Rukwa catchment area in the previous wet season. Similar connections between locust numbers and rainfall may exist for the Brown Locust, *Locustana pardalina* (LEA, 1958) and the Australian plague Locust, *Chortoicetes terminifera* (CASIMIR, 1962).

1.4 The Problems

The central problem of locust populations in the outbreak areas was therefore this: what is the nature of the connection between the multiplication rate in one season and the amount of rain in the previous season? This problem fell apart in two subsidiary problems. Firstly it was unknown exactly where mortalities occur in the locusts' life cycle and how important these mortalities are quantitatively. VESEY FITZGERALD's check list of bird predators (1955 b) gave no indication as to the magnitude of their effect, and ALBRECHT's work (1956 a) revealed only that drought could be fatal for eggs, but not whether this could be anything more than of occasional importance. Only Symmons' work provided an indication, in that the apparent correlation between rainfall and multiplication rate suggested that the really important reduction factor(s) are at work somewhere between the oviposition of the parents and the emergence of the imagines of the filial population. In addition theoretical considerations, such as given by SCHWERTFEGER (1958) and GUNN and SYMMONS (l.c.) make it clear that the violent fluctuations in locust populations from year to year are likely

to be caused by very few, but powerful factors.

Secondly there was the question of which of the factors that would be found to cause severe reductions in numbers, could be correlated with the rainfall and how this correlation could work.

Finally there was the problem of why the outbreak areas differ from one another in their effectiveness as outbreak areas. A solution to this third problem could be of great help in recognising potential outbreak areas, other than the known areas and in estimating their danger level.

Underlying all this work was the basic question, whether there was any likelihood of developing a method of ecological control. In the first two seasons the work focussed entirely on the first problem. When the results appeared to suggest some answers and time permitted, attention was also given to the second and the third question. Since it gradually became more and more likely that a method of ecological control, if one could be developed at all, would not be able to compare favourably with the successful and relatively cheap methods of chemical control as in operation at present, in 1963 the research programme was closed down.

It can hardly be expected that the problems connected with the population dynamics of an insect, that has only one generation per year, could be satisfactorily solved in four years of research. This paper can in fact do no more than record the results of the work and present some probable, or only possible, answers to the questions which were formulated above.

2 Methods and Materials

2.1 Population Assessments using a Land Rover or a Swamp Skipper

The technique of assessing adult locust populations with the help of a vehicle, which is driven along straight and predetermined lines, has been described in detail elsewhere (SCHEEPERS and GUNN, 1958; SYMMONS, DEAN and STORTENBEKER, 1963). An observer counts the number of locusts which are flushed (*i.e.* caused to fly up) in front of the vehicle in a strip estimated to be of the same width as a Land Rover which is about 1.2 yard (1.1 m). It was found that a very high percentage of the population was flushed if one travelled more or less down wind at a speed of about 5 miles (8 km) per hour, with air temperatures between 25° and 35° C and winds not exceeding 12 miles per hour (about 5 m/sec.). The assessments were carried out along parallel lines, the distance between the lines depending on the degree of clumpiness of the locusts' distribution and the accuracy required. The reliability of the estimates was analysed using a method derived from YATES (1949).

When flooding prevented use of Land Rovers, assessments were carried out using a Swamp Skipper, an amphibious vehicle capable of crossing swamps and rivers. The observer was seated on a platform about 12 ft (3.5 m) above the ground and the locusts flushed in front were counted through an inverted V-shaped frame, which limited the view to a strip of about 1.2 yard (1.1 m). On two occasions the flushing qualities of this vehicle were compared with those of the Land Rover. It was concluded that the two vehicles gave close estimates, provided the Swamp Skipper was driven at an angle to the wind. The vehicle is slow and rather noisy and it was found that when it was driven down wind, the locusts flew up too far ahead to be counted accurately.

2.2 Catching of Adult Locusts

Catching of samples of adult locusts used to be done at dawn. African research scouts with nets swept the tall grass which the locusts prefer as roosting sites. Very soon after sunrise, however, the locusts warm up sufficiently to escape and the time available is often too short for catching large samples. In addition, it appears that this method does not give reliable data on the sex ratio. ALBRECHT (1956 a) got a sharp rise in percentage males during December (from 56 % to 96 %), but in January the ratio

dropped back to 54 %. CHAPMAN (1959) found values which fluctuated around unity, but he also got a sharp increase in percentage males in November and December. In 1954 J. H. LLOYD (I.R.L.C.S. records) compared samples of locusts obtained by catching at dawn and by collecting corpses after a control operation in North Rukwa; a sample of 584 corpses contained 52 % females against 38 % in a sample of 382 locusts caught at dawn. Finally data collected by the author showed similar discrepancies (table 1).

Table 1. *Percentage female locusts in samples collected in 1959*

| Area | Month | Size of sample | Percentage females | |
|---------------|------------|----------------|--|-------------------------------------|
| | | | in samples of living specimens collected at dawn | in samples collected after spraying |
| Central Rukwa | April/Nov. | > 4000 | 43.8 | |
| | July | 3670 | | 46.3 |
| | Aug. | 216 | | 44.4 |
| | Sept. | 175 | | 61.5 |
| Wembere | Sept. | 392 | 40.7 | |
| | | 258 | | 50.4 |

In 1959 a more convenient method was adopted. In the Rukwa valley, at night the air cools off considerably and the locusts become sufficiently lethargic to be picked off the grass stems in the light of a Land Rover's headlights. A vehicle was driven slowly through the grass with a group of African research scouts walking ahead. This method was found to provide adequate samples fairly quickly and for comparison samples could be caught at various places during the same evening.

In order to check the reliability of this method, in November 1961 just before the rains began, a sample was obtained one evening and the same population was then sprayed the next morning at dawn. A sample of 585 locusts was caught on the 1st November 1961 between 7.00 and 9.00 p.m. near Mwaze camp in North Rukwa in an area of tall and dense grass. The next morning at 6.00 a.m. the same area was sprayed from the air with DNC (dinitro-orthocresol) and 753 corpses were collected. The results were very close:

catching : 48.1 \pm 2.5 % females,
spraying : 48.3 \pm 2.5 % females.

2.3 The Experimental Plots in Burnt-off Grassland

Nomadacris prefers to lay in bare ground or in soil of which the grass cover has been burnt (SYMMONS and CARNEGIE, 1959). Maturing locusts are known to move distances

of 10 to 15 miles towards burnt-off ground. In order to restrict the size of the area in which laying takes place and in which subsequently hopper control may be required, it had been the policy of the I.R.L.C.S. to protect the North Rukwa plains against annual burning. For the population-dynamics research it was the intention to burn a plot in the middle of the fire-protected plain which could act as a laying trap. This had to be done late in the dry season in order to obtain the necessary clean burn. In

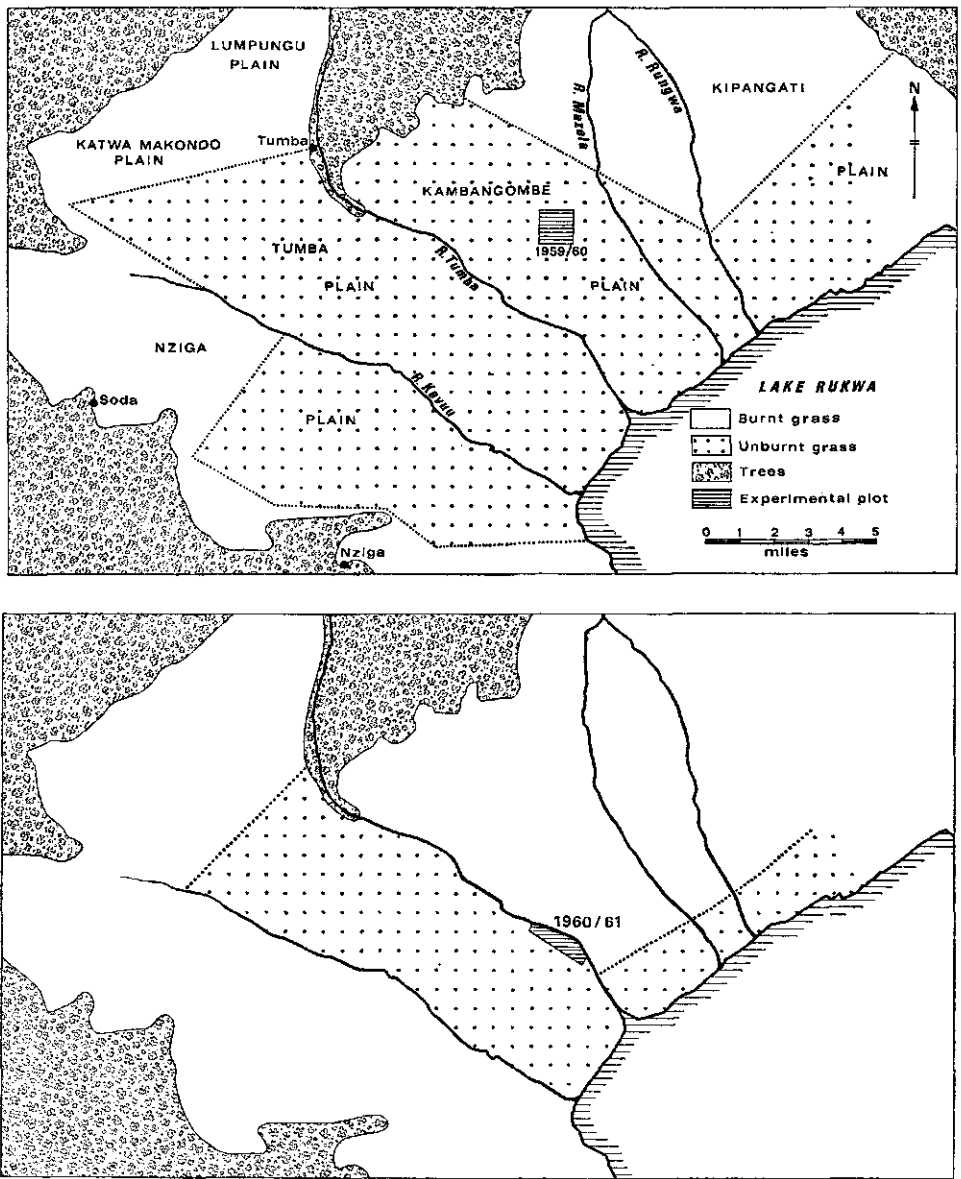


Fig. 4. The North Rukwa plains with the experimental plots used in 1959/60 and in 1960/61

two of the three years, however, accidental fires burnt out large parts of the plain.

In the 1959/60 dry season the fire protection had been largely successful and the central part of the plains was unburnt. In the middle of the Kambangombe sector Symmons burnt a plot of 1 mile square (1.6×1.6 km), which acted as a laying trap for about 2 million parents (fig. 4). The rest of the parental population (about 8 to 9 million) bred in the burnt N.E. part of the Kambangombe and the Kipangate sectors, in the partition firebreaks, and in the western part of the Nziga sector.

The next year the fire protection was not successful and all grass was burnt, except for most of the Tumba sector (fig. 4). Symmons laid out an experimental plot about 1 mile (1.6 km) long and on average 0.5 mile (0.8 km) wide, between the edge of the unburnt grass and the Tumba river. A population of reasonable size gathered and laid there. In that same 1960/61 season the author made some observations in the Kabwe plain in the Mweru wa Ntipa region. All grass in this plain had been burnt, except for a few small patches, which acted as roosting sites for the parents and around which most of the laying took place (fig. 5).

In the 1961 dry season fires burnt out the western half of North Rukwa. With the first rains the entire parent population moved over to the Tumba sector for first oviposition. A number of small plots were laid out there: four in the area of first oviposition (Tumba sector) and one in the southern Nziga sector where part of the second oviposition took place. Each of these plots measured 0.25 mile by 0.3 mile (400×480 m) and was divided into 3 parallel strips of 0.1 mile (160 m) wide each. One of the plots in the Tumba sector became inaccessible before hatching started and the plot in the Nziga sector became flooded during incubation and all egg-pods died. Thus in the end only three plots could be used. Plot 4 in fig. 6 refers to the cage experiment described in section 5.1.

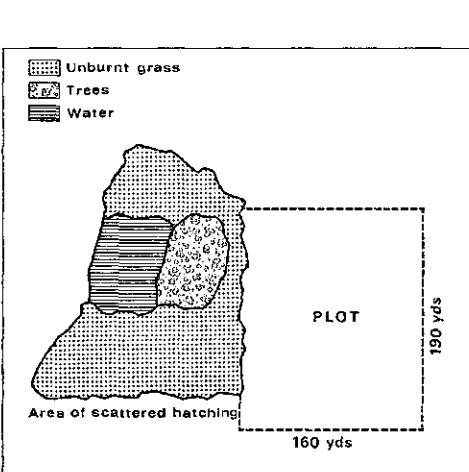


Fig. 5. Experimental plot in the Kabwe plain (Mweru wa Ntipa) 1960/61

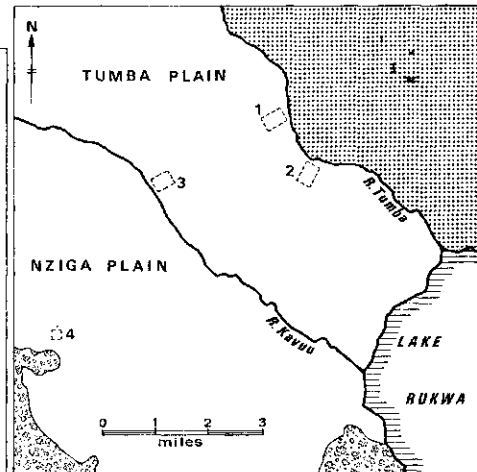


Fig. 6. Experimental plots in North Rukwa, 1961/62. Legend as in fig. 5

2.4 Egg-pod Assessments

Density and distribution of egg-pods were assessed by ploughing sample lines at regular intervals across an experimental plot. This was done by a hand plough, which was pulled by a Land Rover or a tractor and which ploughed a furrow of 3 to 4 in. (7.5 - 10 cm) deep and 5 to 7 in. (12.5 - 17.5 cm) wide. The ploughed-up soil was then examined by African scouts, who cut up the lumps of soil with 'panga's'. It was found that the width of the furrow varied from place to place, depending mainly on the type and the moisture content of the soil, and the furrow was measured in each case. On several occasions Symmons checked examined parts of a plough line, but did not find any more egg-pods. In November 1961 the author also made several checks, but no missed egg-pods were found. It was concluded that virtually all pods in the plough line were found, though perhaps a very small number of pods was destroyed beyond recognition by the plough.

2.5 Estimating the Incubation Success of Eggs and Egg-pods

The incubation success depends (a) on the proportion of the egg-pods that hatch and (b) on the percentage of the eggs in the pod that produce a living and emerging hopper. Study of these two parameters, which are not necessarily correlated, was based on the observation that hoppers, emerging from one pod, stay together and are recognisable as one 'hatched party', usually until the next day. The phase-transients Red Locusts populations in the outbreak areas (section 2.8) scatter before oviposition and high egg-pod densities like in egg-beds of swarms do not occur. Thus the chance is small that hoppers from several egg-pods merge into one party.

The incubation success of the egg-pods was estimated in two ways. Symmons sampled for egg-pods in a subsidiary plot (1959/60), or in several sample strips (1960/61) within the experimental plot and estimated the number of egg-pods that had been laid there. Then, during the period of hatching, the sample area was inspected daily and the hatched groups were counted and killed with BHC-dust (Benzene-hexachloride).

In 1960/61, however, doubt arose on the reliability of this technique under some conditions. The next season the author marked egg-pods at laying, in various parts of the plain. At first females found ovipositing at night were prevented from escaping by placing a cylindrical plastic cage over them. Oviposition of the first and the second pod, however, is usually concentrated in a few evenings and it was found that only few pods could be marked in this way. So instead of looking for ovipositing females, a great many locusts were caught early at night and the very fat females, which appeared to be ready to oviposit, were selected and placed under plastic covers. The next morning the females were dissected and when they had oviposited (over 90 % did so the first night) the top soil was carefully scraped off with a knife until the top of the froth plug was found. The pod was covered again with soil and a wire ring

of 8 inches diameter was placed around it with the pod in the centre. Each site was marked with a long pole and a bundle of grass on top. Thus egg-pods were marked in 7 places in various parts of the North Rukwa plains. Shortly before hatching was expected, a plastic cylinder and lid were placed over the pod and it was inspected daily. Emerged hoppers were killed with BHC-dust and counted. Not less than one week after the last hatchings had been seen, the remaining pods were dug up.

The incubation success of the eggs in the pod was estimated in three different ways. Symmons quickly placed a net over just hatched parties and counted the hoppers, after having killed them with a quick-acting insecticide. The author dug up a number of pods just after hatching and counted the eggs that had not hatched and the hoppers that had not managed to get out. The mean number of eggs that did not produce a hatched hopper was subtracted from the mean number of eggs per pod, and this gave an estimate of the number of hatchlings per pod. With the first method it was likely that some hoppers escaped attention, resulting in an underestimate of the size of the hatched parties. The second method might have given an overestimate, since some eggs may have been lost in the process of digging up the pod. The true figure, therefore, was likely to have been in between the two estimates. In some cases I used a third method. Hoppers have their first ecdysis immediately after emergence, or sometimes when they are still in the ground. Often ants immediately start carrying away the cast skins, occasionally even with a hopper still half inside it. In some areas, however, there was little or no ant activity and the skins could be counted. This method was tested in the Kabwe plain (Mweru wa Ntipa). Of 8 egg-pods the mean number of skins cast was 132 ± 5 . From the same 8 pods an average of 13 ± 5 eggs had not hatched, which gave an estimated mean of $(152 \pm 4) - (13 \pm 5) = 139 \pm 6$ hoppers per hatched party. The marking of egg-pods introduced in 1961/62 offered a fourth method.

2.6 Hopper Mortality Estimates

Natural mortality of hoppers in the first and second instars was assessed by first estimating the total number of hoppers that hatched in a plot and then, about three weeks after the peak of hatching, assessing the population that had survived and had by then entered the third instar. The estimate of the original hatching population was deduced from sample data on the numbers of egg-pods in the plot and on the hatching success of eggs and of egg-pods. The estimate of the remaining population was obtained by drench spraying sample lines from the air with the quick acting contact insecticide DNC. Hoppers died within 20 minutes, but after 10 minutes they were already too sick to move.

Symmons arranged for the aircraft to spray a number of parallel sample lines across his plots (1959/60 and 1960/61). He then placed wire rings, each enclosing one square meter (1.2 sq. yds) every 5 paces and African scouts searched for corpses.

The efficiency of searching was tested by placing 20 rings with a known number of corpses; $89.5 \pm 2.5\%$ of the corpses were recovered in the time normally taken to search a ring. The possibility of scavengers taking corpses between spraying and searching, Symmons checked by placing a known number of corpses in rings before searching began. Inspection at the end of searching showed that in the sample strips no corpses disappeared, but scavenging by ants in the non-sprayed area was rapid.

In 1961/62 I laid out plots, which were divided into 3 parallel strips of 0.25 mile (0.40 km) long and 0.10 mile (0.16 km) wide. When all hoppers had entered the second instar the aircraft laid several swaths of DNC along the middle of the outer strip on the down-wind side and corpses were sampled in square-meter rings, which were laid down at intervals of 15 paces along 6 parallel lines. About ten days later the hoppers had all entered the third instar and a sample strip was sprayed in the other outer strip of each plot. The middle strip acted as a barrier and was not used for hopper mortality assessments.

In 1961/62 the rings were searched by teams of two scouts and each team was tested for reliability by re-searching rings which they had searched without knowing that a check would be made afterwards. In addition, scouts were made to search rings with a known number of corpses; only 2 in 124 hopper corpses were not found, which meant a higher efficiency than in the years before. However, searching conditions were better since the plots were under about one foot (30 cm) of water and it is much easier to see a hopper, when it is floating on the water than when it is lying amongst the debris on dry soil. The possibility of corpses sinking to the bottom when falling in the water was tested by dropping 20 corpses from grass-top level into a tin of water. After 24 hours all corpses were still afloat.

In any case, after the spraying one half to one third of the corpses were found clinging to the grass. Scavenging of floating corpses by catfish (*Clarias mossambicus*) was known to take place and, every time that a plot was sprayed, two test rings were placed, with a known number of corpses. Only one of the 60 corpses, that were laid out, disappeared between the beginning and the end of searching.

On one occasion (Kabwe plain, Mweru wa Ntipa, January 1961) no aircraft was available for spraying and the surviving population had to be assessed by walking through the grass and counting the hoppers. In general this is a very unreliable method, but in this case it was the only possibility and the conditions were as favourable as they could be. The grass was very sparse and thin and only 3-4 inches (7-10 cm) high. Hoppers were counted along parallel lines 15 yards apart and one yard wide and the observer went forward step by step at a speed of about $\frac{1}{2}$ mile (800 m) per hour, while moving the grass in the strip with a twig to disturb the hoppers. On two occasions counts were done, both times between 11.00 a.m. and 2.00 p.m. and under warm and sunny conditions and with little wind.

2.7 Predator Assessments

The Red Locust was found to be preyed upon by a number of predators, mainly insects and birds. Insect predators, like Asilidae and Odonata, were assessed in plots of 20 x 20 yards (18 x 18 m), which were traversed by a line of African scouts under supervision, one arm length apart and walking slowly through the grass. One half of the square was traversed in one direction and the other half in the opposite direction. In order to prevent counting the same insect twice, it was intended to catch every predator, but usually some escaped. In the beginning every square was examined twice but never were any Asilidae seen in the second traverse. The method was thought to be less reliable for assessing Odonata, since these were seen to fly into the plot. Thus it was possible that some predators were chased out of the plot without being seen, but on the other hand there was a chance that a predator escaped capture and was counted twice, though extreme care was taken to avoid this. On the whole it is thought that the estimates were reasonably reliable.

Bird predators like Stork and Egret, were assessed from the air by counting the birds and, if necessary, photographing the flocks as described by DEAN (1964). The Coucal population (*Centropus superciliosus*) was assessed in an approximate way by counting birds sitting in, or flying up from the grass in strips of about 50 yards (46 m) on either side of a scouting line. Dean attempted to assess numbers of Finch lark (*Eremopterix leucopareia*) and *Quelia quelia centralis* and *Q. cardinalis*, but as these birds have an extremely fast and erratic flight in dense groups this was found to be impossible. Since only few hoppers were found in stomachs of shot specimens no attempts were made to improve on the assessments. Bee eaters (*Merops* spp.) are very difficult to assess as they have a very clumpy distribution, but they seem to prefer to stay close to the trees and are not often seen in the middle of the plain.

2.8 Phase Status of Populations Studied

Locusts in swarms are different, both morphologically and behaviourally, from solitary living specimens (UVAROV, 1928). There are many intermediate forms between the solitary and the gregarious phase. The phase status is, therefore, usually described with the help of a morphometrical criterion, such as the Elytron/Femur ratio (E/F). For *Nomadacris* this ratio ranges from about 1.80 in the phase solitaria to about 2.15 in the phase gregaria (CALLAWAY, in GUNN *et al.*, 1948).

A comparison of morphometrical data from various sources learnt that locusts in swarms leaving an outbreak area are morphologically still in phase transiens and reach the morphological phase gregaria only after a number of swarm generations (STORTENBEKER, in preparation). The present research was done largely on populations which were gregarious in behaviour, but the E/F ratio did not exceed 1.96. In North Rukwa the E/F ratio varied from 1.90 to 1.96 and in 1960 the rather solitary population in the Kabwe plain had a ratio of 1.87.

3 Fecundity of the Populations

Four probably independent parameters determine the fecundity of a population: the sex ratio, the mean number of pods per female, the mean number of eggs per pod, and the viability of the eggs.

3.1 Sex Ratio

Parental populations are assessed as a whole. If one wants to know the fecundity of such a population one must know the sex ratio. Samples taken from various outbreak areas of *Nomadacris* showed considerable differences in percentage females (table 2).

Table 2. Percentage females in samples from populations in various areas

| Area | Year | Origin of sample | Time of collecting | Size of sample | Percentage females ¹ |
|---------------------------------|------|---|--------------------|----------------|---------------------------------|
| North Rukwa | 1959 | Experimental plot | November | > 500 | about 50 |
| | | | December | > 500 | about 25 |
| | 1960 | Experimental plot | November | 1210 | 33.6 |
| | | | December | 79 | 22 |
| | 1961 | Hopper concentrations ² | February | 5000 | 52.7 |
| | | | | | |
| | | Immature adults | August | 1011 | 38.9* |
| | | | | 1089 | 60.4 |
| | | Parent population ³ | November | 5236 | 56.4 |
| | | | 1st December | 3484 | 41.2 |
| | | | 14th December | 116 | 31 |
| Central Rukwa | 1959 | Immature adults | 15th January | 39 | about 15* |
| | | | July | 3670 | 46.3* |
| | | | August | 216 | 44* |
| | | | September | 175 | 61* |
| | | | September | 544 | 31 |
| Wembere | 1959 | Swarms | September | 258 | 50* |
| Kabwe plain (Mweru wa Ntipa) | 1960 | Sparse population at 2nd oviposition | December | 245 | 29 |

¹ Samples were obtained by catching at night, except for those marked with *, which were collected after spraying operations.

² In the 1960/61 experimental plot.

³ Samples collected over entire oviposition area.

The sex ratio of the parental population that gathered around the 1959/60 plot has not been assessed accurately, but just after the start of the rains large numbers of locusts were caught for a cage experiment. In the beginning about equal numbers of males and females were obtained. Just before the first oviposition, however, it became increasingly difficult to obtain the required number of females and the sex ratio dropped to about one female in four locusts caught. Later experience showed that the method of catching at night gives reliable results and thus the females either must have moved away from the experimental plot and oviposited elsewhere, or they died, but there was no evidence of such a high mortality.

In November 1960 several samples were taken during two weeks around the first oviposition. Differences in the sex ratio at various distances from the area of burnt grass suggested that females moved to their oviposition sites from more than a mile away, but that males did not move that far (DEAN and STORTENBEKER, in DU PLESSIS, 1960). The overall mean percentage females appeared to be lower than in 1959 and it dropped towards the second oviposition.

In the 1961/62 season there were again strong indications of differential behaviour of the sexes. Around the end of October there were some light showers and maturation started only slowly (cf. fig. 9). Sex ratio and average length of oocytes in samples, taken between 3rd and 7th November, at a number of points between the main locust concentrations and the burnt-off grassland, showed that the males moved ahead and that of the females the more rapidly maturing individuals moved first (fig. 7). When

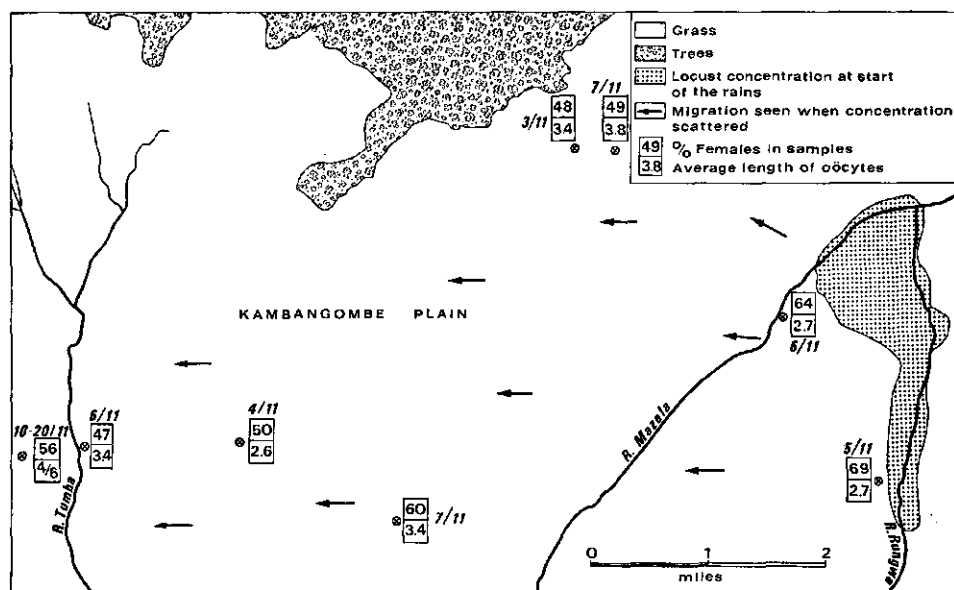


Fig. 7. North Rukwa, 2nd - 10th November 1961. Large-scale movement of individual locusts towards the burnt grass west of the Tumba river after the start of the maturation; percentages females and state of maturation in samples taken at various points. The data for 10th - 20th November reflect the situation after the migration

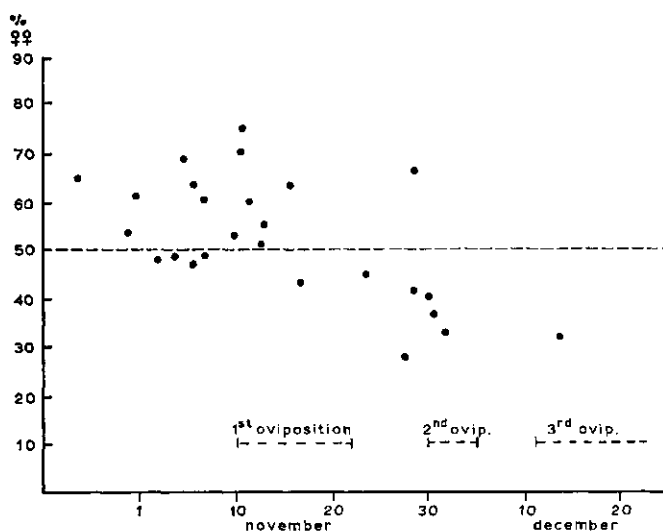


Fig. 8. Percentages females in samples. North Rukwa, 1961

on the 7th November the rains began properly, a mass movement towards the west was observed. Subsequent samples taken in the main concentrations along the Tumba river contained 56% females, which is very close to the mean of the values in all samples collected between 10th and 20th November (57%).

The sex ratio's in two large samples taken earlier that year from two concentrations about 10 miles apart (North Rukwa, August 1961) indicate that even before maturation considerable differences can occur within one outbreak area.

In November and December 1961 samples were taken from all over the area of oviposition and differential mortality between the sexes was apparent (fig. 8). Additional proof was obtained when during a sudden wave of mortality on 30th November 1960, just before second oviposition, 69 out of a sample of 96 corpses were found to be females.

3.2 Mean Number of Egg-pods per Female

In order to assess the mean number of egg-pods per female, one has to know the size of the parental population and the sex ratio at the times of successive layings. The state of maturation and the dates of laying were known from regular dissection of samples of 20 females, as illustrated for 1959/60 and 1961/62 in fig. 9.

In November 1959 the first population assessment was made on 4th November, revealing the presence of 2.8 million parents around the plot. Oviposition started a few days later, reaching a peak around the 9th. Just before second oviposition the

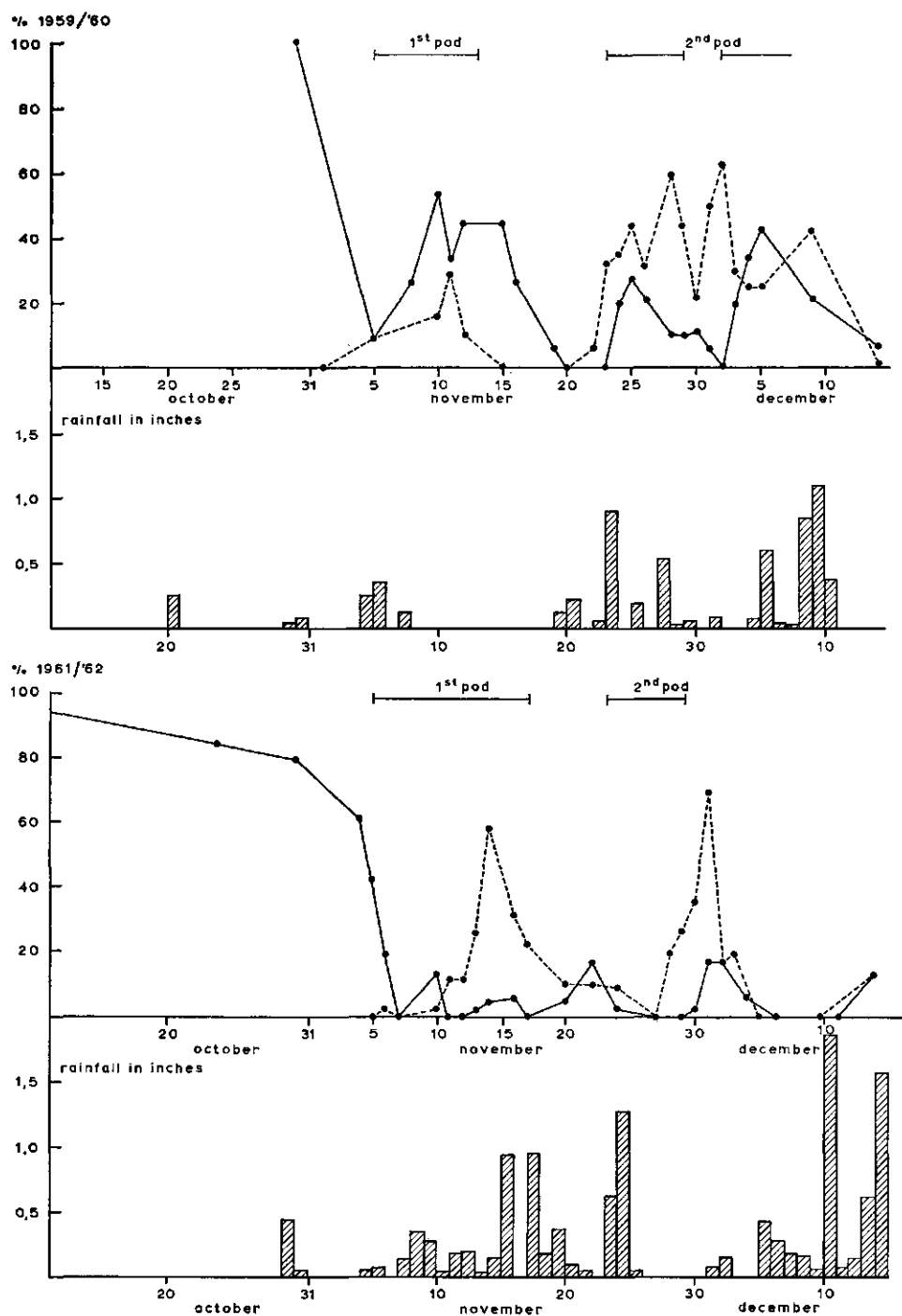


Fig. 9. Oviposition of successive egg-pods as seen from the mean length of the oocytes in the ovaria (at the first sign of development oocytes are about 1.5 mm long and just before oviposition about 6.5 mm); (● - - - ●) is the percentage of the females which held oocytes with a mean length of more than 6 mm, and (● — ●) is the percentage in which the oocytes were in average 2 mm or less

population had dropped to 1.3 million. About 40 % of the females had laid a second pod when there was a period of rather dry weather (which does not show very well in the Tumba rain records, fig. 9), and the second oviposition was interrupted for about a week until 4th December; then only 0.16 million locusts remained. Numbers dropped further to 90,000 just before the third oviposition¹.

The drop in percentage females and the drawn-out second oviposition made it very difficult to calculate the expected number of egg-pods in the experimental plot. Symmons carried out an intensive egg-pod survey after the second laying and estimated the total number of pods in the plot at $420,000 \pm 30,000$. I examined the stage of development of 210 pods and found 134 of them to be of the first oviposition and 67 of the second, whilst of 9 pods the time of laying was uncertain. Thus 67 % was of the first laying, and for the population around the plot the mean number of pods per female was about 1.5.

In the 1960/61 season the experimental plot was part of a large burnt area along the contact line between burnt and unburnt grass. It was, therefore, difficult to estimate the parental population that laid inside the plot. Just before the first oviposition Dean and I carried out 8.5 miles of scouting in an area of 6.8 sq. miles, which covered the plot and the area of adjacent unburnt grass from which females were likely to move to the plot for oviposition. An average count of $4.45 \pm .33$ locusts per 0.1 mile of scouting indicated a parental population of $408,500 \pm 30,300$.

The mortality curve, based on seven successive assessments by Symmons in a 30 square mile area (fig. 10) indicated that at the time of the second oviposition about 80 % of the original population remained and that less than 12 % survived until the time of the third laying.

The percentage females was only 33 % at the start of oviposition and dropped to 22 % towards the second laying. A long drought followed and when the third pod was laid the remaining population had largely moved away from the plot, so that most laying took place further north. Thus the expected number of pods in the plot was: $.33 \times (408,500 \pm 30,300) + .22 \times .80 \times (408,500 \pm 30,300) = 206,650 \pm 15,430$ of which 65 % from the first oviposition. At the first egg-pod search Symmons found a very high density of pods along the southern edge: of all pods found in 12 sample lines 22.5 % were from the most southern line. In order to obtain a more uniform pod density he excluded the southern margin from his experimental plot. Thus approximately 77.5 % of the population, estimated to have been around at the time of oviposition, had laid in the plot as it then became, which brings the expected number of pods down to $160,200 \pm 12,000$. I estimated sterilisation by *Ceracia* larvae at 4 % and thus the final estimate was $153,800 \pm 11,500$ egg-pods expected to have been laid in the plot.

¹ The assessments were carried out by P. M. Symmons. The estimates were based on 18.3, 14.6, 18.9 and 6.8 miles (29.4, 23.5, 30.4 and 10.9 km) of scouting along parallel lines, covering an area of 9 sq. miles (23.3 km²).

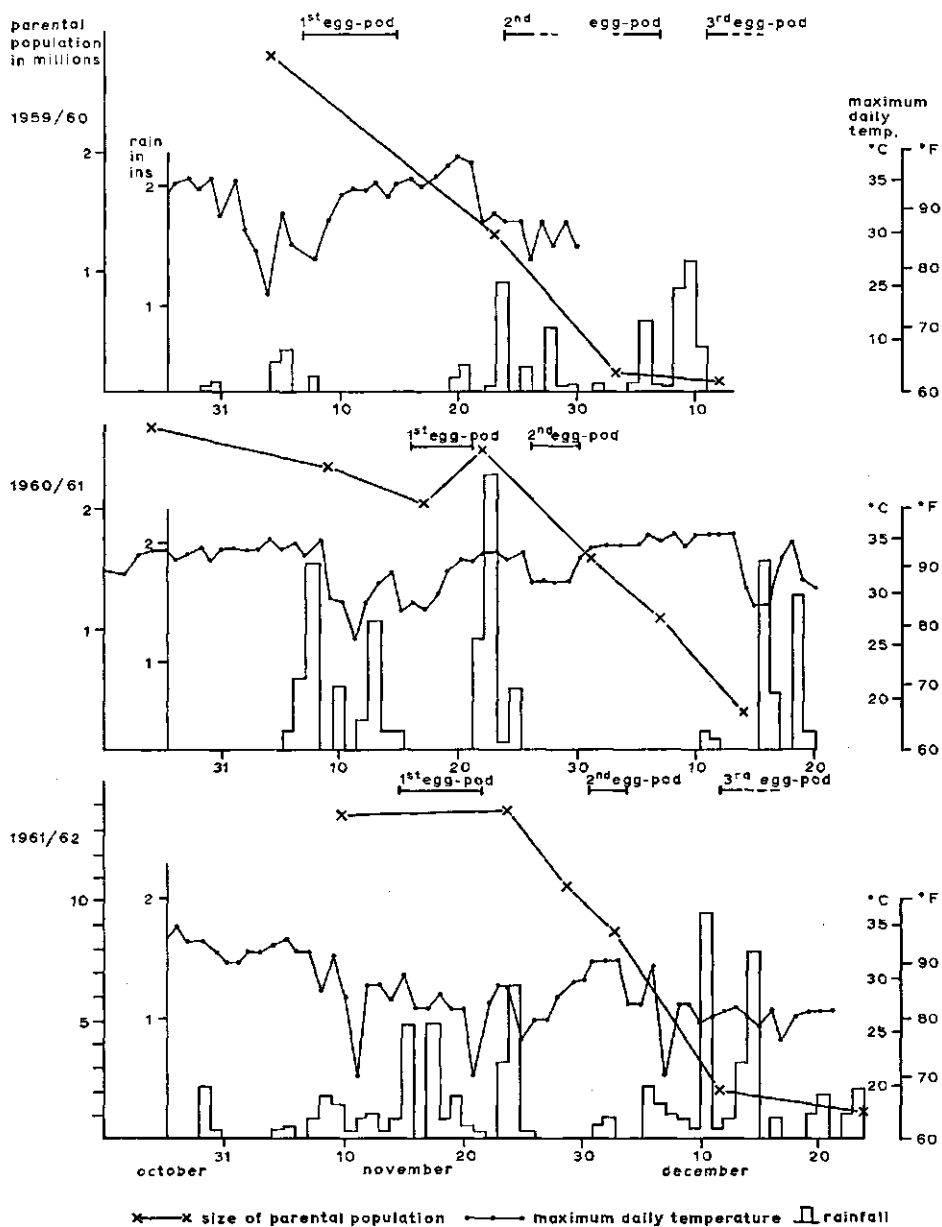


Fig. 10. The decline in numbers of parents compared with rainfall and maximum daily temperature. In 1959/60 the population assessments were carried out in an area of 3×3 miles around the experimental plot, in 1960/61 in an area of 30 sq. miles (78 km²) mainly to the east of the plot, and in 1961/62 in all grassland to the west of the Tumba river. The meteorological data were registered at Tumba camp

Symmons' assessment, based on the number of egg-pods found in 12 sample lines of 0.5 mile (0.8 km) each, and carried out after the second oviposition, gave an estimated total of 157.568 ± 12.751 pods (later assessments showed that in the plot probably about 3500 egg-pods had been laid in the third oviposition). Microscopical examination suggested that about 60 % of the pods were of the first oviposition. Thus in the area of the experimental plot the mean number of egg-pods per female was approximately 1.5 when the estimate is based on the population assessments and sex ratio's, and 1.7 when it is based on the ratio of egg-pods of the first and of the second oviposition as found in the plot. These are slight underestimates, as the third laying has been ignored.

In the 1961/62 season a number of small plots were laid out and not one large plot, as in the years before. In previous years there had been indications that the multiplication rate from parents to filial population might vary considerably from place to place within one outbreak area. Results from one plot might, therefore, be misleading. Thus five plots were laid out within the burnt western half of the North Rukwa plains. It was impossible to relate numbers of pods found in the plots to the parental population, but a rather crude egg-pod survey was made in the area, where the first and some of the second oviposition had taken place. Samples were taken along 4 parallel lines 2 miles apart. Every 0.5 mile (0.8 km), 0.1 mile (0.16 km) of plough line was examined for egg-pods. The average number of pods per 0.1 mile in the sample lines was 4.9, 4.5, 3.5 and 2.5 respectively, giving an over-all average of 3.8 pods per 0.1 mile sample and a crude estimate of about 7 million egg-pods in the area of first oviposition.

From population assessments and sex-ratio estimates the number of egg-pods in that same area could be calculated to be 7.41 million, as 11.75 million parents¹, 56 % of which were females, produced 6.58 million egg-pods in the first oviposition, and 2.78 million parents², 30 % of which were females³, laid 0.83 million second egg-pods. Sterilisation of females by *Ceracia* larvae was negligible, but in view of later findings the total of 7.41 million should be corrected for damage done by predators between laying and egg-pod survey (estimated at between 10 % and 15 %; see section 4.2.1). This brings the expected total number of egg-pods down to between 6.30 and 6.67 million.

On data obtained in the Tumba sector only, one would have estimated the mean number of pods per female at about 1.1. But after the first oviposition the majority of the females moved out of the Tumba sector and laid their second egg-pod in areas to

¹ Based on 34.2 miles (55.1 km) of scouting along 9 parallel lines, 0.5 mile (0.8 km) apart, over an area of 37.5 sq. miles (97.1 km²).

² Based on 17.6 miles (28.3 km) of scouting along 5 parallel lines, 1 mile (1.6 km) apart, over 37.5 sq. miles (97.1 km²).

³ The percentage at the time of the second oviposition for the N. Rukwa population as a whole was 42 (fig. 8), but many females had moved out of the Tumba sector, probably because the grass had grown very tall there.

the north-north-west and west-south-west. For the whole of the North Rukwa (to the west of the Tumba river), population and sex-ratio assessments at the times of successive layings gave total numbers of 7.8, 3.8 and 0.4 million egg-pods from first, second and third ovipositions respectively¹. That meant a total of 12.0 million pods from the original 7.8 million females, which is a mean number of about 1.5 egg-pods per female.

Thus in the three breeding seasons the mean number of egg-pods per female was estimated at about 1.5, between 1.5 and 1.7, and at 1.5 respectively. The estimate for 1961/62 was based on data from the entire North-Rukwa population, but the estimates for the two earlier years were valid for the populations around the experimental plots only. In view of the shifts in populations as described in section 3.1, it is thought that in particular the 1959/60 estimate may have been different from the true value for the population as a whole.

3.3 Mean Number of Eggs per Egg-pod

Acridids are characterised by large numbers of ovarioles and tropical species have greater numbers than temperate ones. WALOFF (1964) recorded 85 + 85 ovarioles for *Nomadacris*, but ALBRECHT (1956 b) found a female with 185 and one with 194 ovarioles. LLOYD (in ROBERTSON, 1954) found one egg-pod with 195 eggs and I got several egg-pods with more than 170 eggs.

In North Rukwa the average numbers of eggs per pod were obtained by counting the numbers of eggs in the pods, but in the Mweru wa Ntipa and in the Uninji Pans estimates had to be based on counts of the developing ovarioles which was done when

¹ The three population assessments were based on 80.8 miles (130.1 km) of scouting over an area of 105 sq. miles (271.9 km²), on 59.6 miles (95.9 km) of scouting over 84 sq. miles (217.6 km²) and on 15.1 miles (23.3 km) over 32 sq. miles (82.9 km²).

Table 3. Mean numbers of eggs per pod

| Area | Year | Origin of sample | Size of sample | Mean | Minimum | Maximum |
|---------------------------------|------|-------------------------|----------------|---------|---------|---------|
| North Rukwa | 1959 | 1st and 2nd oviposition | 84 | 114 ± 2 | 61 | 169 |
| | 1960 | same | 42 | 144 ± 5 | 83 | 181 |
| | 1961 | same | 16 | 133 ± 4 | 100 | 163 |
| | 1962 | 1st oviposition | 5 | 109 | 103 | 117 |
| Kabwe plain (Mweru wa Ntipa) | 1960 | 2nd oviposition | 18 | 152 ± 4 | 109 | 178 |
| Uninji Pans (near Abercorn) | 1961 | 1st oviposition | 7 | 157 | 114 | 178 |

the oocytes were in average at least 4 mm long (table 3). In very sparse populations this is the only way of estimating the size of the egg-pod. Some idea about the reliability of this method was obtained in November 1960 in North Rukwa by counting the developing oocytes in 9 ovaria. This gave an estimate of 132 ± 6 developing oocytes in the first batch against 135 ± 3 eggs per pod found in a sample of 18 egg-pods, dug up in the experimental plot 2 weeks later.

LLOYD (in ROBERTSON, 1954) found a large difference in size between the pods, laid at first and at second oviposition in North Rukwa in 1954: on average 82 and 152 eggs per pod. In Central Rukwa ROBERTSON (l.c.) found an even lower average for the first egg-pod, namely 49. In the 1960 breeding season the oocytes in the first batch were in average 3 to 4 mm long when in part of the population some oocytes began to show signs of degeneration. Corpora lutea appeared, which normally are seen only after first oviposition and the contents of some of the oocytes got the bright yellow flocculated appearance which is not uncommon during the development of the third and later batches. Some signs of degeneration were seen in 39 % of the females and 18 % had a considerable number of degenerating eggs. The egg-pods that were laid in the first oviposition were found to contain in average 135 ± 3 eggs. The development of the second batch was normal and in egg-pods of the second oviposition there were 152 ± 3 eggs. The difference between the two means was highly significant ($t = 3.2$, $p < .005$) (table 4). It seems likely that the reduction of the mean number of eggs in the first pod was the result of the degeneration of a small proportion of the oocytes, but the cause of this degeneration remained obscure. There was no sign of any decrease in quality of the eggs when laid; eggs and pods laid by females, caught in the plot just before first oviposition and transferred to tins with sand or clay soil had a high incubation success. In 1959 the numbers of eggs per pod of the first and the second oviposition did not differ significantly.

3.4 Factors Influencing the Fecundity

There are a number of factors which influence the mean number of egg-pods per female and the fecundity of a population. The most important one is the average longevity of the female locust after the start of the rains. The general impression is that usually the natural mortality is low all through adult life, until some time after the start of the rains. Then there is a rapid increase in death rate and the population is reduced to practically zero in a matter of weeks. For a number of reasons it is not certain that the population curves, given in fig. 10, give the true picture for the whole population.

In the first place assessments could not be carried out frequently enough and they usually had standard deviations which were too high to be sure of the exact point at which the mortality began. Secondly in 1959/60 and 1960/61 oviposition took place over large parts of North Rukwa and the assessments could not be extended to cover the entire area. A complete cover is important since there may be substantial shifts

in the locust distribution. This was suspected to be the case in 1959/60, it certainly happened in the 1960/61 oviposition season and in 1961/62 the parental population shifted continuously.

In this last year the population assessments covered the entire oviposition area. A sudden spectacular mortality was seen on 30th November and 1st December, a mortality that coincided with a marked change in weather; a long period of wet and cool conditions was interrupted by a short spell of dry and very hot weather. In the Nziga sector hundreds of locusts were seen dead or dying and sick individuals could be caught by hand. Marabu Stork (*Leptotilos crumeniferus*) patrolled the area for days, clearing up corpses. It could not be established what the cause of this mortality was. On dissection the dying locusts were found to be free of parasites and their fat-bodies had a normal appearance.

Lack of suitable breeding ground may have some influence on the number of egg-pods per female, but only in years when an outbreak area is still wet and its grass unburnt at the end of the dry season. This may have been the case in 1962, when at the end of the dry season most of North Rukwa was still under water and suitable breeding ground was available only along the north-western fringe. Although millions of locusts managed to find the breeding ground, they were almost certainly less numerous than the April population had been, and there is just a small possibility that lack of suitable breeding ground was a limiting factor that year.

There may be losses due to predation by the White-bellied Stork (*Sphenorhynchus abdimii*) and the European Stork (*Ciconia ciconia*). At the start of the rains locusts swarm out over the burnt grasslands, which offer little protection. Shortly afterwards European and White-bellied Stork arrive in numbers on their southward migration. At the same time the distribution of all Storks becomes more closely associated with the locust's distribution. DEAN (l.c.) saw this in 1959 and his observations were confirmed in subsequent years. In particular the White-bellied Stork was seen to concentrate in burnt grasslands and to patrol oviposition areas consistently. Dean estimated their numbers at about 400 in December 1959 and I counted over 700 in December 1960. The next two seasons hardly any were seen and European Stork also were far fewer in numbers. There is no doubt about it that the predation by these birds is stepped up in this period, but the Red Locust is more agile than most other Acridids and forms only part of the daily catch (DEAN, l.c.). The drop in numbers of parents did not appear to be related to the activity of Stork.

The marsh owl (*Asio capensis*) also catches more locusts when these remain in burnt grassland overnight, but their numbers are too small to have any noticeable effect. In 1959/60 Dean caught rats (*Mastomys natalensis*) in the plot during oviposition peaks, but there were no remains of locusts in the stomach contents.

Females may be parasitised by larvae of the Tachinid fly, *Ceracia nomadacridis*, and this normally means sterilisation (CHAPMAN, 1962; STORTENBEKER, in preparation). The percentage infestation appeared to be slightly higher in females than in males, but the highest recorded percentage sterilisation was only 13% (Kabwe plain, Mweru wa Ntipa, 1960/61), and the percentages for North Rukwa were lower: 1.5%

in 1958/59, 7.7 % in 1959/60, 4.0 % in 1960/61 and 0.3 % in 1961/62. All these figures are based on dissection of hundreds of females.

Finally a reduction of the number of pods per female may occasionally result from the breeding grounds being too dry. Laboratory experiments (WOODROW, 1965 b) showed that some Red Locust females begin to reject a laying site when there is a dry top layer of more than 2 cm thick, and that no more females oviposit when it is over 6 cm thick. If there is no choice, however, after 3 or 4 days females will lay in the dry soil or scatter their eggs. According to ALBRECHT (1956 a) in the field it may take a week or ten days before they do so, but here the ovarian development is retarded. Thus, if the natural mortality goes on while the oviposition is held up, drought could cause a reduction in the mean number of egg-pods per female. This may have been the case in 1959/60 when a period of dry weather split the second laying in two parts (fig. 9).

3.5 Viability of the Eggs

In the laboratory it regularly happens that egg-pods of *Nomadacris* are completely sterile. NORRIS (1959) reported that, in particular females that had no imaginal diapause, laid many sterile pods (up to 39 %). In addition a considerable proportion of the eggs in the fertile pods were not viable (up to 37 %).

In North Rukwa, however, sterile pods were never found and the percentage of not viable eggs was very low, as could be seen from the high percentage of the eggs that hatched, when the pods had optimum incubation conditions (1959/60). In 1960/61 and 1961/62 in the field, these conditions were far from optimal and hatching was poor, but in incubation experiments a high percentage of the eggs hatched, so all eggs were viable at time of laying (table 4).

Table 4. Not hatched eggs, differentiated for stage of development at the moment of death

| Area | Breeding season | Origin of sample | Number of egg-pods examined | Mean percentage of eggs | | | Total % of eggs not hatched |
|---------------------|-----------------|-----------------------------|-----------------------------|-------------------------|---------------|--------------|-----------------------------|
| | | | | not devel. | partly devel. | fully devel. | |
| North Rukwa | 1959/60 | 1st + 2nd oviposition | 34 | 6 | 0 | 0 | 6 |
| | 1960/61 | 1st pod, field | 7 | 20 | 2 | 19 | 41 |
| | | 1st pod, cages ¹ | 36 | 1 | 0 | 5 | 6 |
| | 1961/62 | 1st pod, field | 11 | 1 | 0 | 0.99* | 1-100 |
| | | 1st pod, cages ¹ | 15 | 1 | 0 | 4 | 5 |
| Kabwe plain (Mweru) | 1960/61 | 2nd pod | 31 | 4 | 0 | 5 | 9 |

¹ Pods laid by females, that were caught in the field, just before oviposition and transferred to cages with sand or soil from the experimental plot.

* Incubation success varied from 0 to 99%₀, due to waterlogging of the soil (section 4.4).

3.6 Mean Number of Viable Eggs per Parent

The mean number of viable eggs per parent is the parameter that determines the fecundity of a population. In table 5 this mean has been calculated per parent of the original parental population and it is, therefore, based on the sex ratio as it was at the start of the rains. For reasons of comparison the data collected in the Kabwe plain (Mweru wa Ntipa) have been included, but the values for sex ratio and mean number of egg-pods are not reliable, since the population was studied from the time of second oviposition onwards only. At the moment of first oviposition the percentage females may have been higher and, therefore, the mean number of pods per female is an estimated minimum, based on the observation that the population died off very slowly; even at time of the second hatching there still were scattered parents around.

The mean number of viable eggs per parent is not the number of eggs that actually went into the ground, as larvae of *Ceracia* sterilised 7.7 %, 4.0 %, 0.3 % and 13 % of the females respectively, thus reducing the number of viable eggs per parent to 74, 68, 105 and 64 respectively.

Table 5. Number of viable eggs laid per parent, as determined by various parameters

| | North Rukwa | | | Kabwe ^a |
|--|-----------------------|------------------|-----------|--------------------|
| | 1959/60 | 1960/61 | 1961/62 | 1960/61 |
| percentage females at start of rains | about 50 ¹ | 33 ¹ | 56 | 30 |
| estimated mean number of egg-pods per female | 1.5 ¹ | 1.6 ¹ | about 1.5 | 1.5-2.0 |
| mean number of eggs per pod | 114 | 144 | 133 | 152 |
| Numbers of eggs per parent | 86 | 77 | 112 | 80 |
| mean percentage of eggs viable | 94 | 94 | 95 | 91 |
| percentage of females sterilised by <i>Ceracia</i> | 7.7 | 4.0 | 0.3 | 13 |
| Number of viable eggs laid per parent | 74 | 68 | 105 | 64 |

¹ The values of the %age females and of the mean number of egg-pods per female may not have been valid for the population as a whole, since the data were collected in, and immediately around, the experimental plots only.

^a Data on the Kabwe population refer to the situation at the time of second oviposition.

4 Incubation Success

The incubation success of eggs and egg-pods will be considered from the numerical side first (4.1). Then the causes of the observed mortalities will be described.

4.1 Numerical Data

The 1959/60 season. In order to assess the incubation success of the egg-pods (cf. section 2.5), Symmons laid out a subsidiary plot of 7000 sq.yds (5850 m²) inside the square-mile plot. After the second oviposition he assessed the number of egg-pods in this small area at about 518¹. In a sample of 210 egg-pods from the whole plot I found 67 % to be of the first oviposition (section 3.2); assuming that this percentage was also valid for the subsidiary plot, 346 of the 518 pods should have been 'first' pods. The pods of the first oviposition hatched between 10th and 18th December and 382 hatched parties were found within the subsidiary plot. This suggested that the hatching percentage of the egg-pods was high. There is no reason to suppose that the hatching of the pods of the second oviposition was not equally successful.

The incubation success of the eggs in the pods was estimated in two ways. Symmons counted numbers of hoppers in 27 hatched parties and got a mean size of 88 ± 5 hoppers. I dug up 30 pods immediately after hatching and found that in average 7 ± 2 eggs did not produce a hatching hopper. Compared to the estimated mean of 109 ± 3 eggs in the first egg-pod, this gave an estimated mean size of hatching party of 102 ± 4 . The true value was probably between 88 and 102 which meant that the incubation success of the eggs in the egg-pod was between 81 and 94 %.

I examined 242 egg-pods on natural enemies. Damage appeared to be slight, the total destruction by mites and *Scelio* being less than 7 % (tables 7 and 8). Thus the incubation success of pods and eggs in the 1959/60 breeding season was almost certainly high.

The 1960/61 season. In December 1960 Symmons examined the incubation success of egg-pods in 11 samples strips of 5 yds (4.5 m) wide and in average 0.42 mile (0.68 km) long. The mean egg-pod density over the entire plot had been estimated at one egg-pod per 8.9 sq. yds (7.1 m²), giving an expected number of egg-pods per sample strip of 4116. Only 1635 hatched parties were found, (about 58 % of which were of the

¹ He examined five plough lines, finding 1, 2, 9, 8, and 4 egg-pods respectively.

first oviposition) and this suggested that only 39.7 % of the egg-pods hatched.

The incubation success of the eggs in the pods did not seem to be very high either. Symmons found a mean of 55 ± 3 hoppers hatching per pod (16 pods), and I dug up 13 pods from the first oviposition, finding that an average of 50 ± 6 eggs had not hatched, which subtracted from the mean number of 135 ± 3 eggs per pod gave a mean size of hatched party of 85 ± 7 hoppers. The viability of the eggs had been good, as was shown by the high hatching percentage of both egg-pods and eggs that were incubated in moist soil in tins (table 4).

During incubation there had been a long and severe drought, which lasted from 25th November until 10th December. For the egg-pods of the first oviposition it fell in the second half of their incubation period, those of the second oviposition had only just been laid. In the Central Rukwa plains the drought was even more severe and egg-pods, dug up by field officers, had all completely shriveled.

The small size of the hatching parties was beyond doubt but there were some observations which suggested that the hatching percentage of the egg-pods had been underestimated. Firstly in a sample of 20 egg-pods, which I dug up 20th December, when most of the first egg-pods should have hatched, only two pods were of the first oviposition; one had partly hatched, the other had not, 50 % of the eggs having dried out. If over half of the first egg-pod had not hatched, many more than these two pods should have been found. Secondly Symmons kept in moist cotton wool 26 egg-pods from the second oviposition, dug up just before they were due to hatch, and all but one hatched with some degree of success. Thirdly, immediately after the hatching of the second egg-pod, Symmons ploughed 6 sample lines across the plot, finding only 2 not-hatched pods. This meant that about 3400 egg-pods remained in the plot. If more than 60 % of the egg-pods of the second oviposition had not hatched, he should have found at least 9 times as many unhatched pods (assuming that the not-hatched pods of the first oviposition had all disintegrated by then, otherwise there should have been even more). Finally the ultimate assessment of the numbers of hoppers in the third instar revealed the presence of more hoppers in the plot, but not significantly more, than ever could have hatched if the 39.7 % hatching percentage of the egg-pods had been right.

It thus appeared that the incubation success of the egg-pods had in fact been considerably higher than the assessment suggested. In the sample strips many parties probably had not been recognised as such, possibly because they were small and scattered quickly in the sparse vegetation due to the strong winds.

On the other hand, when the hatching was over and the sample strips were examined for hoppers, hardly any were found; that is, if hatched parties were missed they died all the same. Thus all we can say is that the hatching percentage of the egg-pods almost certainly has been higher than the 39.7 % that was recorded in the sample strips.

The 1961/62 season. In each of the small plots used in the 1961/62 season the incubation success was estimated. The numbers of egg-pods had been counted in 6 sample

Table 6. Incubation success of egg-pods in the 1961/62 experimental plots as estimated a. from numbers of hatched parties counted in sample strips, and b. from the hatching percentage of marked egg-pods.

| | Plot 1 | Plot 2 | Plot 3 |
|--|-----------------|----------------|---------------|
| a. estimated number of egg-pods in sample strips | 432 \pm 45 | 2159 \pm 185 | 642 \pm 104 |
| number of hatched parties counted in sample strips | 83 | 34 | 120 |
| estimated percentage of egg-pods hatched | 19 | 2 | 19 |
| b. number of egg-pods marked | 31 | 21 | 19 |
| number of egg-pods hatched | 7 | 1 | 9 |
| percentage of egg-pods hatched | 23 ¹ | 5 | 47 |

¹This group had been marked in an area to the North of plot I with a different vegetation. From the size of the surviving population (table 11) it was clear that the hatching percentage in this plot had been higher than 23%.

lines of 0.1 mile long (160 m) and 0.05 mile (80 m) apart. Incubation success of the pods was assessed in two sample lines of 0.3 miles (480 m) long and 4 yards (3.6 m) wide, laid out across the plot, 0.12 mile (190 m) apart. In view of the experiences of 1960/61 it was the intention to search these strips twice a day, in order to lower the chance of missing some of the hatched parties, but due to the difficult terrain conditions slowing down transport, there could be only one inspection a day. A cross-check on the incubation success of the pods was obtained from the group of egg-pods which intentionally had been marked close to places where experimental plots were expected to be laid out. This latter method gave higher estimates for incubation success of egg-pods than the daily counts of hatching parties in the sample lines across the plots (table 6). The percentage hatching was low in all plots, and this time it was not caused by drought as in 1960/61, but it appeared to find its cause in waterlogging of the soil.

The 1961/62 season was very wet, with heavy rainfall unusually early in the season. In the slightly lower-lying areas this caused temporary waterlogging or flooding of the soil for periods of up to 10 days. In addition, there was heavy rain over the whole catchment area and the annual flooding arrived two months earlier than usual.

The low incubation percentages in table 6 do not represent a valid average for the whole of North Rukwa, as the plots and the sites of the marked pods all happened to be in the area that was affected by the temporary flooding. Towards the north and west hatching was very much better. On the whole, however, there is no doubt that in the southern part of the Tumba sector, where the majority of the first pods had been laid, the incubation success of the pods was low.

The incubation success of the eggs in the pods that did hatch was high. In contrast with the effect of drought, as seen the year before, flooding did not usually affect the size of the hatched party; either a pod hatched well or it did not hatch at all. For

estimating the mean size of a hatched party the plan was to use the marked egg-pods, but the difficult conditions in the plains hindered transport so much that regular inspection of the plastic cages was impossible. It was found that emerging hoppers died quickly as a result of the hot conditions under the plastic cover, and that their corpses were eaten by ants which seemed to consider the cages a welcome support when building up their nests from the wet ground. Only 7 pods hatched just before an inspection and five of these hatched well, producing an average of 114 hoppers (minimum 100, maximum 132). The other two pods hatched only partly, giving 65 and 15 hoppers respectively. In another 21 cases not-marked pods were dug up just after hatching and these had a mean of 6 ± 1 not-hatched eggs, which, subtracted from the mean egg-pod size of 133 ± 4 , gave a mean size of 127 ± 4 hoppers per hatched party. In estimates of numbers of hoppers hatched in a plot, the average size of a hatched party has been taken as 110.

Thus in the three breeding seasons between 1959 and 1962 the incubation success varied; in 1959/60, when there was sufficient and well spread rain, the incubation success was high for both egg-pods and eggs, in 1960/61, when there was a drought during incubation, it was low for eggs in the pod, but possibly better for the egg-pods, and finally, in 1961/62 in some parts of the plains, heavy rain caused waterlogging of the soil and the incubation success was low for egg-pods, but usually high for the eggs in the pod.

In 1962/63 the breeding grounds were almost inaccessible and only little was learned from a few inspections. A parental population of several million locusts moved on to the only dry ground in North Rukwa's north-eastern part and probably laid there. Hatching was probably poor, which was thought to be the result of waterlogging of the soil. The water table was high and the heavy early rainfall must have saturated the soil for prolonged periods.

4.2 Predators and Parasites on Egg-pods

4.2.1 Rats

On inspection of the marked egg-pods, about one week after they had been laid, it was found that in some cases there was a slight depression where the egg-pod should have been and the pod had disappeared. No more pods disappeared after the first week. This looked very much like the work of rats and traps were put up close to the groups of marked egg-pods. Near four of the groups 20 traps were put out at intervals of 5 paces along four parallel lines 5 yds (4.5 m) apart. Dried fish, the local 'daga', was used as bait. Because of shortage of traps these could be kept in one place for four successive nights only¹. Consequently it is unlikely that the rat populations were trapped out completely and the densities given in figure 11 must, therefore, be underesti-

¹ In plot 2 the traps had been there only for two nights when the area became flooded.

% of eggpods destroyed

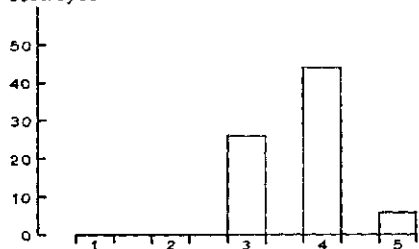
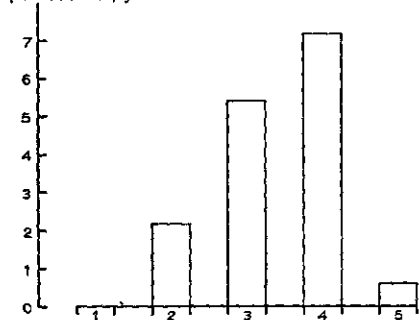


Fig. 11. Estimated rat densities compared to the percentage of the egg-pods that disappeared in each group of marked egg-pods. North Rukwa, November 1961

rats per 1000 sq. yds



Legend:

1. Plot 3 (30 pods)
2. Plot 1 (23 pods)
3. Middle of Tumba plain (26 pods)
4. Kasala (20 pods)
5. Tumba treeline (31 pods)

mates. The results suggested some correlation between rat density and the percentage of marked egg-pods that disappeared. In one place (Kasala) pods had been marked along three parallel lines; one of the outer lines was about 50 paces away from the middle one and there was a depression in between. Only along the two lines on one side of this depression had egg-pods disappeared and only there were rats caught.

The approximate effect of rats on the total number of egg-pods in the Tumba sector can be estimated from the rat densities in the oviposition area. The catching results suggested an average density of between 3 and 4 rats per 1000 sq. yds (836 m²). These could have caused a loss of egg-pods of between 10 and 15 %.

In the previous seasons Dean collected some data on rat densities in the experimental plots. In 1959/60 he estimated their density at 2.4 ± 0.4 per 1000 sq. yds, a population which could have reduced the total number of egg-pods by 6 to 10 %. In the 1960/61 plot, in the same area as plot 1 in 1961/62, rats were virtually absent and damage must have been negligible.

All specimens I caught in North Rukwa were of the species *Mastomys natalensis*, with the exception of four unidentified grey black rats of a larger species, which was found close to the tree line in the Kasala tree point sample only. In the same area the only shrew, of unknown species, was caught.

4.2.2 Mites

Several Acarina species were found in egg-pods, though not all of them preyed on the eggs. Once a pod was infested the mites multiplied rapidly, but not all eggs were destroyed at once and it was not uncommon to find hoppers hatching from an infested pod. More often infection apparently occurred early in incubation, the damage was then extensive and the few hoppers that hatched could not get out of the pod.

Dr. Newell (California University) provisionally identified the predatory species as belonging to the genera *Rhizoglyphus* and *Anoetus* (or possibly *Histiostoma*). Some more genera were represented, but these are known either to be scavengers or to specialise on fungi. They had probably been attracted by decaying eggs in already infested pods or by fungi which are sometimes found to thrive on the froth enveloping the egg-pod.

Damage done to the egg-pod population varied, but was never high (table 7). In 1959/60 and 1960/61 the percentage infestation was estimated in the experimental plot only. In 1961/62 egg-pods were collected from all over the Tumba sector and appreciable differences in infestation level were found, but the overall mean was of the same order of magnitude as in the previous two years. In 1961/62 samples suggested that variation in mite density could be due to flooding conditions. On three parallel lines (cf. section 3.2), two miles apart, the infestation varied from 5 to 25 %. The 5 % was in the area of lowest level, subject to the longest flooding, whilst on river-banks and other higher level areas that are flooded later and dry up earlier, the percentage infestation was higher.

4.2.3 *Scelio howardi*

In a few cases locust egg-pods were found to be parasitised by larvae of the hymenopteran *Scelio howardi* CRAWF. One larva makes its way into one locust egg, eats the contents and pupates inside it. The egg looks normal but it is often darker in appearance. Usually about half of the eggs in one egg-pod were parasitised and the other half hatched, if the hoppers could make their way out. The *Scelio* imagines hatched a few days after the hoppers. The percentage infestation was low (table 8). According to CLAUSEN (1940) Scelionidae that parasitise single-brooded hosts also have only one generation per year, but most Scelionids have several generations per year and in the Rukwa Valley *Scelio howardi* may have one or more grasshoppers as alternative hosts.

No other egg-pod or egg-destroying agents have been found. If any other member of the soil fauna had been destroying egg-pods on a considerable scale, some would have been found in the act of destroying an egg-pod. On a few occasions nematodes or fungi were found in an egg-pod, but these seemed to live either on the froth or on decaying eggs and the healthy eggs had not been affected.

Table 7. *Percentage of the egg-pods that were infested and destroyed by mites*¹

| Area | Breeding season | Origin of sample | During incubation | | At hatching | | Percentage of pods destroyed |
|---------------------------------|-----------------|----------------------------|-------------------|----------------------------------|----------------|----------------------------------|------------------------------|
| | | | size of sample | percentage infested ¹ | size of sample | percentage infested ¹ | |
| North Rukwa | 1959/60 | Experimental plot | 242 | 6 | 34 | 0 | 6 |
| | | Experimental plot | 154 | 21 | 14 | 14 | 7 |
| | 1960/61 | Tumba plain (all samples) | 139 | 11 | 22 | 0 | 11 |
| | | Sample line 1 ² | 20 | 20 | | | |
| | | 2 | 38 | 5 | | | |
| | | 3 | 13 | 23 | | | |
| Kabwe plain (Mweru wa Ntupa) | 1960/61 | 4 | 6 | 17 | | | |
| | | | | | 23 | 13 | |
| | | | | | | | |

¹ After infestation by mites an egg-pod is only gradually destroyed.

² Sample lines of egg-pod survey (section 3.2).

Table 8. *Percentage of egg-pods infested by *Scelio howardi**

| Area | Breeding season | Size of sample | Number of pods infested | Percentage infested |
|-------------|-----------------|----------------|-------------------------|---------------------|
| North Rukwa | 1959/60 | 242 | 3 | 1.2 |
| | 1960/61 | 154 | 5 | 3.2 |
| | 1961/62 | 139 | 0 | 0 |
| Kabwe plain | 1960/61 | 23 | 0 | 0 |

4.3 The Effect of Drought

In the 1960/61 breeding season some field observations were made on the effect of drought on incubating eggs and egg-pods. In the Central Rukwa area the dry spell lasted for more than a fortnight and its effect was enhanced by the poor rainfall preceding it: less than 2 in. (50 mm) in total, of which 1.5 in. (40 mm) fell in the two days before the drought¹. Egg-pods dug up by field officers all had dried out completely; the young hoppers appeared late and they were few in numbers. This suggested that the egg-pods from the first oviposition had all been destroyed, and those of the second oviposition at least for a large proportion.

In North Rukwa the drought lasted even longer (20 days with 0.2 in. (5 mm) rain on the 15th day, but the preceding rainfall was much higher than in Central Rukwa (8.2 in. or 208 mm)². All the same the soil must have been very dry for at least ten days. At that time the pods of the first oviposition were in the last half of their incubation. The pods of the second oviposition were laid during the first week of the drought. Examination of egg-pods that were dug up on 12th December, gave no indication of any ill effects on pods from the first oviposition, but those of the second laying had dried out considerably, the yolk was very thick and it looked as if no development was taking place.

The rains resumed on 15th December and I dug up a sample of 20 egg-pods on 20th December. Now all egg-pods of the second oviposition looked healthy and were apparently developing normally. However, the majority of the egg-pods of the first oviposition had hatched by then and these produced abnormally small numbers of hoppers (section 4.1). Nearly 41 % of the eggs did not hatch; about half of the not-hatched eggs had not developed at all, but the others contained fully developed hoppers (table 4), some partly out of the egg-skin. Data on the hatching of the second egg-pod are not so detailed, but Symmons thought the hatching to be equally poor. The drought probably also affected the incubation success of the egg-pods, but to what extent did not become clear.

In the 1961/62 breeding season a small experiment was carried out on the effect of drought on egg-pods (table 9). Female locusts were caught just before laying and transferred to tins with soil from the experimental plot. They laid 37 egg-pods, but later 4 pods had to be discarded as these were badly damaged by mites.

All tins were watered regularly, but either at the beginning or halfway through or at the end of incubation, they were subjected to 10 days dry conditions; that is, the soil was not watered and the 10 days were counted from the day the top soil had dried out. These conditions were not strictly comparable to drought conditions in the field

¹ Rainfall figures from Milepa station at the edge of the plains and at the foot of the escarpment, where the amount of rain is usually higher than in the plains. In particular in the beginning of the wet season rainfall can be very localised and readings from one single station can be misleading. In this case eye-witness accounts confirmed the Milepa readings.

² Rainfall records from Tumba station, which is situated away from the escarpments. Here also readings were thought to be representative for the whole North Rukwa area.

Table 9. *Effect of desiccation of soil on incubation success of egg-pods and eggs laid in Rukwa soil in biscuit tins*

| | Number of egg-pods | Incubation success in percentage hatched | |
|------------------------------|-----------------------|---|------|
| | | egg-pods | eggs |
| Dry period | | | |
| a. early in incubation | 8 | 100 | 78 |
| b. halfway incubation | 8 | 100 | 71 |
| c. towards end of incubation | 9 | 89 | 77 |
| a + b + c | 25 | 69 | 76 |
| Control group | 8 | 100 | 92 |

of course; the tins were kept outdoors under a cover which shielded them from rain but allowed much of the sun to reach the soil. The average temperature of the soil, however, must have been lower and the humidity of the air higher than is normal during a drought in the field. On the whole, the effect of the dry conditions was small. The incubation percentage of the egg-pods was hardly affected, but there was a small reduction in the survival of the eggs in the pods. This reduction was almost entirely caused by a large mortality among emerging hoppers, which died either half way out of the egg or before first ecdysis. This appears to be characteristic of damage done by drought. It was also seen in a group of 34 egg-pods, which had been taken out of the soil just after oviposition, had been transferred to moist cotton wool and then had been subjected to a period of 'drought' of 3-9 days in dry cotton wool.

4.4 The Effect of Waterlogging of the Soil

Exceptionally heavy rainfall caused temporary waterlogging or flooding of the soil in some parts of the Tumba sector during incubation in November 1961. The water dried up or drained away again, but in several parts of North Rukwa the soil was waterlogged for a period of several days to one week. This caused a considerable mortality among egg-pods and the development of the surviving pods was slowed down, incubation taking about 35 days compared to 30-31 days under normal conditions (1959/60).

The destruction caused by the waterlogging is demonstrated in table 10, which gives the hatching percentages in the groups of marked egg-pods (cf. section 4.1). The not-hatched pods were dug up one week after the last hatching; all were found back. Virtually all eggs contained apparently fully developed hoppers.

Submergence of the egg-pod may not always prevent hatching, as hoppers from one of the marked pods emerged through 2 in. (5 cm) of standing water, but only half of the hoppers managed to get out. This is probably a rare event.

Fig. 12 shows the Tumba sector with the density of laying for the egg-pods of the

first oviposition, as it was estimated from the distribution of the parental population during the peak of oviposition¹, and confirmed by the results of the rather crude egg-pod survey (section 3.2). The ground levels were estimated from depths of water at the time of the assessment of the filial population, which assessment was carried out by Swamp Skipper early in April 1962; they are, therefore, relative levels with the water surface as criterion. Waterlogging of the soil by early rains is not necessarily correlated with the relative soil levels, but in November 1961 the rainfall was well spread. The areas of higher level drained off quickly, but in the lower lying areas the water disappeared slowly. Superimposed on the estimated egg-pod distribution and the ground levels, are the hopper bands seen and destroyed from the air in January, February and March 1962 (pilot's reports). The distribution as seen from the air confirmed observations on the ground. The effect of waterlogging is clearly demonstrated; in the area of lowest egg-pod density, but high groundlevel, the incubation success was highest. There is the possibility that this hopper distribution was the result of displacement of bands from their nursery areas to the North, but this appears extremely unlikely, in the first place because of the distances and secondly because bands showed a significant preference for displacement to the West (DEAN, 1967b).

In the Tumba sector the average incubation success of the egg-pods was probably about 25 %, but this figure is not valid for North Rukwa as a whole. In the other areas the incubation success of pods from the second and following ovipositions was apparently high, judging from the size and density of the hopper populations seen from the air.

The effect of waterlogging of the soil on egg-pods was simulated in two small experiments. Females were caught just before oviposition and made to lay in biscuit tins with soil from the experimental plot. Some of these egg-pods were taken out of the soil immediately after laying and kept in moist cotton wool. In the second half of their incubation period they were submerged for 1, 2 or 4 days. One day submergence proved fatal for one of the three pods involved, 4 days under water was fatal for all three pods. In the second experiment in two tins the soil was waterlogged for 3 days; all 5 pods hatched, but only 77 % of the eggs produced a healthy hopper. In two other tins the soil was kept waterlogged for 6 days; none of the 11 pods hatched.

4.5 Discussion

The observed differences in sex ratio (section 3.1) appeared to be real. The method of catching-by-night was applied in various types of vegetation, both before and after maturation had started and both during periods of oviposition and in between layings, but it never gave the sharp rise in percentage males in November and December and

¹ Assessment of 15th and 16th November; 34.2 miles (55.0 km) of scouting along 9 parallel lines 0.5 mile (0.8 km) apart, over an area of 37.5 sq. miles (97.1 km²).

the subsequent drop in January, as found by ALBRECHT (1956 a), CHAPMAN (1959) and myself with the catching-at-dawn method (chapter 2).

In most cases the sex ratio of the parental population at the start of maturation was close to unity (table 2). There were two exceptions to this; in November and December 1960 the North-Rukwa population consisted for only one-third of females. In December of that same year the Kabwe-plain population also had a predominance of males, but at the time of first oviposition this may have been different.

The sex ratio can differ from place to place within one outbreak area. This was probably the case at the time of first oviposition in 1959, it certainly happened in the 1960/61 breeding season and it was also seen in 1961, both in the dry season and after the first oviposition (section 3.1). Secondly, the sex ratio of the parent population may change due to the apparent higher death rate of females compared to males (fig. 8); this finds its counterpart in experiences with laboratory populations (NORRIS, 1959). For a reliable estimate of the sex ratio, therefore, one has to collect samples of locusts prior to each oviposition and in various parts of an outbreak area.

The mean number of egg-pods per female (section 3.2) also can be accurately estimated only on the basis of several successive population assessments, covering the entire area that is occupied by the parental population. There often are substantial shifts in distribution: in 1960/61 in the Kambangombe plains there was a slow shift of the population to the north-east (observation by P. M. Symmons) and in 1961/62 the parent population largely moved out of the Tumba plains after the first oviposition. Only in 1961/62 the assessments covered the entire population and only for that year the estimated mean number of pods is reliable. In 1960/61 the change in distribution was a slow one and the assessments covered a rather self-contained part of the parent population; thus the estimate for that season probably was close to the real value. In 1959/60 a substantial shift of females possibly occurred before first oviposition, but we do not know whether there was any migration after that, and the estimate for that season may not be correct.

Work of several authors indicates that in the field Red Locust females tend to lay about two egg-pods (ROBERTSON, 1958a). Robertson's own data, collected from 1952 to 1956 in Central Rukwa, showed large variations in numbers of pods per female (2.3, 0.7, 3.1 and 0.9 respectively), but these estimates were based on observations in a relatively small part of the outbreak area and he did not allow for possible migrations and for differential mortality of the sexes. His data are, therefore, not very reliable.

The mean number of pods per female is closely linked with the longevity of the parents after the start of the rains. Predators did not appear to be of much influence and the survival of parents may largely depend on the occurrence of sudden changes in weather. The spectacular mortality early in December 1961 did coincide with a hot and dry spell, and in 1952/53 the number of parents went down abruptly at the resumption of the rains following a severe drought that lasted from 8th to 31st December (ALBRECHT, 1956 a; ROBERTSON, l.c.).

There is a possibility that longevity is not only determined by abrupt changes in

weather, but that it is also predetermined by conditions during the preceding dry season. In the laboratory immature adults must be kept as dry as possible if they are to remain alive (NORRIS, personal communication). It could be that in the field wet conditions lasting for many months into the dry season, weaken the resistance of adults against sudden changes in weather in the following wet season. On the other hand, ROBERTSON (1954) recorded that in 1950 a long dry season had an adverse effect, females producing egg-pods with an average of only 49 eggs.

A parameter that is much easier to determine in the field is the mean number of eggs per pod (section 3.3), and several authors have given information on this point. Generally the number of eggs per egg-pod was found to be high in the phases solitaria and transiens, but low in swarms (ROBERTSON, l.c.). In the laboratory crowding of *Nomadacris* had a detrimental effect on the number of ovarioles; after two generations the maximum had dropped from 196 to 153 and, in addition, the percentage of non-functional ovarioles had increased (ALBRECHT, l.c.).

In my own data on the number of eggs per pod, the state of gregariousness of the females' parents is clearly reflected. The highest averages were produced by the solitary populations in the Kabwe plain and in the Uninji Pans (152 and 157) (table 3). The number of eggs per pod produced by North Rukwa populations were all lower. In the 1958 dry season the immature adults formed many concentrations and the mean number of eggs in pods produced by their offspring (114) was as low as in the years around 1953, when the populations were large and dense. During the 1959 dry season adults were not numerous and there were few concentrations, and the mean number of eggs in pods laid in November 1960 by the next generation were notably higher (144). In 1960 the population had been very dense in the hopper stage, but in the dry season adults lived rather scattered and there was a slight decrease in numbers of eggs per pod in the 1961 parents (133). Finally, after an unsuccessful hopper-control campaign, adults lived through the 1961 dry season in a few fairly dense concentrations and the mean in the small sample that could be obtained in November 1962 was lower again (109). The number of eggs per pod did not appear to be influenced by the state of gregariousness of the parents themselves.

Thus, when parents are dense, their children produce fewer eggs per pod, but the lowest mean I found was still nearly twice as high as the means given by various authors for swarming locusts (ROBERTSON, l.c.). This demonstrates that *Nomadacris* swarms may have a high reproductive potential at the moment of emigration from an outbreak area. It confirms ALBRECHT's conclusion (l.c.) that *Nomadacris* is most dangerous when there is sudden concentrating of locusts that have had a low level of gregariousness for a number of generations, as it is only in the second generation of crowding that the number of eggs per pod decreases. From morphometrical data (STORTENBEKER, in preparation) it appeared that swarms leave an outbreak area in the phase transiens. It is likely, therefore, that this high reproductive potential will help emigrating swarms in establishing a plague, but it will not be a factor of great importance probably.

The viability of eggs hardly varied (section 3.5). When in the field for some reason the number of eggs per pod was reduced (section 3.3), the viability of the eggs laid was still high. This forms a contrast with experiences of NORRIS (1959) and ALBRECHT (l.c.), that in the laboratory usually many egg-pods and eggs are not viable, percentages of 20 to 30 % being no exception.

The four parameters which determine the fecundity of Red Locust populations would not allow very much higher multiplication rates in periods of dry years. Not the viability, as in the described seasons of low multiplication rates it was very high; not the sex ratio, since the percentage females can not be much higher than it was in 1961/62; not the number of eggs per pod, as in periods of dry years, with increasing population densities, this number would decrease rather than increase, and finally not to a very great extent the number of pods per female, as here an increase would merely give an extension of the period during which egg-pods are laid and subsequently hoppers hatch. It would mean, therefore, that predators would be able to find their prey during a longer period of time (cf. chapter 5.).

It is unlikely that between assessing the number of gravid females and finding the egg-pods in the ground a reduction in numbers escaped attention. In two of the three seasons the total number of egg-pods that had been laid in an experimental area (as estimated from egg-pod sampling) could be compared with the number expected from population assessments and estimates of the sex ratio at the times of oviposition. In both 1960/61 and 1961/62 the total number of egg-pods, estimated to have been laid, was very close to the estimate derived from egg-pod assessments (section 3.2). This suggested that all females in fact laid their pods.

In the three breeding seasons between 1959 and 1962 the incubation success of eggs and egg-pods varied from very high to very poor. Predators were not responsible for this; their effect was fairly constant. Rats (*Mastomys natalensis*) were probably responsible for the destruction of some of the marked egg-pods (section 4.2.1). The observation that all destroyed pods disappeared in the first week of their existence, could indicate that rats can discover the pods only just after they have been laid, and that their effect is restricted to a small part of the incubation period only. This appears to be confirmed by the situation in 1954/55, when *M. natalensis* was abundant in the Rukwa Valley, such as to constitute a proper pest; the breeding of the Red Locust, however, was very successful that year (table 34). The density of mite predators appeared to be related to the level of the soil and this would indicate that they cannot survive prolonged flooding.

Dessiccation and waterlogging of the soil were found to be the most effective reduction factors during incubation. Drought was responsible for the poor hatching in the plot in 1960/61, as was waterlogging in the next season. Egg-pods from females that were transferred from the field to cages just before laying, hatched well when given optimum moisture conditions (table 9).

Percolation in clay is extremely slow and temporary waterlogging of the topsoil can

result from very heavy rainfall, even when the water table is several feet under the surface. This was the case in November 1961 and (according to I.R.L.C.S. Council minutes) possibly also in 1947 and 1948, when heavy rainfall early in the wet season may have been the cause of poor hatching in the Milepa plains in Central Rukwa.

Temporary flooding and waterlogging is likely to affect mainly egg-pods in the lower parts of the plains, which are on the whole extremely flat. In addition, rainfall is often of a patchy nature and only part of the breeding area may be affected. Consequently there will be a great variation in incubation success from place to place, as was seen in 1961/62, when the hatching percentage of the egg-pods varied from 0 to 100%.

A typical characteristic of damage done by water-logging appeared to be that egg-pods either hatched well, or not at all (section 4.1). Eggs in not-hatched pods contained what appeared to be fully developed hoppers that were unable to get out. This was probably a result of oxygen deficiency during the incubation. Lack of oxygen during the larval stage has been reported to have a similar effect on *Calopteryx* (Odonata) (ZAHNER, 1959). Eggs of *Nomadacris* are likely to be sensitive to waterlogging of the soil, since they are not embedded in froth¹, the froth plug being attached to, but not continuous with the egg mass. Thus in waterlogged soil the egg-pod will for its oxygen requirements be largely dependant on any air bubbles that are by chance in contact with it.

In contrast with waterlogging a drought did not appear to affect the egg-pods as a whole, but more the eggs in the pod, reducing the number of hatchlings per pod. In November 1960 the effect of the drought on the hatching percentage of the egg-pods remained uncertain, though weighing the arguments pro and contra, I would be inclined to think that a large proportion of the pods hatched. When it is severe, a drought will eventually destroy the egg-pods completely (as in 1952/53 and in 1960/61 in Central Rukwa). Waterlogging may have a local effect only, but a drought is more likely to affect the entire area. Not only the amount of rain is important, but also the spread over the incubation period; in 1959/60 the incubation was successful under conditions of moderate but fairly well-distributed rainfall, but in the next season hatching was poor, when there was more but not so well-spread rain (fig. 10).

Several authors have studied the water uptake of Acridid eggs. Non-diapause eggs like those of the Desert Locust (*Schistocerca gregaria*) take up an initial amount of water within the first 24 hours after oviposition, but the main water uptake falls in the second quarter of the incubation, when the eggs more than double their original weight (SHULOV and PENER, 1963; HUNTER JONES, 1964). If the eggs are unable to imbibe the required minimum amount of water² the development is arrested, the eggs

¹ This is in contrast with eggs of many other Acrididae found in the Rukwa Valley (CHAPMAN and ROBERTSON, 1958), such as the eggs of *Locusta migratoria migratorioides* which have been reported to survive flooding for some time (UVAROV, 1928).

² They normally take up considerably more water than the minimum amount needed for the completion of the development.

remaining healthy and viable for up to 100 days provided they are kept at 100 % humidity (HUSSAIN, AHMAD and MATHUR, 1941; SHULOV and PENER, l.c.). At lower % R.H. the percentage hatching decreased rapidly. Of eggs that were transferred to between 80 and 100 % R.H. with one third of their incubation completed, about 50 % or more hatched; eggs that were given moist conditions during the first two-thirds of their development had hatching percentages of 50 or more at a R.H. as low as 40 %. SHULOV and PENER (in preparation) repeated these experiments with eggs of the Red Locust and obtained somewhat similar results.

In the field, observations on the effect of drought confirmed these findings. The egg-pods of the first oviposition were in the second half of their incubation when the drought started. They probably had imbibed the required amount of water and their development was not arrested as their incubation period was of normal length. The humidity in the soil, however, must have been well under 100 % for several days and this caused a reduction in the number of eggs that hatched. The second egg-pods had not yet imbibed the minimum amount of water when the drought started, the development was arrested (resulting in an increase in incubation period by about 5 days), the eggs lost water (the yolk was found to be very thick), but on the resumption of the rains the development started again and appeared to be normal for all eggs.

Effective as drought and waterlogging occasionally may be, they are factors that have the character of a calamity rather than of a regular occurrence. There may be one exception to this; in a series of very wet years the lake may expand and eventually cover the plains, leaving a narrow fringe of grassland along the edge of the woodland and in some subsidiary plains only. At the end of the dry season the water table there will be close to the surface and only moderate November rains could saturate the soil. This may be a major factor in keeping the locusts down in periods of high lake level, even in a productive area like North Rukwa.

Basing conclusions on three years of research only, it appears that large mortalities during incubation occur only incidentally and that the factor responsible for the correlation between multiplication rate and the rainfall in the previous season, operates elsewhere in the life cycle of *Nomadacris*.

5 Natural Mortality in Hoppers in the First and Second Instars

5.1 Mortality Assessments

In the gregarious phase Red Locust hoppers go through six and in the solitary phase through seven instars (BURNETT, 1951). In the phase-transiens populations, as normally found in the outbreak areas, a variable proportion of the hoppers pass through six instars and the rest through seven or exceptionally eight (STORTENBEKER, in preparation). The duration of the successive instars varies somewhat, but in the field the first and the second instar were taken to last about ten days each.

In laboratory populations of *Nomadacris* and other Acrididae often high mortality rates occur early in hopper life from as yet unknown causes (SPRADBERY, 1959). In the field a similar mortality had never been observed, but in order to check this, assessments were made of the populations that survived after the first two instars. This point in the hopper life was chosen for two reasons. Firstly band formation usually becomes manifest in the third or later instars and this gives very clumpy distributions and high standard errors in the assessments. Secondly at the end of the second instar the corpse of a hopper is no longer so small as to be easily missed. Estimates of the natural mortality were obtained as described in chapter 2.

The 1959/60 season. In the 1959/60 experimental plot an estimated total of $0.94 \times (420,000 \pm 30,000) \times 95 = 37,500,000 \pm 2,700,000$ hoppers had hatched, in which 0.94 represents the percentage of the egg-pods that hatched¹, 420,000 is the estimated total number of egg-pods in the plot², and 95 is the estimated mean number of hoppers hatched from one pod³. For the 0.94 and the 95 no standard errors can be given, but it is thought that these estimates were near enough not to affect the standard error of 2.7 million seriously.

Twenty six days after first hatching Symmons assessed the surviving population. After drench-spraying sample strips with DNC, he counted over 16,000 corpses in nearly 6000 square meter rings, which meant that in the whole plot 8.5 ± 0.5 million hoppers were still alive. Thus $(37.5 \pm 2.7) - (8.5 \pm 0.5) = 29.0 \pm 2.8$ million hoppers had died between emergence and the third instar, or 77% of the population.

¹ Based on SYMMONS' estimate that virtually all pods must have hatched (section 4.1), corrected for losses caused by mites (table 7).

² Estimated from egg-pods found in 12 plough lines of 1 mile (1.6 km) long and 0.2 mile (322 m) apart, laid out in a grid.

³ The mean of two independent estimates (section 4.1).

The 1960/61 season. In the 1960/61 experimental plot a total number of $0.397 \times (157,568 \pm 12,751) \times 70 = 4,382,000 \pm 354,300$ hoppers had hatched. This figure must be corrected for egg-pod destruction caused by mites (table 7), which brings the total down to about 4.16 million hoppers. The number of egg-pods in the plot had been estimated by Symmons¹; the number of hatchlings per pod is the mean of two independent estimates, and 0.397 represents the percentage of the egg-pods that had hatched, but as has been said above (section 4.1), this percentage probably was an under-estimate.

When the hoppers were in the third and fourth instar, Symmons drench-sprayed a number of sample lines across the plot and searched 880 square meter rings. He found 3300 corpses and this indicated a surviving hopper population of about 4.49 million. This was more (but not significantly more) than there ever had been if the 39.7% hatching of the egg-pods had been correct. Whatever happened, we do not know which percentage of the hopper population died, that is, if there was any considerable mortality at all.

Also in the 1960/61 breeding season, the author carried out two mortality assessments in the Kabwe plain in the Mweru wa Ntipa (chapter 2). Hatching in the small plot (fig. 5) took place between 8th and 11th January 1961. Three times per day the hatched parties were counted and then scattered. On 8th, 9th and 10th January 38 egg-pods hatched, giving a total of $38 \times (118 \pm 10)^2 = 4484 \pm 380$ hoppers. On the morning of 11th January the population was assessed at 2953 ± 591 hoppers. Thus 1531 ± 703 hoppers had died (about 34%).

On 11th January another 9 egg-pods hatched, which brought the population at $(2953 \pm 591) + 9 \times (118 \pm 10) = 4015 \pm 598$. A final assessment on 13th January gave an estimated population of only 785 ± 137 hoppers². During the second mortality period of 2 days, therefore, 3230 ± 620 hoppers died (about 80%). The overall mortality in five days had been $47 \times (118 \pm 10) - (785 \pm 137) = 4761 \pm 490$ or 86% of the population.

The 1961/62 season. During the 1961/62 breeding season I tried to assess the mortality in separate plots in four different places (chapter 2, fig. 6). In three of these plots the survivors were assessed after the first instar and then again after the second instar, and in the fourth plot only after the first instar. Hatching of the first egg-pod began 16th December and showed a peak from 17th to 19th. Since little second oviposition had taken place in the Tumba sector the hopper population in the plots was fairly uniform in age. The first series of assessments was carried out on 2nd, 4th and 5th January when between 91 and 98% of the hoppers had entered the second instar,

¹ Estimate based on egg-pods found along 11 parallel plough lines, of in average 0.42 (0.67 km) long and 0.1 mile (0.16 km) apart.

² Mean number of hoppers hatching from 10 pods.

³ Assessment carried out along 12 parallel lines, 1 yard (0.91 m) wide and 15 yards (13.7 m) apart.

Table 11. Mortality of hoppers during the first and second instar in experimental plots

| | Egg-pods | | | Hoppers | | | Mortality | | |
|---------------------|------------------|---------------------|------------------------|--------------------------|--------------------------|----------------------|------------|-----------------------------|------------------------------------|
| | estimated number | hatching percentage | number hatched per pod | estimated number hatched | mortality period in days | surviving population | numbers | in % of original population | in numbers per 1000sq. yds per day |
| North Rukwa | | | | | | | | | |
| 1959/60 | 420,000 | 94 | 95 | 37,500,000 | 26 | 8,500,000 | 29,000,000 | 77 | 359 |
| 1960/61 | 157,570 | ? | 87 | ? | 25 | 5,010,000 | ? | — | — |
| 1961/62 plot 1-1 | 9,030 | ? | 110 | ? | — | 295,200 | — | — | — |
| plot 1-2 | 14,730 | ? | 110 | 496,300 ¹ | 9 | 352,800 | 143,500 | 29 | 206 |
| plot 2-1 | 48,180 | 5 | 110 | 264,990 | 18 | 160,200 | 104,790 | 39 | 75 |
| plot 2-2 | 46,850 | 5 | 110 | 257,680 | 24 | 111,160 | 146,520 | 57 | 79 |
| plot 3-1 | 17,100 | 47 | 110 | 884,100 | 16 | 538,200 | 345,900 | 39 | 279 |
| plot 3-2 | 18,200 | 47 | 110 | 940,940 | 27 | 482,400 | 458,540 | 49 | 219 |
| plot 4 | 100 | 100 | 110 | 11,000 | 11 | 4,270 | 6,730 | 61 | 610 |
| Kabwe plain (Mweru) | | | | | | | | | |
| 1960/61 1st period | — | — | 118 | 4,484 | 3 | 2,953 | 1,531 | 34 | 17 |
| 2nd period | — | — | 118 | 4,015 | 2 | 785 | 3,220 | 80 | 53 |

¹ The hopper population in 1-1 as assessed on 4th January was larger than it ever could have been, if the hatching percentage of the egg-pods had been the same as in the group of marked egg-pods nearby. Thus the original number of hoppers was unknown and plot 1-1 could not be used for a mortality assessment. However, the result of the assessment was used to calculate the hopper population still alive that day in plot 1-2. The total number of egg-pods in 1-2 and 1-1 had a ratio of 1.63 : 1, and the number of hatched parities in the two plots (52 and 31) had virtually the same ratio (1.66 : 1). It was, therefore, assumed that on 4th January the hopper populations still had that same ratio.

and the second series on 11th, 13th and 14th January when between 84 and 92 % of the hoppers had reached the third instar.

All data on numbers of egg-pods, hatching percentages and surviving hoppers in the plots are given in table 11. In 1961/62 once again the method of estimating the hatching percentage of the egg-pods, by counting the number of hatched parties in sample strips, gave under-estimates. Two weeks after hatching there were many more hoppers in the plots, than there ever could have been according to the number of hatched parties seen. Thus the estimate of the hatched population had to be based on the hatching percentages in the groups of marked egg-pods, but for plot 1 even that figure was an obvious under-estimate. The marked egg-pods near this plot had been on the other side of a channel on lower-level ground and they suffered badly from the temporary waterlogging. Thus the southern part of plot 1 could not be used for assessing the hopper mortality in the first instar, but the estimate of the hopper population, present on 4th January in that part of the plot, was used to calculate the hopper population that was present on that same day in the other, northern part of the plot. This population was then assessed 13th January and so the mortality could be estimated over a period of 9 days during the second instar.

In plot 2 the numbers of egg-pods in the two parts of the plot were very similar and so were the numbers of hatched parties. This plot suffered from prolonged waterlogging of the soil, and the hatching was extremely poor: the number of hatched parties accounted for only 1.6 % of the estimated number of pods in the sample strips and of the 21 marked egg-pods only 1 hatched (5 %) (table 6). Consequently, the total number of hoppers, hatching in the plot was smaller than in any of the other plots, though the egg-pod density had been highest. In plot 3 the hatching parties accounted for 18 to 19 % of the egg-pods; the group of marked egg-pods gave a hatching percentage of 47 (9 out of 19 egg-pods).

Finally a mortality assessment could be made during an experiment by Dean, who studied band formation at very high hatching density (plot 4). He made hundreds of females lay their second egg-pod in a cage built over 10×10 ft (3×3 m) of burnt grassland in the Nziga sector. There had been virtually no laying within 0.5 mile (0.8 km) of the cage. The hoppers hatched on 1st and 2nd January 1962 and on 12th January the survivors were sprayed with DNC, when they were in their second instar; 133 corpses were found in 52 wire rings of 1 m^2 , laid out in the 2000 sq.yds (1670 m^2) which the cage population occupied by then. The same day the cage area was dug up and the remains of 100 successfully hatched pods were found. It is almost certain that originally the number of pods was much higher and it is suspected that rats destroyed a large proportion of the pods.

Unfortunately in 1961/62 there was an exceptionally early band formation, in which both the gregarious history of the parents and the unusually rapid growth of the grass, and consequent early manifestation of the mosaic, played a part. The clumpy distribution resulted in a disproportionately high number of zero's, relatively few counts from one to ten and a few high and very high counts, which greatly influenced the total. As an example the frequencies of counts in four assessments are given in table 12.

Table 12. Frequencies of numbers of hopper corpses per m² in 180 samples. Hopper survival assessments in 4 experimental plots in North Rukwa 1961/62

| Number of hoppers per m ² | Frequencies | | | |
|--|-------------|----------|----------|----------|
| | plot 1-1 | plot 2-1 | plot 3-1 | plot 3-2 |
| 0 | 78 | 103 | 75 | 102 |
| 1 | 19 | 23 | 26 | 22 |
| 2 | 20 | 15 | 16 | 14 |
| 3 | 14 | 9 | 16 | 9 |
| 4 | 6 | 5 | 4 | 3 |
| 5 | 6 | 2 | 5 | 2 |
| 6 | 5 | 5 | 4 | 1 |
| 7 | 1 | 3 | 3 | 3 |
| 8 | 2 | 1 | 3 | |
| 9 | 2 | 3 | 2 | 1 |
| 10 | 3 | 1 | 2 | 1 |
| 11 | 2 | | | |
| 12 | 2 | 1 | 1 | |
| 13 | 2 | | 2 | 2 |
| 14 | 4 | 2 | 2 | 1 |
| 15 | 2 | 1 | 11 | 1 |
| 16 | 2 | | | 1 |
| 17 | 1 | | 2 | |
| 18 | 1 | | | |
| 19 | | | 1 | 1 |
| 20 | 1 | 2 | 2 | |
| 21 | | 1 | | 1 |
| 22 | 1 | 1 | | |
| 24 | 1 | | | 1 |
| 25 | | | | 1 |
| 27 | | | 1 | 1 |
| 29 | | | | 1 |
| 30 | | | 1 | |
| 31 | | | 2 | |
| 33 | | | 1 | |
| 36 | 1 | | | |
| 38 | | | 1 | |
| 40 | 1 | 1 | | |
| 43 | | | | 1 |
| 46 | | | | 1 |
| 48 | | | 1 | |
| 50 | 1 | | 1 | 1 |
| 52 | | | | 1 |
| 53 | 1 | | | |
| 55 | 1 | | | |
| 56 | 1 | | 1 | |
| 57 | | | | 1 |
| 61 | | | 1 | |
| 62 | | 1 | | |
| 65 | | | 1 | |
| 81 | | | | 1 |
| 92 | | | 1 | |
| 93 | | | | 1 |
| 110 | | | | 1 |
| 200 | | | | 1 |
| 205 | | | | 1 |
| 505 | | | 1 | |
| Total number of corpses in 180 samples | 830 | 446 | 1495 | 1341 |

The counts obviously do not follow a Poisson distribution and with the exception of one case, they do not fit a log-normal distribution either. An additional difficulty in the latter type of distribution is that one cannot attach any meaning to the zero counts, unless one assumes that they represent a density of between zero and one, but this gives an over-estimate. Apparently there is no statistical model, which fits this type of distribution and it is extremely difficult to attach any limits of confidence to these hopper-population estimates. All that can be said is that according to the observers impression the 180 samples did seem to give a fair representation of the distribution and the density of hoppers in each plot. The estimated populations in table 11 are based on the arithmetic mean of the counts. In total nine cases resulted in which the mortality among first and second-instar hoppers could be estimated.

In all three years, therefore, there was a considerable mortality during the first and second instar in at least one of the experimental areas. In section 5.4 the daily mortality rates will be compared with the densities of various predators.

5.2 Predators on First and Second-Instar Hoppers

5.2.1 Asilidae (Diptera)

The first and only mention of a Robberfly as a natural enemy of *Nomadacris* hoppers was by BREDO (1947), who reported *Alcimus* sp. preying on hoppers in the Mweru wa Ntipa.

Asilidae are known as voracious predators on insects and some of the larger species have been reported to live primarily on Acridid hoppers and adults (CLAUSEN, 1940). HOBBS (1936) analysed the diet of a number of Asilidae, caught with their prey by Swynnerton in S. Rhodesia and he found that *Alcimus setifemoratus* and *Philodictus swynnertoni* fed primarily on Acridids, while in the diet of *Philodictus nigripes* Hymenoptera were about as prominent as Acridids. LER (1958) studied the effect of the Asilid *Stenopogon porcus* on populations of the Acridids *Caliptamus* sp. and *Dociostaurus* sp. in Kazakhstan and he concluded that this Asilid is able to reduce the populations of these Acridids by 40-60 %.

Very little is known on the biology of Asilidae in general. According to CLAUSEN (l.c.) some species lay in decaying wood, others on grass or in the soil. The incubation period is short, at any rate for those species in which it has been studied. The larvae of Asilidae live in decaying wood or in the soil. The vermiform free pupa moves to the surface just prior to the emergence of the adults.

Clausen also states that larvae of some, not specified, species feed on locust eggs. STOWER, POPOV and GREATHEAD (1958) did find Asilid larvae in or near egg-pods of the Desert Locust, but there was no evidence of any damage to the eggs.

In the Rukwa Valley larvae of Asilidae certainly do not feed on locusts eggs, possibly because they are active at another time of the year. Adults, however, showed a clear

Table 13. *The prey of Asilidae in areas of different hopper densities*

| Prey | Hoppers of <i>Nomadacris</i> and other Acrididae abundant ¹ | Hoppers of <i>Nomadacris</i> absent, of other Acrididae not abundant ² |
|---------------------------|--|---|
| <i>Nomadacris</i> hoppers | 17 | |
| Other Acrididae hoppers | 3 | 5 |
| Diptera | 1 | 1 |
| Lepidoptera | 1 | |
| Odonata | 1 | 4 |
| Coleoptera | | 2 |
| Other | 1 | |

¹ Asilidae collected with prey in North Rukwa, 1960/61 and 1961/62 and in the Kabwe plain (Mweru wa Ntupa) in 1960/61.

² Asilidae collected with prey around the Uninji Pans (near Abercorn, Zambia) in 1960/61.

preference in their diet for Acridid hoppers, when these were available.

Two Asilid species were found to be dominant in both the North Rukwa plains and the Mweru wa Ntupa: *Omnatius variabilis* ENGEL and *Philodiscus nigripes* RICARDO. Both species are of medium size, measuring from 16 to 21 mm and they catch *Nomadacris* hoppers when these are in the first and second instar, that is up to a maximum length of 12-15 mm. On rare occasions *Philodiscus* was seen to take a third-instar hopper. Hoppers in the first two instars are available as prey over a period of normally 5 to 7 weeks, somewhere between 15th December and 15th February. During this period Acridid hoppers formed over 80 % of the prey (table 13). In the grass around the Uninji Pans near Abercorn Acridid hoppers were far from abundant, but they still made up nearly half of the diet. Outside the period in which small hoppers were

Table 14. *Distribution of Asilidae in relation to the abundance of hoppers. North Rukwa, 1959/60*¹

| Area | Date of assessment | State of grass at start of the rains | Hoppers | Asilidae per 1000 ² sq. yds (836 m ²) |
|--|-----------------------|--|--|--|
| Experimental plot Kambangombe plain | 15th December | burnt | very dense, 1st + 2nd instars | 12.1 |
| Idem | 17th January | burnt | few 1st + 2nd instars, mostly 3rd + 4th instars | 1.8 |
| Grass immediately around plot | idem | unburnt | none | 0 |
| Short grass 2 miles south of plot | idem | burnt | none | 0 |

¹ Based on unpublished data collected by G. J. W. Dean.

present, the Asilidae were seen feeding mostly on Tabanidae and small Lepidoptera, but no detailed data on this were collected.

The distribution of Asilidae in an area appeared to be correlated with the distribution of their prey. This was first seen in 1959/60 in North Rukwa (table 14). Another example was found in the Uninji Pans in 1960/61 (fig. 13).

A slow adaptation of the density distribution of Asilidae to that of the hoppers was apparent from assessments made in North Rukwa between 10th December 1960, the date of first hatching, and 3rd February 1961, when virtually all hoppers were past the second instar (table 15).

An example of Asilidae, actively concentrating in a small area with high prey density was seen in the Mweru wa Ntipa in January 1961. As described above (chapter 2 and 5.1) concentrated hatching of hoppers took place in a small area of about 190 × 160 yds (173 × 146 m). After three days the numbers of Asilidae had gone up considerably and on the 6th day after the first hatching their density had increased

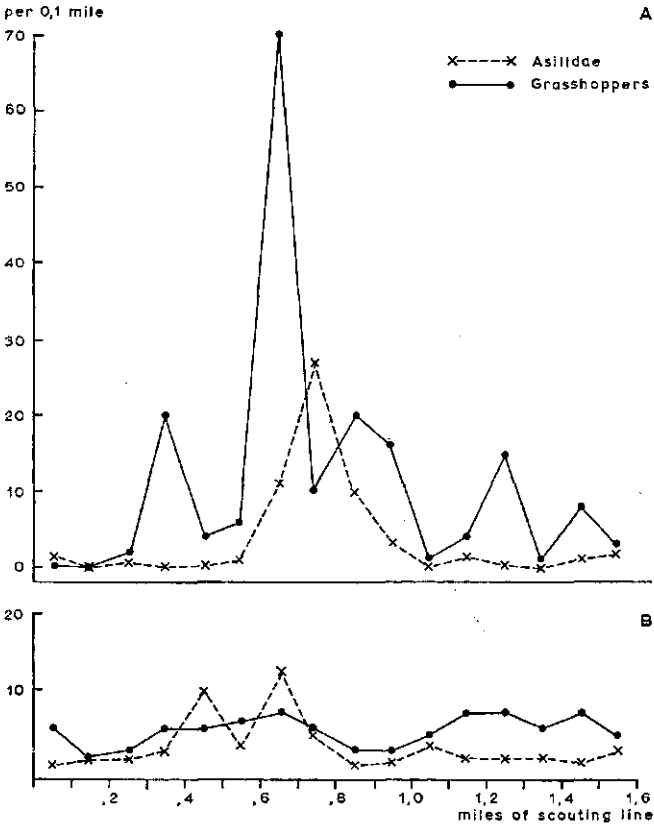


Fig. 13. Distribution of Acridid hoppers (●—●) and of Asilidae (× - - ×) along a 1.6 mile (2.6 km) long transect, in the larger of the Uninji Pans. A represents the numbers recorded every 0.1 mile (0.16 km) on 17th January 1961, and B gives the situation along the same transect one month later (14th February)

Table 15. Changes in distribution of Asilidae as compared with the hopper distribution. North Rukwa, 1960/61

| | Hopper density | Asilidae per 1000 sq.yds (836 m ²) | | | |
|--|----------------|--|-----------|----------|-----------|
| | | 14th Dec. | 20th Dec. | 5th Jan. | 3rd Febr. |
| 1 Area of experimental plot of the year before | Low | | 14.0 | | 6.0 |
| 2 Experimental plot 1960/61 | Medium | 0.2 | 0.7 | 1.4 | 5.0 |
| 3 Midway between 1. and 2. | Low | | 1.7 | 2.1 | 2.5 |
| 4 Trans Valley firebreak | Low | | 9.4 | 3.5 | |

by fifteen times. At the same time the mortality among young hoppers showed a progressive increase (fig. 14). Also on the morning of the 13th December three assessments of Asilid densities were made outside the plot. While in the plot there were 8.3 Asilids per 1000 sq.yds, 40 yds to the south-west, where few hoppers hatched, there were only 2.9 Asilids, 200 yds to the south-west there were no Asilids at all, but at a distance of 400 yds the density was the same as in the rest of the plain, about 0.6 Asilids per 1000 sq.yds. This suggested that Asilidae had moved into the plot from a strip of between 200 and 400 yds around it. On a superficial inspection of the whole Kabwe plain it was found that Red Locust hoppers were confined to the northern half, where the Asilid density was 0.6 per 1,000 sq. yds, and that in the southern half

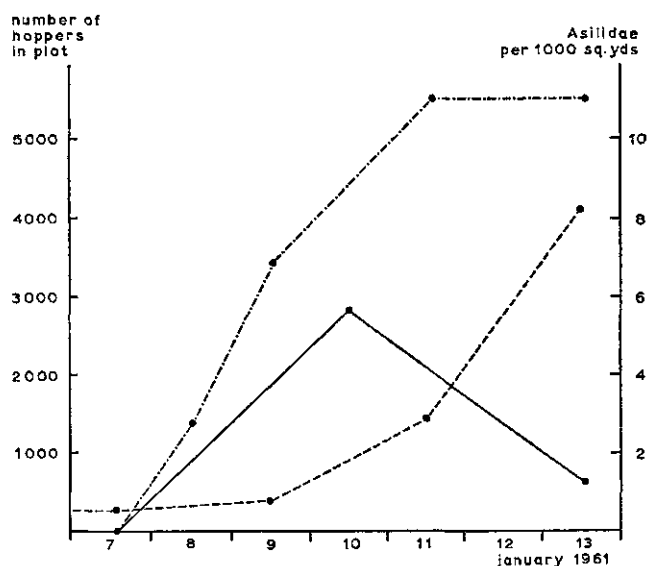


Fig. 14. Numbers of Red Locust hoppers, known to have hatched (● - - - ●) and those estimated to have survived (● — ●), compared to the density of Asilidae (● - - - ●). Experimental plot Kabwe plain, January 1961

only very few hoppers of other Acridids were present and here no Asilidae were seen.

The following observations give some indications as to the biology of *Omnatus* and *Philodicus* in the Rukwa Valley. Adults appeared in numbers only a few weeks after the first rains, well before the hatching of the hoppers (fig. 15). They were at their peak density during about the same period that hoppers go through the instars that are suitable as prey. In January their numbers appeared to go down and at the end of February and in March few were seen any more. Web-building spiders and Anisoptera (Odonata) appeared to be their main natural enemies.

Copulation was seen from a few weeks after appearance of the adults onwards. The eggs are presumably laid in the soil of the Rukwa grasslands; firstly, around the end of December 1961 the Tumba plain became progressively flooded (plot 1 first, plot 3 later), and there was a gradual decrease in numbers of Asilidae there which coincided with an increase in numbers in the dry Nzigu plain (table 16). Secondly, 19th-21st December 1960, that is only few weeks after the appearance of the Asilidae, assessments were made at six points in the Tumba and Kambangombe plains; the different Asilid densities appeared to be related with the hopper distribution in the previous season,

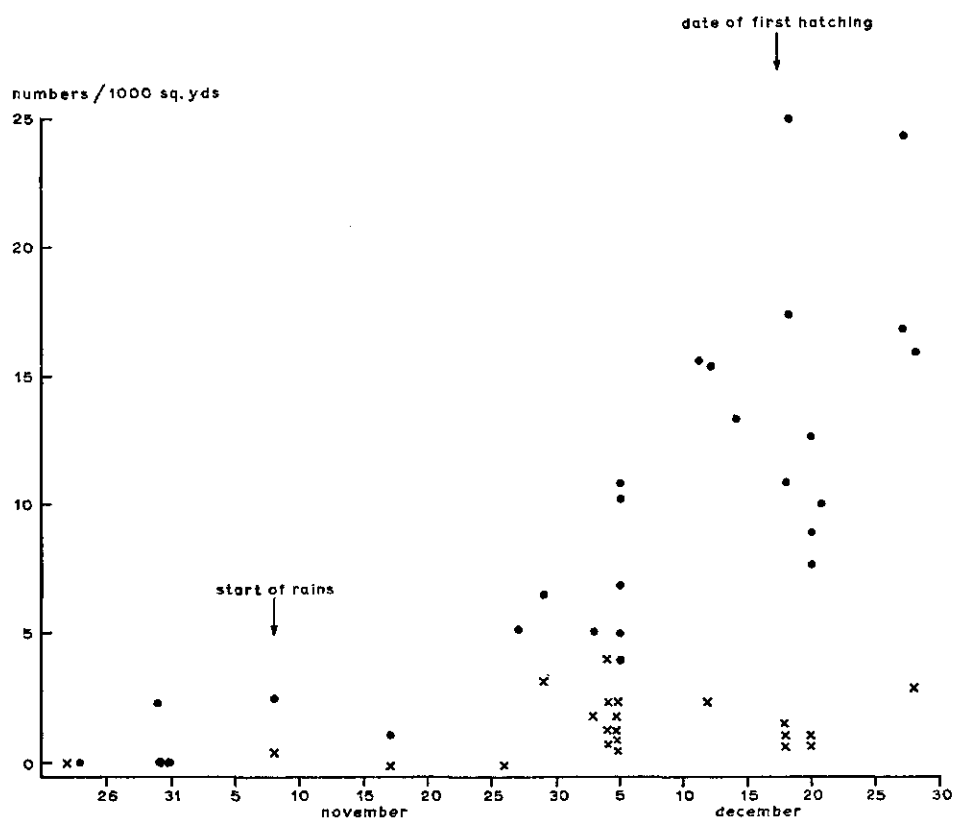


Fig. 15. Appearance of Asilidae (x x) and Anisoptera (● ●) at the start of the rains. North Rukwa, 1961

Table 16. Changes in distribution of *Asilidae*. North Rukwa 1961/62

| | Asilidae per 1000 sq.yds (836 m ²) | | | | |
|-------------|--|---------|---------|--------|---------|
| | 5 Dec. | 18 Dec. | 29 Dec. | 9 Jan. | 12 Jan. |
| Tumba plain | | | | | |
| plot 1 | 2.5 | | 1.8 | | 0 |
| plot 2 | 1.3 | 1.7 | 3.3 | 1.0 | |
| Nziga plain | 2.5 | | | 4.2 | |

Table 17. Asilid densities early in the rainy season, compared with hopper densities in the previous breeding season. North Rukwa, 19th-21st December 1960

| Area | Hopper density in the 1959/60 breeding season | Asilidae per 1000 sq.yds |
|-----------------------------------|---|--------------------------|
| Bank of the Tumba river | zero | 0 |
| Area of experimental plot 1959/60 | very high | 14.0 |
| Experimental plot 1960/61 | zero | 0.7 |
| Trans-Valley firebreak | very high | 9.4 |
| Nziga plain | very low | 1.7 |
| Middle of Tumba plain | zero | 0 |

Table 18. Relative abundance of *Omnatius variabilis* and *Philodictus nigripes* in various areas¹

| Area | | Number of Asilidae caught | <i>Omnatius</i> in % | <i>Philodictus</i> in % |
|---------------------|--------------------------|---------------------------------|-------------------------|----------------------------|
| North Rukwa 1960/61 | Exp.plot Dec.-Jan. | 23 | 56 | 44 |
| | Near treeline, late Jan. | 45 | 98 | 2 |
| | 1961/62 | 41 | 98 | 2 |
| | 1962/63 | 0 | — | — |
| Kabwe plain | 1960/61 | 19 | 68 | 32 |
| Iku plains | 1960/61 | 15 | 80 | 20 |
| Uninji Pans | 1960/61 | 55 | 2 | 98 |

¹ No data are available for the 1959/60 breeding season, but both species were abundant.

1959/60 (table 17)¹. This inferred local breeding of Asilidae, not immigration from the forest.

Philodicus and *Omnatius* differed in relative abundance from year to year and area to area (table 18). In 1961/62 the only specimen of *Philodicus* was caught just before the rains began and *Omnatius* was only seen several weeks later. The 1960/61 rains had been heavy and large parts of North Rukwa were under water for several months. The 1961/62 rains were even heavier and virtually the whole of North Rukwa remained under water until the 1962 rains started. During the 1962/63 season no specimens of either of the species were seen. Thus it would appear that prolonged annual flooding is unfavourable for both species, in particular for *Philodicus*.

Two observations gave some direct information on the daily consumption of Asilidae. Once in a cage a specimen of *P. nigripes* was seen to take about 20 minutes for sucking out a first-instar hopper and, secondly on a two-hours traverse through the Nziga plains which area had a medium dense hopper population, 16 *O. variabilis* were seen, of which four were in the process of consuming a hopper. This would suggest that an Asilid takes one hopper per 80 minutes, or about 9 hoppers per 12 hour day.

Asilidae, therefore, were active predators on Red Locust hoppers. They were at optimum density at the right time (fig. 15), they were more often than other predators seen to catch hoppers, these formed the major part of their menu, their distribution showed great similarity with that of their prey, they were even seen to concentrate actively in spots with a high hopper density and finally their density level appeared

¹ Later on, the distribution of the Asilids adapted itself to the hopper distribution in 1960/61 (table 15).

Table 19. Approximate density levels of Asilidae in December and January in different breeding areas

| Area | Breeding season | Density per 1000 sq.yds ¹ |
|----------------|-----------------|--------------------------------------|
| North Rukwa | 1959/60 | 6 |
| | 1960/61 | 5 |
| | 1961/62 | 1.5 |
| | 1962/63 | 0.1 |
| Central Rukwa | 1959/60 | 0 |
| | 1960/61 | 0 |
| Mweru wa Ntipa | 1960/61 | 0.3 ² |
| Iku plains | 1960/61 | 3 |
| Uninji Pans | 1960/61 | 1.3 |
| | 1961/62 | 0.3 |

¹ Mean of all samples in the period that first and second-instar hoppers of *Nomadae* were present in areas where the grass had been burnt before the rains.

² Mean of samples taken in the Kabwe perimeter plain and along the western fringe of the Mweru wa Ntipa proper.

to be high enough to make them a mortality factor of some importance.

However, in the Central Rukwa plains hardly any Asilidae were seen and in the North Rukwa area their numbers decreased to virtually zero in the course of the last two years which were very wet (table 19). In addition, in 1959/60 they could not really have caused the death of 28 million hoppers in 36 days, though their numbers were high; this would have meant a daily consumption of about 50 hoppers per Asilid. Although HULL (1962) reports that consumption can be rapid (EDWARDS, 1883, watched one Asilid catch and eat 8 Geometrid moths in 20 minutes), it appeared unlikely that medium-sized Asilidae like *Omnatius* and *Philodicus* would have so great an appetite.

5.2.2 Odonata

Prey. During the rainy season Odonata (both Zygoptera and Anisoptera) are among the most abundant insects in the outbreak areas. Occasionally Anisoptera were seen to make dashes at groups of just emerged hoppers, but they rarely seemed to catch any. At the same time Asilidae were found to feed largely on hoppers, and at first attention was focussed on these predators. However, during the 1960/61 breeding season it became evident that, on their own, Asilidae could not cause the recorded hopper mortalities and it was decided to make a closer study of other possible predators and in particular of the Odonata.

It is well known that capture of flying prey is the normal feeding behaviour of dragonflies. However, a number of observations have been recorded which suggest that capture of sitting prey is not uncommon (CORBET, 1962). This is particularly so for members of the sub-family Zygoptera which have been described to take settled Aphids from plants (TÜMPAL, 1910)¹ and Coleoptera larvae from leaves of bushes (CORBET, 1960)¹. The Anisoptera are said to specialise on prey flying overhead, but capture of resting prey has also been observed and CORBET (l.c.) is of the opinion that this is more common than is generally thought. In the compound eye of Anisoptera the facets in the upper half are usually larger than in the lower half, and there is a gradual transition in size; in some libellulids there is a narrow zone of transition, often showing up as a nearly straight horizontal line. It has been suggested (EXNER, 1891)¹ that the upper part of the eye is used for flying prey and the lower part for perceiving the form of sitting prey.

In the North Rukwa plains the abundant Zygoptera² are *Enallagma subtile* RIS and *Agriocnemis exilis* SELYS (Coenagriidae), very small and fragile insects of about 20 mm long, and *Lestes pallidus* Rambur and *Ceriagrion glabrum* (Burmester) (Lestidae) which are about 40 to 50 mm long. The smaller species are often seen flying up and

¹ Quoted from CORBET (1962).

² I am greatly indebted to Dr E. PINHEY of the National Museum of Rhodesia, Bulawayo, for naming all Zygoptera and Anisoptera species I collected.

down grass stems and their behaviour suggests that they normally capture sitting prey, but they are too small and too fragile to master prey of the size and strength of a first-instar hopper and they probably feed on very small insects up to the size of a mosquito. *L. pallidus* and *C. glabrum*, however, appear to be big enough to catch at least a first-instar hopper and they also seem to search for their prey in the grass. Between 1959 and 1961 these bigger species formed only a small part of the population, but in the 1961/62 season their numbers increased considerably; all but two of the twenty-two specimens caught with their prey were collected in that season, in which there were few hoppers.

Their choice of prey was as follows:

| | |
|----------------------|----|
| Lepidoptera | 13 |
| Diptera (mosquito's) | 6 |
| Arachnoidea | 1 |
| Unidentified | 2 |

Acridids did not appear on the diet and indeed none of the victims approached a first-instar Red Locust hopper in size. The Anisoptera on the other hand, were found to have a preference for Acridid hoppers, when these were present (table 20). The data were split up for three different sets of conditions in which feeding Anisoptera were caught.

It is self-evident that table 20 cannot give a fair representation of the overall diet of all Anisoptera species in the North Rukwa plains. Firstly several species catch and devour their prey in flight; only with a large prey they may alight. Many other Anisoptera species are perchers, waiting for prey on some protruding stick or grass stem and making numerous reconnaissance flights from there. These species were seen to return to their perch with the prey, even if it was as small as a mosquito. Secondly some species were easy to catch and some were not. This is clearly demonstrated in table 21 where the prey of different species is given: in 1961/62 *Orthetrum brachiale* accounted for well over half of the total number of Anisoptera caught with prey, while in the areas of catching they formed only between 9 and 15% of the population (table 23).

In the 1962/63 season the composition of the Anisoptera population differed greatly from that in the previous year, as is evident from tables 21, 23 and 24.

Feeding behaviour of the common Anisoptera species. Those species that are commonly seen in North and Central Rukwa, in the Iku plains and in the Mweru wa Ntipa have been grouped according to their feeding behaviour (table 22). The following annotations should go with it.

- a. It is possible that *Hemianax ephippiger* feeds mainly on the wing, but catches hoppers that it disturbs when alighting in the grass.
- b. In large numbers *Trithemis annulata* has been seen only in North Rukwa and only in 1962/63 when the area had become permanently flooded; this species possibly breeds there only in series of very wet years.

Table 20. Diet of *Anisoptera* that were caught with their prey in areas of different hopper densities¹. North Rukwa, 1961/62 and 1962/63

| Prey | 1st and 2nd instar hoppers of <i>Nomadacris</i> abundant, few hoppers of other Acrididae (plots 1 and 3, 1961/62) | Few <i>Nomadacris</i> hoppers, but other Acridid hoppers abundant (Nziga plain, 1961/62) | Virtually no <i>Nomadacris</i> hoppers, few other Acridid hoppers (Nziga plain, 1962/63) |
|------------------------------|---|--|--|
| Orthoptera | | | |
| hoppers of <i>Nomadacris</i> | 24 | 5 | 0 |
| hoppers of other Acrididae | 2 | 9 | 7 |
| Diptera | | | |
| Asilidae | 1 | 2 | 1 |
| Tabanidae | 2 | 2 | 3 |
| Culicidae | 2 | 1 | 3 |
| Odonata | | | |
| Zygoptera | 0 | 3 | 4 |
| Anisoptera | 1 | 1 | 1 |
| Lepidoptera | 3 | 2 | 14 |
| Other | 2 | 3 | 4 |

¹ All samples were collected between 10 a.m. and 4 p.m.

Table 21. Choice of prey of different Anisoptera species in North Rukwa

| | Number caught with prey | Acridid hoppers | | Diptera | Odonata | Lepi- doptera | Other |
|--------------------------------|-------------------------------|-------------------|-------|---------|---------|------------------|-------|
| | | <i>Nomadacris</i> | other | | | | |
| 1961/62 | | | | | | | |
| <i>Orthetrum brachiale</i> | 44 | 18 | 5 | 5 | 2 | 2 | 12 |
| <i>Philonon luminans</i> | 12 | 7 | 2 | 1 | 0 | 0 | 2 |
| <i>Crocothemis erythraea</i> | 4 | 2 | 1 | 0 | 0 | 0 | 1 |
| <i>Hemistigma albipunctata</i> | 4 | 2 | 1 | 0 | 0 | 1 | 0 |
| <i>Tholymis tillarga</i> | 3 | 1 | 0 | 2 | 0 | 0 | 0 |
| <i>Hemianax ephippiger</i> | 3 | 1 | 2 | 0 | 0 | 0 | 0 |
| Total | 70 | 31 | 11 | 8 | 2 | 3 | 15 |
| 1962/63 | | | | | | | |
| <i>Orthetrum brachiale</i> | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Crocothemis erythraea</i> | 8 | 0 | 4 | 1 | 1 | 2 | 0 |
| <i>Hemistigma albipunctata</i> | 19 | 0 | 2 | 3 | 1 | 10 | 3 |
| <i>Acisoma panorpoides</i> | 6 | 0 | 0 | 1 | 2 | 1 | 2 |
| <i>Trapezostigma basilaris</i> | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Diplacodes lefevrei</i> | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Hemianax ephippiger</i> | 2 | 0 | 2 | 0 | 0 | 0 | 0 |
| Total | 38 | 0 | 8 | 7 | 4 | 14 | 5 |

Table 22. Anisoptera species common in Red locust outbreak areas, their hunting behaviour and their role as predators on hoppers

| | Hunting behaviour | Predating on hoppers (= ×) |
|--|---|----------------------------|
| Aeschnidae | | |
| <i>Anax imperator</i> LEACH | Flying fast and high over grass, roosting in bushes | |
| <i>Hemianax ephippiger</i> (BURMEISTER) ^a | Flying high and fast, but often alighting in short grass | × |
| Libellulidae | | |
| <i>Trapezostigma basilaris</i> (BEAUVOIS) | | |
| <i>Urothemis edwardsi</i> (SELYS) | | |
| <i>Acisoma panorpoides assalaphoides</i> (RAMBUR) | All four species roost on high observation posts, but more often they are seen flying. | |
| <i>Trithemis annulata</i> (BEAUVOIS) ^b | <i>T. basilaris</i> and <i>U. edwardsi</i> have a very fast flight | |
| <i>Philonon luminans</i> (KARSCH) | | × |
| <i>Hemistigma albipunctata</i> (RAMBUR) | Both species are perchers. They are often seen perching on protruding grass stems in the shorter grasses of mosaics and making dashes at their prey from there | × |
| <i>Orithetrum brachiale</i> (BEAUVOIS) ^c | | × |
| <i>O. trinactia</i> (SELYS) ^c | All three species are often seen perching in lower grasses of a mosaic or in tracks; in particular <i>Orithetrum</i> is frequently seen flying slowly through tall grass as if looking for prey | × |
| <i>Crocothemis erythraea</i> (BRULLÉ) | | × |
| <i>Tholymis tillarga</i> (FABRICIUS) | Known as a crepuscular species and ♀♀ found roosting low in grass, often in groups, rarely seen flying; ♂♂, however, often seen flying through grass as if hunting like <i>Orithetrum</i> | (×) |
| <i>Brachythemis leucostrigata</i> (BURMEISTER) | Patrolling over open or bare ground, mud patches, puddles and ditches | |
| <i>Diplacodes lefebvrei</i> (RAMBUR) | Usually found in very short and sparse vegetation, over swamps or near water | |

¹ For notes a, b, c and d see text.

- c. In North Rukwa *Orthetrum brachiale* was by far the most abundant of the two species, but *O. trinacria* was more common in the Central Rukwa plains. The latter has not been caught with prey, but the behaviour of the two species is so similar that almost certainly their choice of prey is identical.
- d. *Tholymis tillarga* is considered to be a crepuscular species (CORBET, 1962). However, in the Rukwa Valley the males were often seen flying during the hot hours of the day, but always low through usually tall grass. It may be that those flights were caused by the observer or by intolerable temperature conditions in the roost, but *T. tillarga* was once caught with a Red Locust hopper as prey. The female was rarely seen flying during the day, but was twice caught with a Dipteran as a prey.

The following species were also recorded, but formed a very small proportion of the population: *Orthetrum abbotti*, *O. caffrum*, *Zygonyx torrida*, *Nesciothemis farinosum*, *Trithemis hecate*, *Crocothemis sanguinolenta*, *Acisoma panorpoides*, and *Trithemis annulata*. *Pantala flavescens* also breeds in the Rukwa Valley, but was usually seen only at the beginning of the rains and from February onwards. The period during which hoppers are in the first two instars probably does not coincide with the adult period of *P. flavescens*. In 1960/61 *Anax imperator* could be seen roosting on bushes in fair numbers, but they were never abundant during the day.

Those Anisoptera that are predators on Red Locust hoppers belong to the group of species that either perch in the shorter grasses of mosaics, or fly low through the grass (table 22). It appears that it is movement rather than form to which the dragonfly reacts, since on several occasions *O. brachiale* and *P. luminans* were seen perched within a few feet of a group of hoppers, none of which were caught as long as they did not move. A jumping hopper, however, was dashed after and caught even after it had landed. The frequent patrolling along a track and in particular the habit of flying through the grass, as seen mainly from *Orthetrum*, is likely to have a disturbing effect on hoppers. In the tropics *Brachythemis leucostrigata* is well known for its habit of flying closely around the legs of man or beast moving over open ground; presumably it catches small insects flushed by the disturbance. *O. brachiale* has been seen to show a similar behaviour in that it flies a few paces ahead of a moving observer in an irregular undulating flight, frequently alighting and waiting until the observer has caught up.

The compound eyes of the common Rukwa species were examined, in view of Exner's idea about the function of the larger and smaller facets. In *O. brachiale* very small facets occupy the lower two-thirds of the eye, then there is a clear, narrow transition zone to facets of medium size and finally a gradual transition to very large facets in the dorsal part. The eye of *O. trinacria* is very similar. In the eye of *Crocothemis* a horizontal line indicates the transition from small to medium sized facets, the small facets taking up the lower two-third of the eye. *Philonomon* has a very clear, horizontal division between small and large facets, dividing the eye in more or less equal parts. *Brachythemis*' eye is almost identical. *Hemistigma* has very small facets in the lower two thirds of the eye and a clear straight line marks the transition to the top part,

which has very much larger facets. *Hemianax* has a very gradual transition from smaller to bigger facets about halfway up the eye. *Tholymis tillarga*, *Trapezostigma* and *Urothemis* have large and very much smaller facets separated by a clear, narrow, U-shaped transition zone dividing the eye in more or less equal parts.

Thus, in general, Anisoptera that specialise on prey in the grass have smaller facets and the region of small facets occupies a larger portion of the eye. This confirms work recently published by PRITCHARD (1966). He made an elaborate study of the numbers and size of facets in a great many species, and his conclusion was that there is a close relation between the hunting behaviour and the size and numbers of facets in the different parts of the eye.

Distribution of Anisoptera in relation to hoppers and vegetation. The distribution of the Anisoptera did not seem to be closely linked with that of hoppers, as was the case with the Asilidae. In 1959/60 in North Rukwa, DEAN (in DU PLESSIS, 1960) assessed densities of Anisoptera in three places: (a) in an area where the grassland had been burnt before the rains and hoppers were dense, he estimated the population at $48,100 \pm 4,400$ per sq. mile; (b) in a similar area but without hoppers at $37,400 \pm 2,100$, and (c) in an area adjacent to (a) where grass had not been burnt and where there were no hoppers, at $19,400 \pm 5,000$ per sq. mile ($2,59 \text{ km}^2$). This suggested an affinity to burnt grassland rather than to hopper concentrations. On the other hand, in the case of the 1960/61 plot in the Kabwe perimeter plain of the Mweru wa Ntipa I found that not only the Asilidae concentrated in the plot but that to some extent the Anisoptera did the same; their density went up from 1.5 per 1,000 sq. yds on the 9th January to 3.3 on 13th January. Any possible concentration would be less obvious than with Asilidae since only part of the Anisoptera population would respond to hopper concentrations. This appeared to be confirmed by observations made in January 1963 during a reconnaissance by Swamp Skipper through the Katwa Makondo plain which was the only part of North Rukwa that had been dry at the beginning of the rains and where locusts had laid. Anisoptera were dense everywhere, but *Orthetrum brachiale* was almost exclusively seen near the hopper bands which were far apart and not very dense.

In general, species differed in the selection of their feeding habitat and consequently the composition of the Anisoptera population varied from area to area, as is demonstrated in table 23 for the 1961/62 season. Since catching does not give representative samples and collecting corpses after spraying gave too few specimens, the composition of Anisoptera populations was determined by counting the number of each species seen in a strip of 10 yds wide along transects of about 0.5 mile long.

Comparison of tables 23 and 24 shows (a) that Anisoptera populations in North Rukwa and in other areas were largely composed of the same species, but that the relative abundance varied, and (b) that in 1962/63 the population in North Rukwa differed considerably in composition from that in the previous wet season, probably due to the drastic changes in flooding conditions.

Table 23. Relative abundance of Anisoptera species in different types of vegetation, in % of all Anisoptera seen in the area. North Rukwa 1961/62

| | Tall vegetation of almost pure <i>Echinochloa</i> | Mosaic of tall <i>Echinochloa</i> , <i>Cynodon</i> and <i>Cyperus longus</i> | Mosaic of tall <i>Echinochloa</i> , <i>Sporobolus ro-</i> <i>bustus</i> , <i>Diplachne</i> and bare ground | Mosaic similar to that in plot 3 | Mosaic of short grasses near the lakeshore, mainly <i>Cyperus longus</i> and <i>Diplachne</i> | Mosaic of short grasses, mainly <i>Cynodon</i> and <i>Cyperus longus</i> |
|---|---|---|--|--|---|---|
| | plot 1 | plot 3 | Near Soda | Nziga plains | plot 2 | plot 4 |
| * <i>P. luminans</i> | 48 | 64 | 65 | 60 | 69 | 56 |
| * <i>O. brachiale</i> | 1 | 9 | 9 | 9 | 9 | 15 |
| * <i>C. erythraea</i> | 19 | 7 | 11 | 8 | 4 | 2 |
| * <i>H. albipunctata</i> | 2 | 5 | 4 | - | - | - |
| <i>D. lefeburei</i> | - | 4 | 1 | 12 | 12 | 5 |
| <i>T. basilaris</i> + <i>U. edwardsi</i> ¹ | - | 3 | 3 | 9 | 4 | 12 |
| * <i>Th. tillarga</i> | 30 | 9 | - | 1 | - | - |
| <i>B. leucostrigata</i> | - | - | 7 | - | - | - |
| * <i>H. ephippiger</i> | - | - | 1 | 1 | 2 | 10 |
| Total numbers of Anisoptera in sample | 156 | 153 | 76 | 138 | 269 | 156 |

* Species that were found to prey on *Nomadasteris* hoppers.¹ These species have been taken together, since in flight they are very difficult to distinguish.

Table 24. Relative abundance of Anisoptera species in various areas, in % of all Anisoptera seen in the area

| Species | Central Rukwa 1962 | | Iku February 1962 | | Uninji Pans Febr. 1962 | North Rukwa January 1963 | | |
|---|------------------------------------|---|----------------------|-----------------------|--|---|--|--------------------------------|
| | February, short grass mosaic | September, in burnt grass and along fringe of un- burnt grass (dry season) | tall grass mosaic | short grass mosaic | very short open grass, along water | tall grass along edge of woodland, west side | short grass mosaic, Nziga plains | open space in wood- land |
| <i>P. luminans</i> | 36 | — | 28 | 15 | — | 2 | 1 | 43 |
| <i>Orthetrum</i> spp. ¹ | 9 | 20 | 12 | 12 | 1 | 15 | 4 | 1 |
| <i>C. erythraea</i> | 5 | 33 | 19 | 28 | 1 | 15 | 15 | 13 |
| <i>H. albipunctata</i> | — | — | 5 | 24 | 2 | 51 | 63 | 40 |
| <i>D. lefebvrea</i> | 6 | 7 | 15 | 5 | 75 | 1 | 12 | — |
| <i>T. basilaris</i> + <i>U. edwardsi</i> | 11 | 26 | 7 | — | 18 | — | 3 | 1 |
| <i>Th. tillarga</i> | 3 | — | 12 | 11 | — | — | — | — |
| <i>B. leucostrigata</i> | — | 15 | — | — | — | 2 | 4 | — |
| <i>P. flavescens</i> | 2 | — | 2 | 5 | — | — | — | — |
| <i>H. ephippiger</i> | 28 | — | 1 | — | 2 | 1 | — | — |
| <i>Rhyothemis semitylata</i> | — | — | — | — | 1 | — | — | — |
| <i>Acisoma panorpoides</i> | — | — | — | — | — | 3 | — | 1 |
| <i>Trithemis annulata</i> | — | — | — | — | — | 10 | — | — |
| Total number of Anisoptera in sample | 185 | 46 ² | 129 | 75 | 181 | 89 | 200 | 76 |

¹ *Orthetrum brachiale* dominant in North Rukwa, *O. trinaria* relatively more abundant in Central Rukwa.

² Density very low. *O. trinaria* in unburnt *Sporobolus robustus* along edge of retreating flooding, other species in area of burnt grass away from water, with *Brachythemis* near and around clumps of trees, mainly flying at dusk.

In table 25 densities are given at different times and in different places, and in the last column all available assessments have been combined to give an indication of the density level over the entire area.

Importance of Anisoptera as predators on hoppers. In order to relate the daily mortality in the experimental plots to densities of Anisoptera, one has to take the composition of the population into consideration. In addition, some of the species that prey on Red Locust hoppers are more effective than others and this is of course extremely difficult to assess. In fact it could only be attempted for *Orthetrum* and *Philonomon*, two species which were abundant in the samples in 1961/62. Table 26 shows that *Orthetrum* is much more easy to catch than *Philonomon*, in fact about $3.1/0.85 = 3.5$ times as easy. Assuming that the species are of equal abundance and equal effectiveness as a predator, one would expect to catch 35 *Orthetrum* with prey for every 10 *Philonomon* with prey. *Philonomon*, however, formed on average 60 % of the population and was, therefore, roughly 8.5 times as abundant as *Orthetrum*, which on average formed only 7 % of the population. Thus one could expect to catch 35 *Orthetrum* with prey against 85 *Philonomon* with prey, but instead of 85 only 9 were caught (table 21). This indicates that as a predator *Orthetrum* is about ten times as effective as *Philonomon*.

The available data do not allow similar detailed comparisons between these and other species, and the weighting of the different species as to their effectiveness as a predator had to be based on general observations and impressions. *Crocothemis erythraea*, *Hemistigma albipunctata* and *Hemianax ephippiger* were considered to be equally effective predators as *Orthetrum brachiale*, and *Tholymis tillarga* was, with *Philonomon luminans*, counted at one-tenth of the effectiveness of *Orthetrum*. On these assumptions the effective part of the Anisoptera populations in the 1961/62 experimental plots could be calculated from table 23. This gave 29.8, 21.9, 28.3 and 32.6 % for plot 1, 2, 3 and 4 respectively.

In addition, it should be realised that the effectiveness of a species may not be constant, since it may depend on density and height of the grass. Perching species like *Philonomon* are more likely to catch hoppers in a sparse and low vegetation, resulting from poor early rainfall, than in a rapidly growing vegetation (like in the wet December and January 1961/62) when the killing of hoppers will largely be left to species like *Orthetrum*, which fly low through the grass.

From all data given in this section, it appears that certain Anisoptera species prey on hoppers of *Nomadacris* and that they are present in considerable numbers at the right time. There remains the question, whether they can measure up to the problem; that is, could they have caused the hopper mortalities that occurred? This point will be considered in section 7.4.

Life cycle. A positive correlation between the rainfall in one season and the abundance of a predator in the next rainy season could provide an explanation for Symmons' negative correlation between rainfall and *Nomadacris*' multiplication rate (section 1.4).

Table 25. *Anisoptera* densities in different areas and years

| Area | Time | Experimental plots | | | Large parts of outbreak areas | | | |
|---------------|---------|--|----------------|----------------------------|-------------------------------|--------------------------------|---|---|
| | | plot number of squares ¹ | vegetation | Anisoptera per 1000 sq.yds | part | number of squares ¹ | vegetation | estimated number of Anisoptera per 1000 sq.yds ² |
| North Rukwa | 1959/60 | middle December | uniform, short | 13.1 | Kamba-ngombe plain | — ³ | various types | about 8 |
| | | | | | | | | |
| | 1960/61 | middle January middle December end January | uniform, short | 15.5 | Kamba-ngombe plain | 32 | various types | about 10 |
| | | | | | | | | |
| | 1961/62 | early January | uniform, short | 2.5 | Nziga plains | 43 | tall grasses | about 17 |
| | | | mosaic, tall | 15.8 | | | | |
| | | | uniform, short | 18.8 | | | | |
| | | | mosaic, tall | 17.1 | | | | |
| Central Rukwa | 1962/63 | Dec./Jan. | mosaic, short | 30.8 | Nziga plains | 19 | mosaic, short | about 65 ⁴ |
| | | | | | | | | |
| | | | | | | | | |
| Iku | 1959/60 | early February | | | northern part | 16 | mosaic, short | 8 |
| | | | | | | | | |
| | | | | | | | | |
| | 1960/61 | early February | | | | 5 | | 7 |
| | | | | | | | | |
| Uninji Pans | 1961/62 | February | | | Various sectors | 10 | mosaic, tall open, sparse mosaic, tall mosaic, short | 26 5 20 32 |
| | | | | | | | | |
| | | | | | | | | |
| | | | | | | | | |
| | | | | | | | | |
| Uninji Pans | 1961/62 | February | | | Along the edge | 10 | short, sparse | 63 |
| | | | | | | | | |

¹ Technique described in chapter 2.

² Based on assessments both in burnt and unburnt grassland, and on the ratio of the two types of grassland.

³ Data from G. J. W. Dean who used a different technique.

⁴ Numbers ranging from 25 to several hundred per 1000 sq.yds. but mostly between 25 and 90.

Table 26. Relative abundance of *Philonomon* and *Orthetrum* in samples taken in the experimental plots. North Rukwa, 1961/62

| | <i>Philonomon luminans</i> | | | <i>Orthetrum brachiale</i> | | |
|--------|---|-----------------------------------|---------------------|---|-----------------------------------|---------------------|
| | % of Anisoptera population ¹ | % in samples of Anisoptera caught | Ratio caught : seen | % of Anisoptera population ¹ | % in samples of Anisoptera caught | Ratio caught : seen |
| plot 1 | 48 | 42 | 0.88 | 1 | 8 | 8.0 |
| plot 2 | 69 | 58 | 0.84 | 9 | 13 | 1.4 |
| plot 3 | 64 | 44 | 0.69 | 9 | 12 | 1.3 |
| plot 4 | 58 | 59 | 1.0 | 9 | 23 | 1.6 |
| Mean | | | 0.85 | | | 3.1 |

¹ As seen in transects (table 23).

Consequently the life cycle of the Anisoptera in an outbreak area of the Red Locust is of singular interest.

In temperate zones the life cycle of Odonata is characterised by a short adult life and a prolonged larval life which involves a period of quiescence or diapause in winter. Little is known about the biology of dragonflies in the semi-arid tropics, but the few available publications indicate a short aquatic life for the larvae, and a long adult life span to bridge the dry season.

GAMBLES (1960) made observations on some dragonflies in Nigeria and came to the provisional conclusion that emergence of adults is most common at the beginning and at the end of the rainy season (for Nigeria May and October respectively). From captures through the year he found that both the Zygopteran *Lestes virgatus* and the Anisopteran *Acanthagina vesiculata* spend the dry season away from the temporary pools, which are their breeding places, and move to areas where the tree cover offers sufficient protection. *Lestes* possibly spends some of the time in a state of quiescence. From the slow, but marked changes in body colour in three species of *Crocothemis* (including *C. erythraea*), Gambles concludes that the specimens seen ovipositing at the beginning of one rainy season had emerged at the end of the previous rains. *Trapezostigma basilaris* was found to breed not only in temporary pools but also in permanent waters. Nevertheless it appeared to have a one year life cycle and oviposition was seen only at the beginning of the rains. In all these cases the adult life span must have been around nine months.

As to the length of larval life, again only isolated observations exist. Gambles found a larva of *Anax imperator* which hatched in the laboratory five months after first appearance of water in the pool where it was caught. Similar observations gave just over three months for *Anax tristis* and *Hemianax ephippiger*. It has been suggested (TILLYARD, 1910)¹, that in arid regions drought resistance in larvae might be common among pool dwelling Anisoptera, but work by HODGKIN and WATSON (1958)

¹ Quoted from CORBET (1962).

made it clear that normally larvae do not survive in the mud. They proved that three pool-dwelling Australian species complete their aquatic life in two or three months, and GARDNER (1956) working with the African species *Orthetrum stemmale* and *Palpopleura lucia* got similar results.

The following data from CORBETS review on the biology of dragonflies (1962) are also of interest here. The incubation period of the eggs of those few tropical species, for which it is known, is about five days. Larvae are facultative feeders on whatever is available and suitable. Cannibalism occurs as a function of population pressure, but is probably rare under natural conditions. Most larvae are bottom dwellers, but some (Aeschnidae) move into the vegetation and others (many Libellulidae) bury themselves in the debris or mud. After emergence the adults normally scatter and later congregate again for mating. There is habitat selection and there are indications that some species may have a way of 'homing', returning for oviposition to the area of their emergence. Others, however, wander freely and new habitats are colonised promptly, up to distances of perhaps 35 miles (60 km). Some are well known migrants and in many parts of Africa *Hemianax* and *Pantala* are commonly seen migrating in dense swarms, occasionally mixed with *Philonomon luminans*. *Trapezostigma basilaris* is another strong migrant.

My own observations on dragonflies in the Rukwa Valley and around Abercorn confirmed the conclusions of the above authors. Many Anisoptera could be seen in the plains until well into the dry season. When the grasslands dried up, the dragonflies concentrated around those ditches that still contained water, but when these dried out and all grass was burnt, only a few *Crocothemis erythraea*, *Trapezostigma basilaris*, *Brachythemis leucostrigata* and occasionally an *Orthetrum brachiale* were still to be seen¹. At the same time dragonflies were still commonly seen in the open woodland surrounding the plains.

Immediately after the first rains they appeared in numbers in the open and the most striking example of this was seen in 1962, when the first rainstorm came on 16th October and hundreds of Anisoptera were seen the next day flying over the lawns around the headquarters of the International Red Locust Control Service in Abercorn. In the Rukwa Valley just before the rains began, numbers went up slightly near dried up rivers and ditches, but only after the first rains the densities gradually increased over the entire North Rukwa plain (fig. 15). All this suggests survival of adults during the dry season, away from the plains in the open woodland. Maximum densities were reached before any breeding waters were formed and emergence elsewhere is unlikely, since in the second half of the dry season the entire area is extremely arid. At this time of the year there is water left only in the very alkaline lake Rukwa, in some muddy rivers which cannot even support much fish, and in a few of the rivers that come down from the plateau.

Altogether the available breeding waters appear completely insufficient to produce

¹ Cf. the dry-season population in Central Rukwa, September 1962, table 24.

populations of the observed densities over such large areas at the start of the rains. Observations on the body colour of *Crocothemis erythraea* also suggested survival over the dry season. In November and December all males were bright red and the first straw-coloured specimens (as they are when just emerged) were not seen before January.

Copulation was seen from around the first rains onwards. Density assessments were made until early in February, but numbers did not show a clear decrease and it appeared that most adults lived for at least two or three months after sexual behaviour started. This was certainly so for *C. erythraea*. At this stage Anisoptera have apparently little to fear from natural enemies, since no other effective predators were seen than web-building spiders, which regularly caught dragonflies of those species that alight in the grass.

During 1962 some information on length of larval life was obtained. Emergence of *Pantala flavescens* and *Hemianax ephippiger* was seen in a ditch near Soda on 31st January. The rains had started around the usual time early in November. Normally pools and ditches do not fill up until several weeks later, but in 1961 there was some very heavy rainfall around 17th November and it is just possible that the ditch did hold water from then. More likely, however, is that it did not fill up until about 15th December. Larval development for these species, therefore, took possibly only 47 days, but certainly not more than 75 days.

On 1st February samples were taken on four points in the Nziga sector which was under water by then:

- a. in 2 ft. (60 cm) deep water with very tall and dense grass¹,
- b. in 1 ft. (30 cm) deep water with a mosaic of shorter grasses,
- c. in 6 in. (15 cm) water with short grass, and finally,
- d. in 1 to 2 in. (2.5-5 cm) water in very short grass.

Due to slowly advancing floods these points had become flooded successively over a period of weeks, roughly between 20th December and 20th January. In the first sample 18 *Hemianax* larvae were found of in average about 1.5 in. (3.8 cm) long, in the second sample the mean length of the 38 larvae was just over 1 in. (2.7 cm), and there were also 2 *Pantala* larvae of $\frac{1}{2}$ and $\frac{3}{4}$ in. (1.3 and 1.8 cm). In the third sample there were only 5 *Pantala* larvae of between about $\frac{1}{2}$ and $\frac{5}{8}$ in. (1.2 to 1.6 cm), and in the last sample there were no larvae at all. The larvae of highest age were, therefore, found in the places which flooded first and, since the adults at Soda emerged from larvae of just over 1.5 in. (4.0 cm) long, the larvae in the first Nziga sample had nearly completed their development.

During a reconnaissance for hopper bands made by Swamp Skipper on 3rd February 1962 samples were taken at five points in the Tumba and Nziga plains in water of one to two feet deep (30-60 cm). *Hemianax* larvae were found everywhere in

¹ Each sample consisted of 20 sweeps of 5 paces long, with a fine gauze net of 1 ft (30 cm) in diameter, which was scraped along the bottom. The collected debris was carefully searched for larvae.

densities estimated at roughly one per sq. yd (0.8 m^2). Again larvae of the greatest length were found in the places which had been flooded first. Only in one place *Pantala* larvae were found.

I could not spend the 1962 dry season in the Rukwa Valley, but our African research scouts regularly took samples of larvae near Soda, at the only accessible point of the submerged North Rukwa plains. Due to poor communications only 5 samples could be sent to Abercorn, in February, April, May, June and August respectively, and all larvae in the April sample arrived dead. Larvae were bred in the laboratory in Abercorn, where they were kept in Kilnar jars, at water temperatures of 19 to 25°C during the day with an average of about 21° . In the Rukwa Valley water temperatures in the flooded plains were in the region of $24\text{--}26^{\circ} \text{C}$ during the day. Larvae were fed mainly on tadpoles and small fish. In addition, some samples were taken from the Uninji pans and some larvae were caught in Lake Chila, both near Abercorn.

Lake Chila had been of virtually the same size all through 1961 and the time of emergence of the species from there may not be used for conclusions on length of larval life, but in the Uninji pans at the beginning of the 1961 rains some water was left only in the centre and in 1962 all samples were taken at the water's edge several hundreds of yards away from the dry-season water line. The unprecedented flooding and submergence of the Rukwa plains prevented the collecting of more data in the 1962/63 season.

Altogether over 600 larvae were reared, of which 157 emerged successfully. Of these more than half (88) had been collected near Soda in North Rukwa. Unfortunately the majority of the emerging adults from the Rukwa belonged to only two species, *Crocothemis erythraea* and *Diplacodes lefebvrei*. It is unlikely that the other common species did not breed in the Rukwa plains at all, since sexual behaviour was commonly seen. However, the area in which the samples were caught was relatively small and although it contained several types of vegetation, the grass was tall and dense in most places. Another possibility is that the larvae of several species buried themselves below the layer of debris and topsoil that was scraped off with the net. This is supported by the observation, that these same species were equally absent in samples from the other collecting places.

The results of these breeding experiments do not cover all species, but they allow some conclusions on the approximate duration of larval development of a number of Anisoptera species, including some of those predating on hoppers (fig. 16). If one takes the time of oviposition at somewhere in December, the duration of larval life of *Hemianax* and *Pantala* was 2 to 3 months, of *Crocothemis erythraea* and *Tholymis* about 3 to 4 months and of *Hemistigma* and *Diplacodes* about 6 to 7 months. If the data of emergence of the Uninji-pans larvae are taken as reliable indications for duration of larval life, *Trapezostigma* took 5 to 6 months. In the field the actual larval period may be shorter, as there the average water temperature during breeding is higher than it was in the laboratory.

Thus, for many species the duration of the larval life is of the same order as the

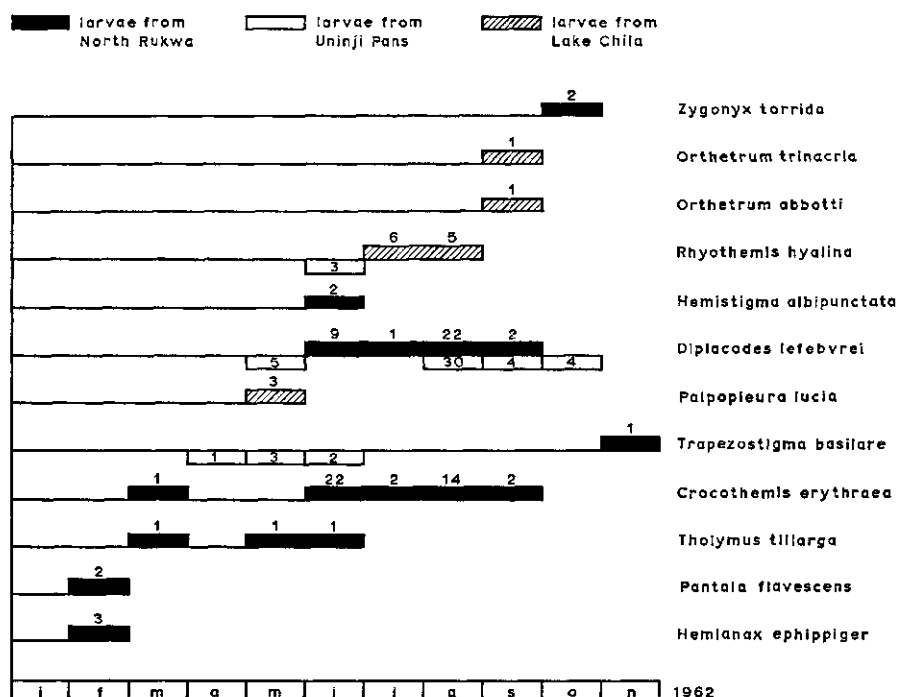


Fig. 16. Time of emergence of the imagines of various Anisoptera species, bred in the laboratory (the figures give the numbers that emerged in a certain month). In the field many *Pantala* and *Hemianax* were seen to emerge on 31st January and in the first week of February 1962

mean duration of the flooding over large parts of the plain, as it is in periods of about average rainfall. Consequently the extent and duration of the flooding in a certain season will directly determine the proportion of the larval population that completes its development in time. And since it appears that the imagines survive the dry season, it will, therefore, indirectly be of great influence on the size of the adult Anisoptera population at the start of the following rains.

5.2.3 Other Predators

Spiders prey on hoppers, but in the outbreak areas only web-building spiders seemed to be of any importance. Wolf spiders and jumping spiders were present, but their numbers were always low (table 27). Web-building spiders were abundant in some years; they were found to catch not only the first and second instar, but also hoppers in later instars and even adults. The 47 preys found in 30 webs in the experimental plots in December 1961¹ could be split up in:

¹ There were very few webs in the plot at that time.

| | |
|-----------------|----|
| Acridid hoppers | 32 |
| Anisoptera | 12 |
| Coleoptera | 2 |
| Hymenoptera | 1 |

In January 1962, when the hoppers were in the third and fourth instar the number of webs had gone up considerably and more detailed observations were made. In two places an area of 3,000 sq. yds (2500 m²) was searched for webs, first in tall grass (mainly *Echinochloa pyramidalis*) and then in a short grass mosaic (*Cynodon dactylon* and *Cyperus longus*). The areas contained 44 and 20 webs respectively. Of those 64 webs 37 (58 %) contained prey, of which 27 held one or more hoppers and 10 had only other prey, mainly Anisoptera. A total of 35 hoppers was found in the 64 webs, which is just over one per two webs. This obviously represents the catch of several days. At a density of 44 webs per 3,000 sq. yds (2500 m²) in tall grass, and, assuming a catch of one hopper per two webs every 5 days, this would mean a hopper mortality of approx. $1000/3000 \times \frac{1}{2} \times \frac{1}{5} \times 44 = 1.5$ hoppers/1000 sq. yds/day. This represents the catch in a hopper population of fairly low density; the effect of one web will no doubt go up with increasing hopper densities.

Table 27. Approximate densities of spiders in North Rukwa, 1961/62 and 1962/63

| Year | Area | Number of spiders per 1000 sq. yds | |
|---------|-----------------|------------------------------------|------------------|
| | | web-building | non-web-building |
| 1961/62 | end of December | plot 1 | 0.7 |
| | | plot 2 | 2.0 |
| | | plot 3 | 1.3 |
| | | plot 4 | 0.1 |
| | end of January | Nziga plain: short grass | 0.3 |
| | | tall grass | 0 |
| 1962/63 | January | Nziga plain: short grass | 14.7 |
| | | tall grass | 0.2 |
| 1962/63 | January | Nziga plain: short grass | 0.7 |
| | | tall grass | 7.7 |
| 1962/63 | January | Nziga plain: short grass | 1.0 |
| | | tall grass | 3.0 |

Mantidae prey on hoppers, but from the third or fourth instar onwards these become too big to handle. In small cages the consumption was about 10 first or second-instar hoppers per day, but in the field catching of hoppers might not be so easy. It was difficult to get an idea of the densities of Mantids, but these were undoubtedly low. On one occasion their numbers were roughly estimated in an indirect way. Mantid females lay their egg-capsules in the second part of the rainy season. These capsules are attached to grass stems in the top level of the vegetation and they are clearly visible; they were often seen in groups of 2 or 3 fairly close together, and since *Mantidae* produce 4 to 5 capsules per female (IMMS, 1951) it was assumed that these groups had been laid by one and the same female. In August 1961 egg-capsules were counted in a strip of 20 yds (18 m) wide, along 67 miles (112 km) of Land Rover scouting in

the Tumba and Kambangombe plains; 149 egg-capsules, or groups of capsules, were seen, which gave a mean density of about 0.07 Mantid female per 1000 sq. yds at the time of laying. Assuming a 1 : 1 sex ratio and a daily consumption of 10 hoppers per Mantid, such a population could have killed one or two hoppers / 1000 sq. yds / day.

Hemipterans of the Reduviidae and Pentatomatidae were seen preying on hoppers but they were not common.

Ants have been seen to drag away hoppers that were in their first ecdysis just after hatching, but normally the hopper jumped free again once it had completed the moulting.

It has been suggested that *birds* may take part in the destruction of young hoppers (VESEY FITZGERALD, 1955 a). DEAN found remains of first-instar hoppers in the stomach contents of *Quelia quelia centralis* and Finch lark or Fisher's sparrowlark (*Eremopteryx leucopareia*), but he came to the conclusion that they are only facultative feeders on hoppers. Their numbers are difficult to assess since they move in dense flocks which have a very fast and erratic flight. During the mortality period in the Kabwe plain, Mweru wa Ntipa, only one small flock of Finch lark was seen around on two successive days, but they never came in or near the plot. In 1961/62 only one flock was seen in plot 3 on 23rd December and again in the same place on 25th December.

The *Egret* (mainly the Buff-backed Egret *Bubulcus ibis*) is a well known predator on Acrididae but they have rarely been found to eat first and second-instar locust hoppers (DEAN, 1964). In the Kabwe plain on 10th January 1961 at about 11 a.m. I shot two Egrets which had been feeding in and around the plot. Their stomachs contained adult locusts, grasshoppers and Coleopterans, but no Red-Locust hoppers; in general there was no prey under 7 mm in length. Another specimen was shot on 14th January 1963 at noon in the Nziga sector, North Rukwa. It had fed on Coleopterans, spiders and grasshoppers; the smallest Acridid was 14 mm long and in general the stomach contained no prey under 8 mm in length. It is, therefore, extremely unlikely that these birds cause any mortality among first and second-instar hoppers.

5.3 Other causes of mortality

Other causes of mortality among hoppers in the first few weeks after emergence have not been found. In laboratory populations high mortality rates during the first and second instar are common (SPRADBERY, 1959), but so far it has been impossible to find the cause. Recently GREATHEAD (1966) reported such a high mortality (50%) STOWER and he observed among first and second-instar larvae of *Schistocerca*, both in cages and in the field. This mortality could not be accounted for and the author suggests that it was due to a natural elimination of unsuitable genotypes. In the

field in *Nomadacris* there never was the slightest evidence of such a mysterious mortality; never were sick, dying or dead hoppers seen. Admittedly scavenging of corpses can be quick, but it appears unlikely that such a mortality, had it occurred, would not have been spotted during the numerous working hours, spent in experimental plots where large numbers of hoppers disappeared.

SYMMONS (unpublished work) placed gauze cages over four hatching parties in the 1960/61 plot, thus keeping them under fairly natural climatical conditions, but screening them from at least some if not most of their predators. He counted the survivors, when they were in the third instar and estimated the reduction in numbers to have been only 6 % over 3 weeks. Unfortunately it could not be proved with certainty that during the same period any large mortality occurred outside the cages, though in my opinion there probably had been (section 5.1).

In that same breeding season in the Kabwe plains, Mweru wa Ntipa, the author caught 25 hoppers on the first day of hatching. These hoppers were kept outdoors in a cylindrical plastic cage with a perforated lid and they were shielded from direct sunlight during the hot hours of the day. After five days only one had died and the others appeared to be in good health, but in the experimental plot numbers had dropped by 86 % over the same period (section 5.1).

There remains the possibility of hoppers being killed unseen during the night. This is difficult to examine, but if it were the case the unknown agent would probably have a disturbing effect on hoppers around the victim. On a number of occasions both in North Rukwa and in the Kabwe plain a group of hoppers, which had hatched that day and had remained together, were marked and mapped in their position at dusk and inspected again at dawn the next morning. Never was the group found to have been disturbed or to have altered its formation.

5.4 Hopper Mortalities and Predator Densities

Nearly all data on hopper mortality suffer from large standard errors and other sources of uncertainty, but with the present techniques this is inevitable. The estimated number of hoppers, originally present in a plot is the product of the number of egg-pods, the percentage of these pods that hatched and the mean number of hoppers hatching from one pod.

Usually the egg-pod distribution is not very clumpy and the estimate of the total number of pods in a plot should not be more than 10 % wrong. The hatching percentage of the egg-pods often formed a source of larger errors of estimate; in 1959/60 a standard deviation could not be given, but the estimate in the subsidiary plot suggested that virtually all pods hatched. In the following two seasons this method probably failed, apparently giving serious under-estimates. In 1960/61 this meant that no reliable estimate of the original hopper population could be given. In 1961/62 it meant that the hatching success had to be estimated from the groups of marked pods, but there were only relatively few pods in each group and hatching percentages differed

greatly from place to place, due to variations in duration of waterlogging of the soil. Only in plot 4 the absolute total of the hatched egg-pods was known and the same applied to the Kabwe-plain plot in 1960/61.

The mean number of hoppers produced by one pod had relatively small standard deviations, but here the estimate depended on the assessment technique used; Symmons' estimates were consistently lower than mine. The mean of these two independent estimates probably was close to the true value. On the whole the standard deviation in the estimate of the hopper population, originally present in a plot, must have been in the region of 15 to 30 %.

The hopper populations that survived after the first and/or second instar could be estimated more accurately (in 1959/60 with a standard error of 6 %, in 1960/61 in the Kabwe plain with standard errors of 20 and 17 %), except in 1961/62 when there was an unusually early band formation.

Thus on the whole the mortality estimates, as obtained by subtracting the surviving from the original population, can not claim any great accuracy. However, it is beyond doubt that in all three years a very large mortality took place in at least one part of an area: in 1959/60 in the square mile plot in North Rukwa, in 1960/61 in the Kabwe plain (Mweru wa Ntipa) and in 1961/62 in plot 4. In the other cases a substantial reduction had taken place during incubation, and the subsequent mortality in the first two instars was appreciable but not dramatic.

In contrast with reductions during incubation it is difficult to link reductions in numbers of hoppers directly with one or more mortality factors. Predators like mantids, hunting spiders and hemipterans could be ruled out because their numbers were too small; web-building spiders were sometimes abundant, but in the years under discussion they were not, or they were too late. Birds could also be excluded (section 5.2.3).

The only predators that could possibly cause a large hopper mortality were the Asilidae and the Anisoptera. Not only were they seen to kill hoppers and were they found to specialise on Acrididae when these were abundant, but their numbers were high enough to be a mortality factor of importance. In fig. 17 their densities are compared with the hopper mortalities per unit area per day, as it was estimated in the nine cases of a known reduction. Only the combined densities of Asilidae and weighted¹ Anisoptera showed a correlation with the hopper mortalities. The only apparent discrepancy was the case of the second mortality period in the Kabwe plain, but the ultimate prey density was very low and even with a 100 % hopper mortality this case would not have fitted in.

Both Anisoptera and Asilidae are facultative feeders on a wide range of prey and the frequency with which a certain prey is caught depends on its relative abundance. Thus one would expect the hopper mortality to vary with the hopper density. In addition, at higher densities hoppers offer a more conspicuous target on account of their gregariousness. Gregarisation results in a higher activity, in a coloration of the

¹ Cf. section 5.2.2.

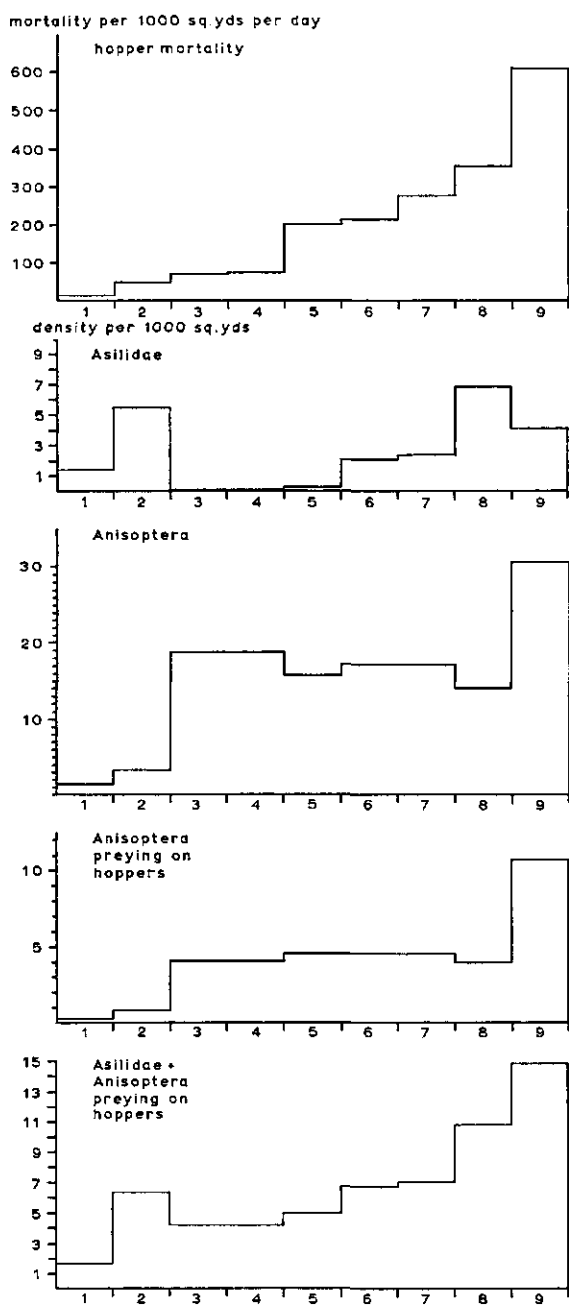


Fig. 17. Hopper mortalities in experimental plots compared with predator densities. Mortalities arranged according to increasing magnitude

Legend:

1. Kabwe plain, 1960/61, first mortality period
2. same, second mortality period
3. North Rukwa, 1961/62, plot 2-1
4. North Rukwa, 1961/62, plot 2-2
5. North Rukwa, 1961/62, plot 1-2
6. North Rukwa, 1961/62, plot 3-2
7. North Rukwa, 1961/62, plot 3-1
8. North Rukwa, 1959/60
9. North Rukwa, 1961/62, plot 4

Table 28. *Hopper mortality and predator density in experimental plots 1959-1962*

| | Hoppers | | Predator densities per 1000 sq.yds | | | |
|-----------------------------------|--|---|------------------------------------|-------------|--------------------------|--|
| | mortality per 1000 sq. yds per day | mean density per 1000 sq. yds over mortality period | Asilidae | Anisoptera | | Asilidae and Anisoptera species |
| | | | | all species | predator species only | |
| North Rukwa 1959/60 | 359 | 7000 | 6.9 | 14.3 | 4.0 ¹ | 10.9 |
| 1961/62: plot 1-2 | 206 | 7500 | 0.3 | 15.8 | 4.7 | 5.0 |
| plot 2-1 | 75 | 2700 | 0.1 | 18.8 | 4.1 | 4.2 |
| plot 2-2 | 79 | 2400 | 0.1 | 18.8 | 4.1 | 4.2 |
| plot 3-1 | 279 | 9200 | 2.4 | 17.1 | 4.7 | 7.1 |
| plot 3-2 | 219 | 9200 | 2.1 | 17.1 | 4.7 | 6.8 |
| plot 4 | 610 | 15000 ² | 4.2 | 30.8 | 10.7 | 14.9 |
| Kabwe plain 1960/61: first period | 17 | 120 | 1.4 | 1.5 | 0.3 | 1.7 |
| second period | 53 | 70 | 5.6 | 3.3 | 0.8 | 6.4 |

¹ The composition of the Anisoptera population in this breeding season is not known. In the other cases the Anisoptera species preying on hoppers formed between 22 and 33% of the population with an average of 28%.

² The original density was very much higher, but the hoppers dispersed rapidly.

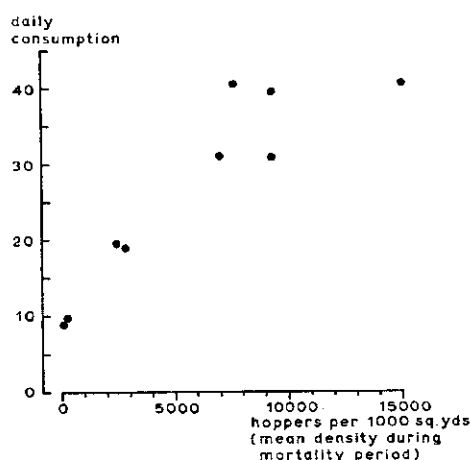


Fig. 18. Daily consumption per head of Asilidae and Anisoptera predators compared with prey density. (The daily hopper mortality is supposed to have been caused exclusively by these predators)

hoppers with black, brown-red, green and yellow, which is rich in contrast, and in band displacement. Fig. 18 compares the daily 'consumption' per predator¹ with the average hopper density over the whole mortality period.

The mortality among hoppers appeared to be correlated both with their own density and with the density of Asilids plus Anisoptera. A multiple regression was carried out, using the data given in table 28². This gave the regression formula

$$Y = -75.54 + .01906 x_1 + 25.37 x_2$$

in which Y represents the hopper mortality per 1000 sq. yds (836 m²) per day, x_1 is the mean hopper density per 1000 sq. yds over the entire mortality period and x_2 is the numbers of Asilidae and weighted Anisoptera per 1000 sq. yds. Both regression coefficients are clearly positive, the values of the variance ratio F_6^1 being 22.03 and 24.69 (at $p = 0.01$, F_6^1 is 13.74).

¹ That is the number of hoppers that died per day, divided by the number of Asilidae and Anisoptera predators.

² My thanks are due to Dr M. A. J. VAN MONTFORT of the Department of Mathematics of the State Agricultural University at Wageningen.

6 Natural Mortality in Later-Instar Hoppers

6.1 Numerical Data

It is difficult to assess any natural mortality, that takes place between the beginning of the third instar and the final moult. Normally band formation produces a clumpy distribution and this gives very large standard errors to any intermediate assessments. The clumpiness may decrease somewhat just before and after fledging, but at that stage the spread in development is considerable and the last hoppers have their final moult several weeks after the appearance of the first fledglings. By that time usually some migration has taken place and it is not always possible to separate the immature adults stemming from the plot and those bred elsewhere.

In January 1960, at the beginning of the third instar, the population had been assessed by Symmons at 8.5 ± 0.5 million. In May 1960 Symmons assessed the fledgling population in and around the plot (which formed an isolated breeding area) at just under 9 million. It appeared, therefore, that no natural mortality of any importance had taken place during the third and subsequent instars.

In 1960/61 and 1961/62 the experimental plots in North Rukwa formed part of much larger breeding areas and the fledgling population stemming from the plots could not be separated from the rest. In 1960/61 in the Kabwe plain (Mweru wa Ntipa) the hopper population was assessed in a very crude way. On 12th January 12.7 miles (20.4 km) of foot scouting were done along 8 parallel lines, varying in length from 1.0 to 2.2 miles (1.6 to 3.5 km), and laid out in a zig-zag pattern across the plain, which is about 7.5 sq. miles (19 km²) in size. In a strip of 2 yds (1.8 m) wide each hopper or group of hoppers, separated by at least 50 paces from the next hopper or group, was recorded and counted as representing one hatched egg-pod. This appeared to be valid, since everywhere the hatching density had been very low, except in the small experimental plot. Apart from a small number of just hatched parties, all hoppers seen were in their second or third instar and never were more than five hoppers seen together. Thirty-five such groups or single hoppers were seen and this suggested an estimated total of $17,500 \pm 3,700$ egg-pods hatched.

If in the Kabwe plain as a whole the mortality among the hoppers during the first and second instar was at least as high as that in the experimental plot in only five days (86 %), then not more than about 300,000 hoppers could have reached the third instar. At the end of April 1961 the surviving fledgling population was assessed; 553 locusts were counted in 10.1 miles (16.3 km) of scouting, which gave a total of $238,500 \pm 40,000$. The two estimates are not significantly different and thus there

probably was no mortality of any importance during the later hopper instars.

6.2 Birds

Of the numerous birds that feed on the later-instars Red Locust hoppers (VESEY FITZ-GERALD, 1955 b) Stork and Egret are the most important and in particular the European Stork *Ciconia ciconia*, the Marabu Stork *Leptotilos crumeniferus*, the White-bellied Stork *Sphenorhynchus abdimii* and the Buff-backed Egret *Bubulcus ibis*.

During 1959 and 1960 DEAN (1964) carried out some aerial surveys and he estimated the number of Egret in North Rukwa in January, February and March 1959 at about 5,000, the European Stork at 100-200, the Marabu Stork at 30-60 and the number of White-bellied Stork at 410 in January, but in March the latter had left the area. He described a number of cases in which these birds destroyed hopper bands, but generally the distribution of birds bore little or no relation to the hopper distribution.

In March 1962 the author made an aerial survey of North Rukwa and estimated the Egret population at 2,000-3,000 and Stork at less than 100. That season there had been scattered laying in the short grass mosaic in the Nziga area, and in the 2nd and 3rd instar a considerable number of small and not very dense hopper bands, of only a few square yards each, had been formed. In January Egret patrolled the area for weeks and destroyed all these small bands, leaving only a few scattered hoppers behind. However, the much denser hopper population in the taller grass, a few hundred yards to the East, was not attacked.

DEAN (l.c.) estimated the daily consumption of Egret at 100-200 hoppers and other insects, and that of European and Marabu Stork at about 800 to 900. In the two years in which their numbers were estimated, they could therefore have destroyed over half a million hoppers per day, that is if they ate nothing but hoppers. If they had done this during all three months, in which hoppers were available, they could have destroyed about 50 million hoppers. Therefore locally they can cause large drops in numbers. However, in years of a high hopper population the death of 50 million hoppers is of no importance and, in addition, in North Rukwa the majority of the hoppers usually is found in the area with taller grasses.

6.3 Other Causes of Mortality

Larvae of a *Tachinid* fly have been reported in hoppers from Tanganyika and this included some cases found in the South Rukwa plains (MICHELMORE, 1936). MICHELMORE and ALLEN (1934) found hoppers parasitised by Nematodes in Northern Rhodesia.

I dissected more than 1800 hoppers in the third and later instars¹ and found only

¹ In 1958, 1959 and 1960, and from both North and Central Rukwa.

one case of a Tachinid larva parasitising a hopper (STORTENBEKER, in preparation). *Nematodes* were found in a *Nomadacris* hopper only once, but these parasites were not uncommon in grasshoppers from the same area of Central Rukwa.

Web-building *spiders* catch hoppers of all instars, but there is no reason to suppose that they will be of any greater effect on later instars than on the first two.

Some *fungus* diseases caused a high mortality among adult locusts under cage conditions (section 7.3), but they did not affect hoppers. It is, therefore, very unlikely that they will be of any effect in the field.

As an occasional predator catfish (*Clarias mossambicus*) can be mentioned. Once in February 1962 hoppers were chased across a channel, and when they 'rowed' across, many were seen to be caught by the locally abundant cat fish. Rarely will this be a serious hazard, since hoppers seem to be extremely reluctant to cross water spontaneously, though in later instars and at high densities they may do so more often.

7 Natural Mortality in Immature Adults during the Dry Season

7.1 I.R.L.C.S. Records 1953-1963

The data, available from records of the International Red Locust Control Service, on assessments of adult-locust populations carried out between the emergence of the adults and the beginning of maturation at the start of the rains, have been grouped for the period of the first few months of adult life (table 29) and for the dry season proper, from about the end of May onwards (table 30). It should be remembered that in this type of population assessment standard errors of 15 to 20 % or more are inevitable. In three cases some chemical control took place between assessments and in two of these cases the resulting mortality had to be estimated from the amount of insecticide used. In both cases, however, the assumed kill per gallon insecticide was a low estimate and the amount of insecticide used could easily have been solely responsible for the drop in numbers since the previous assessment.

Figures in table 29 suggest that in Central Rukwa considerable reductions in numbers during the first few months of adult life may not be unusual. In both 1957 and 1958 it was beyond doubt that a large mortality severely reduced the young adult populations. In 1959 the reduction may not have been a real one, since it could well have been the result of an overestimate in the Swamp Skipper assessments (chapter 2).

This was certainly not the case in 1958, when the population was comparatively evenly distributed and there were no dense concentrations. Additional proof that the mortality indeed had taken place was obtained in September that year, when Dean and the author searched an area of unburnt *Sporobolus robustus* and found the remains of 90 corpses (usually hindlegs and wings). This indicated a natural mortality of $268,000 \pm 80,000$ per sq. mile (2.59 km^2) in that area¹. A similar mortality over only 10 % of Central Rukwa, occurring between May and July, would have been sufficient to explain the disappearance of about 10 million locusts in that period. In another grass island (mainly *Hypparrhenia rufa*) on the other side of the plain 6 corpses were found in 390 sq. yds (326 m^2). In the burnt grass around the islands no remains of corpses were found.

During the dry season proper the percentages reduction varied considerably (table 30), but the absolute mortalities per month were very similar in all years. It was the sort of mortality one would expect from a rather constant predator population, such as resident birds.

¹ There had been no control in Central Rukwa for over one year.

Table 29. *Natural mortality amongst immature adults during the first few months after fledging*¹

| | | Population estimates | | | | Approximate mortality in millions per month | |
|---------------|------|--|----------|-------------------------------|------------------|---|----------------------|
| | | first estimate after fledging ² | | nearest following estimate(s) | | | method of assessment |
| | | month | millions | month | millions | | |
| North Rukwa | 1958 | late April | 44.5 | early June | 46.8 | S.S. ³ | negligible |
| | 1959 | March | 13.7 | April | 11.8 | S.S. | |
| | | | | May | 12.2 | S.S. | |
| | | | | | June | 15.1 | |
| Central Rukwa | 1957 | April | 16 | Sept./Oct. | 2.5 ⁵ | L.R. | 3 |
| | 1958 | May | 18.8 | July | 7.6 | L.R. | 5 |
| | | | | August | 8.7 | L.R. | |
| | | | | September | 9.9 | L.R. | |
| 1959 | | | | May | 24.4 | S.S. | 2 |
| | | April | 27.4 | June | 21.4 | L.R. | 2 |

¹ Based on data collected by the technical and the research staff and recorded in the Annual reports of the Director International Red Locust Control Service.² All assessments in this column were carried out by Swamp Skipper.³ Swamp Skipper⁴ Land Rover⁵ This assessment was done after a fire, which burnt out the entire fire-protected area. The drop in numbers, however, occurred before the fire, since a superficial assessment in August gave only 1.6 million.

Table 30. *Natural mortality amongst immature adults during the dry season*¹

| | Populations | | | | Mortality | | | |
|---------------|---|----------|--------------------------------|-----------|---|-------------------|-------|-----------------------|
| | first estimate after fledgling control ² | | last estimate before the rains | | estimated kill from control in millions | natural mortality | | in millions per month |
| | month | millions | month | millions | | in millions | in % | |
| North Rukwa | | | | | | | | |
| 1953 | July | about 20 | October | about 18 | — | about 2 | 10 | 0.7 |
| 1956 | August | about 4 | September | about 2.5 | — | about 1.5 | 38 | 0.7 |
| 1957 | May | about 7 | October | betw. 2-4 | — | betw. 3-5 | 44-71 | 0.6-1.0 |
| 1958 | June | about 46 | November | about 8 | 33 ^a | about 5 | 11 | 1.0 |
| 1959 | June | about 15 | October | about 11 | — | about 4 | 27 | 1.0 |
| 1960 | May | about 68 | October | about 27 | 37 ^a | about 4 | 6 | 0.8 |
| 1961 | May | about 60 | October | about 20 | 38 ^a | about 2 | 3 | 0.4 |
| Central Rukwa | | | | | | | | |
| 1958 | July | about 8 | November | about 10 | — | negligable | — | — |
| 1959 | July | about 10 | October | about 8.5 | — | about 1.5 | 15 | 0.4 |

¹ Based on data collected by the technical and the research staff and recorded in the Annual reports of the Director I.R.L.C.S.² All assessments in this column were done by Land Rover, except those in 1960 and 1961, which had to be carried out by Swamp Skipper.³ Mortality as a result of some control experiments by W. N. Yule, who estimated the kill from daily assessments at close to 33 million.⁴ In these cases the mortality had to be estimated from the amounts of insecticide (DNC) used (1927 and 2961 gallons resp.) Estimates of kill per gallon insecticide varied from 27,000 in populations of swarm density (LLOYD, 1959) to 11,000 in small concentrations of low to medium density (DEAN, 1963). In 1960 most targets were rather dense swarms and it seems reasonable to estimate the average kill at about 19,000. In 1961 control was carried out against scattered concentrations of slightly higher density than in Dean's experiments and a kill of 13,000 locusts per gallon appears to be a reasonable estimate.

There may have been a high mortality during the 1962 dry season in North Rukwa. The 1961/62 rains had been heavy and the lake rose to a level which it had not reached since 1937. In April the fledgling population was assessed at about 79 million locusts occupying the Western half of the plains. These scattered so quickly over the whole area that hardly any sprayable targets could be found. In July no more locusts could be seen from the air and the area appeared to be empty. However, when the dry season ended with some heavy rainstorms early in October, a massive movement was seen by an African research scout, who had been stationed in Tumba camp for meteorological readings. He watched a migration across the Soda-Tumba road into the Katwa Makondo and Lumpungu plains¹ (fig. 4), which lasted for about a week and which was comparable in scale with a similar ovipositional movement in October 1961, involving 12 million locusts. It seems doubtful though, whether in October the population was still anywhere near the April population in size, even if one allows for a possible migration into some smaller perimeter plains to the north-east. Thus a considerable mortality may well have occurred during the dry season. Egrets had been seen moving around in flocks in the flooded plains, alighting regularly in the clumps of tall grass and they may have caused a large drop in numbers.

Before a control service was set up, at high population densities, a substantial drop in numbers used to result from swarm emigration.

7.2 Birds

A large number of bird species prey on Red Locust adults and these have been listed by VESEY FITZGERALD (1955 b). DEAN's (1964) work on distribution, numbers and consumption of Stork and Egret showed that in 1959 numbers of Egret and Marabu Stork increased greatly from April to July, but that their distribution during those months showed less and less connection with that of the locusts; the birds tended to concentrate along the lake edge and in the adjoining lake-shore grasslands as the flooded parts of the plains dried up. The European and White-bellied Stork are wet season migrants from the Northern Hemisphere, but every year some European Stork stay behind as a resident population around Lake Rukwa.

As in the case of the later-instar hoppers, Dean gives a few examples of Stork feeding on adult locusts, in particular in Central Rukwa in the 1959 and 1960 dry seasons. My own observations in the following years confirmed Dean's conclusions.

It has been suggested, that coucals (*Centropus superciliosus* and *C. toulou*), which are common residents in the flood-plain grasslands, feed largely on adult locusts during the dry season, as they inhabit the islands of unburnt grass like the locusts do (VESEY-FITZGERALD, l.c.). In August 1961 I combined an assessment of the locust populations in the Tumba, Kambangombe and Mazela sector of North Rukwa, with

¹ These plains have a high level, the soil was dry and the grass had been burnt. The rest of North Rukwa was still completely under water.

counts of numbers of coucals. The birds were counted in a strip of about 50 yds (46 m) on either side of the scouting line; 88 coucals were counted in 72.9 miles (117.3 km) of scouting. The over-all mean was 0.12 per 0.1 mile (176 m) of scouting, which gave an estimated total of nearly 3,300 coucals over the whole of North Rukwa. This compared well with an estimate of 3,000, made by Dean exactly two years before.

Roughly speaking the majority of the coucals stayed in the Southern part of the plains, where also the majority of the locusts were. On closer analysis of the data, however, there did not appear to be the slightest association with locust concentrations. A far less detailed survey in October of the same year confirmed the August observations; more than 70 % of the coucal population was in areas with less than 5 locusts per 0.1 mile and 27 % in places where no locusts were seen at all. In addition, coucals are only occasionally seen to chase and catch a locust.

Kites and harriers often accompany a Land Rover for miles, catching locusts that are flushed by the vehicle. However, their numbers were too small to let them play any part in the population dynamics of the locusts, and the same applies to bee-eaters and bustards. Fragments of locusts were also found in the faeces of hyena and jackal (DEAN, in DU PLESSIS, 1959).

7.3 Other Causes of Mortality

The results of an intensive search for parasites during three years and in four areas were meagre. Several thousands of locusts were dissected, but only larvae of the Tachinid fly *Ceracia nomadacridis* were sometimes found in some numbers. They seem to be harmful only in so far as to prevent normal maturation (section 3.4), but during the dry season they do not seem to harm their hosts. The same applies to the *Eugregarines*, which were occasionally found in numbers of up to 20 or 30 in the midgut of hoppers and, rarely, of adults. It is generally believed that these parasites, which were much more common in grasshoppers of the same area, are harmless to the host (CANNING, 1956), but in very high numbers they may severely damage the gut wall and make the insect more susceptible to disease.

In two cases larvae of an unidentified Sarcophagid were found in the body cavity of a locust in Central Rukwa and in the Mweru wa Ntipa. In Central Rukwa there was a case of an immature adult being parasitised by a Nematode, and in November 1961 in the Uninji Pans there were two more cases in female locusts; these were not maturing normally.

Several species of mites parasitise on locusts. The most spectacular are the well known red mites attached to the wing membrane. They are the larvae of *Eutrombidium* sp. Their numbers were always low on hoppers and on adults during the dry season, but around the start of the rains the percentage infestation and the numbers per host went up sharply to a 100 % infestation and an average of 16 per host (North Rukwa population, November 1960). However, even 30 or 40 mites did not influence the maturation of the females which they parasitised.

Yellowish mites were found near the base of the wings of adults from the Mweru wa Ntipa and in North Rukwa. They belonged to probably two genera of the Podapoli-podidae (Dr. I. M. NEWELL, personal communication).

Observations in the field supplied evidence of the presence of at least three fungal diseases. In May 1959 corpses of the grasshopper *Cataloipus oberthuri* were found clinging to grass-stems, in the Nkamba-Kati area of Central Rukwa. This is the characteristic attitude of Acridids dying from *Empusa gryllii* (SKAIFE, 1925). LEA and WEBB (1939) had found corpses in similar circumstances in 1937, but they expressed doubt as to whether these were really cases of *Empusa*. In the same area there had been, and still was, a *Nomadacris* population of low density, but they obviously had not been affected. Infection experiments gave no results.

At the end of April 1959 in North Rukwa one corpse of a locust was discovered in a search of several thousand square yards. After a few days this corpse developed symptoms of a fungus disease, which closely resembled the description of *Sporotrichum* sp. given by MACMARTIN (1952). Infection experiments with a suspension of spores in water were not successful.

In August of that year locusts were kept in outdoor cages in Kafukola research station. Among the corpses of the locusts that died there were some which assumed a pinkish red colour. These were kept in glass tubes and after a few days a fungus broke through the joints of legs and abdominal segments and covered the body in a white, woolly growth. The spores were formed a few days later and these turned the colour of the fungus to creamy white. At about the same time in the field a sick locust was collected, which had a pinkish colour and which developed the same symptoms after its death. These were exactly as described by MACMARTIN (1935) and SCHAEFFER (1935) for *Beauveria* sp.

Infection experiments were successful, giving high mortalities among locusts in cages; it was in fact difficult to keep the fungus out of the control cages (table 31). In general it is extremely difficult to keep locusts alive in cages under field conditions and the mortality in the control cages was high during the 14 days of the experiment. In the field no more cases of infection with this fungus were ever found. It is believed that fungi can attack locusts successfully only when these are not in optimal condition.

Table 31. Effect of *Beauveria* sp. on locusts in cages

| | Number | Died | Died from <i>Beauveria</i> | Died from other causes |
|----------------------------------|--------|------|-------------------------------|---------------------------|
| Infected with a spore suspension | 117 | 115 | 90 | 25 |
| Control | 41 | 14 | 6 | 8 |

7.4 Discussion. The Correlation between Multiplication Rate and Rainfall

Populations of *Nomadacris* and other Acrididae can occasionally have spectacular multiplication rates, despite a relatively low reproductive potential. In the years 1959 to 1962 the mean number of viable eggs per parent was at maximum 100, and there are no indications that in series of dry years this figure will be very much higher, if at all different. In North Rukwa the multiplication rate from parents to fledglings has been lower than one in some years, and over fifty in others. The highest value is not known with certainty, but in 1953/54 it was thought to have been at least fifty if not seventy-five times (table 34). Thus in some years only one out of every hundred potential offspring reaches the fledgling stage, but in other years fifty or even seventy-five succeed. This means that we must look for a mortality factor which in some years is capable of destroying very large numbers, but in other years is largely or completely absent and then allows spectacular increases in numbers of locusts from one generation to the next. This key factor¹ itself, therefore, will have to show spectacular fluctuations in numbers or in intensity, fluctuations that must be positively correlated with the rainfall in the previous wet season. The data presented in this paper cover too few years to warrant analysis as done by MORRIS (1959) or by VARLEY and GRADWELL (1960), but in the years under discussion the multiplication rates were low (cf. table 34) and, therefore, the key factor had to be actively at work.

In the discussion following chapters 3 and 4 the conclusion was drawn that the factor, responsible for the correlation between multiplication rate and rainfall in the previous season, does not operate between the maturation of the parents and the hatching of the eggs. Now the mortalities occurring during the remaining part of the *Nomadacris*' life cycle can be evaluated (tables 32 and 33).

During the first and second-hopper instars there appeared to be a regular and large mortality. Only in the 1960/61 season we could not establish with certainty whether there was any mortality or not, but as has been discussed above (section 4.1), the incubation success of the egg-pods was probably higher than was recorded and consequently there probably was an appreciable reduction in numbers of hoppers.

There was no evidence of a substantial mortality during the last four or five hopper instars and in fact the available numerical data suggested that the reduction in numbers was small or negligible (section 6.1). The only incidental predators were Stork and Egret, but often their distribution did not show any correlation with that of the hoppers. In areas of short grass they can, and did, reduce the local hopper population effectively and it could be that in Central Rukwa, which has more short-grass mosaics than North Rukwa, birds do often cause appreciable reductions. However, even at peak consumption they could not have destroyed more than about 50 million hoppers in one season, that is, at their present population level they may destroy a high propor-

¹ In the sense introduced by MORRIS (1959).

Table 32. Natural enemies of *Nomadacris* and the stage of the life cycle during which they attack

| Natural enemy | Eggs | Hopper instars | | | | | | Immature adults | Mature adults |
|--------------------------------|------|----------------|---|---|---|---|---|-----------------|---------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | | |
| Rats | + | | | | | | | | |
| Mites | + | | | | | | | | |
| <i>Scelio howardi</i> | ○ | | | | | | | | |
| Ants | | ○ | | | | | | | |
| Asilidae | | × | × | ○ | | | | | |
| Anisoptera | | × | × | ○ | | | | | |
| Mantidae | | ○ | ○ | ○ | ? | | | | |
| Hemiptera | | ○ | ○ | ? | | | | | |
| Spiders: web-building | | ○ | ○ | ○ | ○ | ○ | ○ | ○ | |
| wolf and jumping sp. | | ○ | ○ | | | | | | |
| <i>Quelea quelea centralis</i> | | | | | | | | | |
| + Finch lark | | ? | | | | | | | |
| Stork | | | | | ? | + | + | + | + |
| Egret | | | | | ? | + | + | + | + |
| Harriers | | | | | | | | ○ | |
| Kites | | | | | | | | ○ | |
| Bustard | | | | | | | | ○ | |
| Coucals | | | | | | | | ○ | |
| <i>Eugregarina</i> sp. | | | | | | ○ | ○ | ○ | |
| <i>Trombidium</i> sp. | | | | | ○ | ○ | ○ | ○ | |
| Jackal | | | | | | | | ○ | ○ |
| Hyena | | | | | | | | ○ | ○ |
| Pathogenic fungi | | | | | | | | ○ | |
| <i>Asio capensis</i> | | | | | | | | | ○ |
| <i>Ceracia nomadacridis</i> | | | | | | | ? | ○ | + |

× effective and important natural enemy.

+ occasionally and locally of at least some importance.

○ enemy with little or no effect.

tion of the hopper population only in years when due to other factors the locust population level is low anyway.

There probably is a small mortality at each moult, but it has not been measured. For *Schistocerca* GREATHEAD (1966) puts it at about 5%.

Neither numerically nor qualitatively was there any evidence or likelihood that large reductions occur during the life of the immature adults. This confirms the conclusion drawn from Symmons' work that the root of the violent fluctuations in numbers is not to be found in the adult stage. Of all predators, parasites and diseases that have been found to attack immature adults (table 32), only Stork and Egret can occasionally and locally be of some importance, but neither their numbers nor normally their distribution allow them to inflict losses that are greater than the regular

Table 33. *Accumulative reductions in numbers between maturation of the parents and appearance of the imagines of the next generation, in percentage of the original potential numbers (the figure in brackets is the reduction in numbers in the period concerned)*

| Mortality period cause of reduction | 1959/60 | | 1960/61 | | 1961/62 (North Rukwa) | | | |
|---|-------------|------------------------|--------------------------------------|---------------|-----------------------|------------------|------------------|-------------------|
| | North Rukwa | | North Rukwa Kabwe plain ¹ | | plot 1 | plot 2 | plot 3 | plot 4 |
| Maturation | | | | | | | | |
| sterilisation | 8 (8) | 4 (4) | 13 (13) | | (—) | (—) | (—) | (—) |
| Incubation | | | | | | | | |
| inviability | 14 (6) | 10 (6) | 21 (9) | | 5 (5) | 5 (5) | 5 (5) | 5 (5) |
| rats | 21 (8) | (—) | (+) | | (—) | (—) | | |
| drought | (—) | (?) ² | (—) | | (—) | (—) | 31 (27) | (+ +) |
| eggs | (—) | 33 (31) | (—) | | (—) | (—) | (—) | (—) |
| waterlogging | (—) | (—) | (—) | | 53 (98) | 95 (95) | 68 (53) | (—) |
| eggs | (—) | (—) | (—) | | (—) | (—) | (—) | (—) |
| mites | 26 (6) | 42 (7) | 27 (7?) | | (—) ³ | (—) ³ | (—) ³ | (—) |
| Scelio | 27 (1) | 44 (3) | (—) | | (—) | (—) | (—) | (—) |
| Nymphal instars | | | | | | | | |
| 1st + 2nd, predators | 83 (77) | (?) ² | 90 (86) | ab. | 77 (29) ⁴ | 98 (57) | 84 (49) | (61) ⁵ |
| 3rd - 7th, predators | (—) | (+) | (—) | | (—) | (—) | (—) | (+ +) |
| Total reduction at appearance of imagines | over 83 % | over 80 % ² | probably over 90 % | about 77 % | about 98 % | about 98 % | about 84 % | well over 80 % |
| ? = reduction unknown; — = negligible reduction; + = possibly or probably a small reduction; + + = possibly or probably a large reduction | | | | | | | | |

¹ Observations on egg-pods of the second oviposition only.

² It did not become clear to what extent the incubation success of the egg-pods was affected by drought (section 4.1). Consequently it was not possible to determine the mortality of the first and second-instar hoppers. (section 5.1). Whatever happened there was a reduction of about 60% during incubation and/or during the first two instars.

³ Effect included in the destruction by waterlogging.

⁴ Mortality during the second instar only was 29%. During the first and second instar together probably at least 50% died.

⁵ Mortality during the first instar only. Up to the end of the second instar probably more than 80% of the hoppers died.

and rather constant absolute mortalities that appear to take place (table 30, section 7.1).

There may be exceptions to the rule, as suggested by the probable drop in numbers in North Rukwa in 1962, when the plains remained under water during the dry season (section 7.1), and by the reductions in numbers in Central Rukwa early in adult life (table 29). Stork and Egret have been seen to catch Acridids and other insects that escape from grass fires and afterwards systematically attack those locusts that had concentrated in the remaining little islands of unburnt grass. The fact that in 1958 the remains of corpses were found only in the standing grass and not in the burnt area would agree with such a technique of attack. From DEAN's data (1964) it appears that in Central Rukwa in 1959 the distribution of Stork and Egret, at the end of the wet season and early in the dry season, showed some similarity with that of the locusts but this was not the case in North Rukwa; this is probably due to differences in vegetation, the mosaics in North Rukwa being composed of denser and taller grasses (section 8.3). Thus the most likely explanation for the disappearance of several millions of fledglings in Central Rukwa would be that Stork and Egret attack concentrations early in the dry season. The fact, that in 1957 the mortality occurred before there were any fires, would indicate that the birds are equally effective in unburnt grass. In Central Rukwa such a mortality may be rule rather than exception, but it should be noted that the impact of birds on a locust population can be of some importance only when the locust-population level is fairly low (section 6.2).

Thus, in the three years of above average rainfall and low multiplication rates of the locusts, regular and large mortalities did take place only when hoppers were in their first and second instar (table 33). Also these mortalities were 'irreplaceable' in the sense that at a later stage there did not appear to be any mortality that could have replaced the young-hopper mortality, had it not occurred. Thus, it appears reasonable to draw the conclusion that one or more key factors are at work at this stage of the life cycle. In addition, only at this stage effective predators were found to be numerous and the observed hopper mortalities showed a correlation with their densities.

Although it appeared that Asilidae and some Anisoptera species were largely responsible for the recorded hopper mortalities, their 'daily consumption' seemed high. The predator densities, however, were probably underestimated, as it is more likely that predators were disturbed by the assessment and left the plots without being noticed, than that they were counted twice. Secondly, at high prey density it could well be that Asilidae do not suck out hoppers to the last drop, and that Anisoptera only eat the juicy parts of a hopper and then catch another one. Finally predators like spiders and mantids make only few victims per head, but their combined effect must have accounted for several dead hoppers per 1000 sq.yds per day (section 5.2.3).

Considered in terms of numbers of predators over the whole of North Rukwa outbreak area, the populations of Asilidae and Anisoptera were of the right order of magnitude. In 1959/60 a parent population of about 11 million locusts produced about 80 viable eggs per head (table 5). Up to the moment of hatching there were reduc-

tions totalling about 20 % (table 33); thus 11×10^6 (80—16) = about 700 million hoppers hatched. That season about 100 square miles of grassland had been burnt, but the hoppers occupied only about half of it. There were about 1.5 million Asilidae and about 1 million Anisoptera of the hopper-killing species in the burnt grassland¹. In the period of about 40 days during which there were first and second-instar hoppers present, 80 % of the hoppers could have been killed with a daily consumption of $.80 \times 700 \times 10^6 / \frac{1}{2} \times 2.5 \times 10^6 \times 40 = 11$ hoppers per predator.

In 1960/61, 27 million parents produced about 1750 million hatched hoppers over an area of about 160 sq. miles². Assuming that predator densities over that area were similar to those in and around the plot, there were about 5 million predators, which could have killed 80 % of the hopper population with a daily consumption of only 7 hoppers per head.

In 1961/62, under optimum incubation conditions³, 12 million parents could have produced a total of about 1080 million hoppers, emerging in an area of just under half of North Rukwa, roughly 100 sq. miles. If the means of the predator densities in the plots are taken as representative for the whole burnt area, there were about 2 million predators and these could have killed 80 % of the hoppers in a period of 40 days with a daily consumption of 13 hoppers per head.

All these calculations are approximations of course, but they indicate that in all three years the predator populations were large enough to kill a high proportion of the hopper population.

Assuming then that the first and second-hopper instars are the stages in *Nomadacris*' life cycle where the fluctuations in numbers originate, and that two Asilid and several Anisoptera species are the main cause of the mortality at this stage, there still remains the question of whether the numbers of Asilidae and/or Anisoptera could have a positive correlation with the rainfall in the previous wet season.

For the Asilid species such a correlation does clearly not exist. Although apparently their larvae and/or pupae can survive a relatively short period of waterlogging of the soil⁴, their numbers were reduced to virtually zero after two seasons with prolonged flooding. Thus the breeding success of the Asilidae is likely to be correlated negatively, rather than positively with the rainfall of the previous season, at any rate in periods of wet years; this predator cannot, therefore, be the key factor in *Nomadacris*' population dynamics. This detrimental effect of the annual flooding and waterlogging, however, will cease to cause reductions when the water is stabilised at a high level and the remaining Asilidae are forced to lay their eggs along the fringes of the now flooded grasslands. In areas where the water level had been high for many years (Iku plains,

¹ Based on Dean's estimates (table 14, section 5.2.2).

² That is if there had not been a drought during incubation, but this reduction is ignored here.

³ Ignoring the adverse effect of the period of waterlogging during incubation.

⁴ In December 1960 Asilidae appeared in areas that had been flooded for several months at the end of the previous wet season and it was likely that they had been bred there.

Uninji Pans, Mweru wa Ntipa) reasonably high Asilid densities were found along the edge of the woodland in 1960/61 and 1961/62 (table 19).

The Anisoptera are in a completely different position. From work of previous authors and from my own observations it appears likely that Anisoptera survive the dry season in the adult stage. For their reproduction they depend on water in rivers, temporary pools or temporary flooded grasslands. An intriguing aspect of Symmons' correlation between the rainfall in one season and *Nomadacris*' multiplication rate in the next season is, that it does include not only the rainfall over the Rukwa Valley, but also (and as a factor of equal importance) the rainfall over the entire catchment area of 31,000 sq. miles. This could only mean that the total amount of water coming into the basin is of crucial importance, and this total amount of water governs the extent and duration of the annual flooding in the grass-plains around Lake Rukwa.

From both previous researches and my own observations, it appeared that the duration of the larval stage in the life cycle of tropical Anisoptera lasts from two to six months and, therefore, is of the same order as the annual flooding over large parts of North Rukwa, as it is in periods of about average rainfall. Thus, a direct and positive correlation between the duration of the flooding and the breeding success of Anisoptera is not at all unlikely.

Population assessments of Anisoptera were made in and around the experimental plots only. Assuming that the values obtained there were representative for the whole of North Rukwa, the densities of Anisoptera in December and January indeed reflected the flooding situation in the preceding dry season to some extent. In 1959 the flooding was extensive but not of long duration. In the 1959/60 season the rainfall was considerably above average and the flooding was extensive and lasted for many months into the dry season; in December 1960 numbers of Anisoptera had gone up compared to the previous season. The rainfall in the 1960/61 season was about average, but again the flooding was prolonged; in December of that year the Anisoptera level had gone up again. In 1961/62 again the rainfall was well above average and the major part of North Rukwa submerged and did not dry up at all; and in December 1962 the Anisoptera population level had gone up to a very high level.

Thus the Anisoptera population level appeared to be associated with the duration of the flooding, but one would have expected a greater rise after the very 'wet' 1960 dry season. In 1959, however, samples were taken in a burnt area in the middle of a large area of unburnt grass and since the Anisoptera showed a clear preference for burnt grass, the density in the plot may have given an exaggerated idea about the density level in the other burnt areas.

Thus, a tentative explanation of the fluctuations in numbers of the Red Locust in the North Rukwa outbreak area (section 1.4) could read like this. Three sets of circumstances can be recognized. In a period of wet years the lake will rise and spread out over the surrounding grass-plains, which may remain submerged for a period of several years (North Rukwa from 1962 to time of writing, and the Mweru wa Ntipa,

from 1957 onwards). The locusts will find breeding space restricted to some perimeter plains and to narrow fringes of grassland along the edge of the woodland. The water table in the soil is high and egg-pods will run a great risk of asphyxiation through early waterlogging of the soil; in my opinion, this may well be the most effective reduction factor at this stage. A similar idea has been put forward by GUNN (1955 a). In addition, the Anisoptera find optimum breeding conditions and they will be numerous, and several other predators will concentrate along the edge of the water and take their share in keeping the locust population well down¹.

The situation will become different when a period of about average rainfall totals follows. The lake recedes and the grass-plains come under a regime of annual flooding for periods of varying duration (such as in the Rukwa between about 1940 and 1950, and from 1956 to 1962). *Nomadacris* finds ample breeding space and in general the incubation of eggs and egg-pods is successful; only an occasional drought or a short period of waterlogging may cause a reduction in incubation success. There are appreciable fluctuations in multiplication rates, governed largely by similar, but inverse fluctuations in the size of the Anisoptera populations.

The situation will change again when a period of years with sub-average rainfall follows. In the beginning there will still be wide-spread flooding (inducing wide-spread oviposition by Anisoptera), but of so short duration that large percentages of the larvae will be unable to complete their aquatic life period. This will give a sharp fall in the population level of Anisoptera imagines, and corresponding increases in the multiplication rates and the population levels of the Red Locust. After a number of dry years the plains will not be flooded any more during the rains, since the rivers that drain the catchment area transport all water across the plains into lake Rukwa without overflowing, and Anisoptera will find their breeding space limited to ditches and pools and to some rivers².

Thus, in periods of dry years conditions become optimal for rapid multiplication of the locusts (such as around 1950 and again around 1955). Abundance of burnt-off grasslands for oviposition coincides with optimum survival chances for young hoppers, since at least one of the two most important predators has virtually disappeared. There are only incidental reduction factors left, like a drought that prevents oviposition or affects the incubation of the eggs. This happened in 1952/53, when a severe drought

¹ There are a number of mechanisms which protect *Nomadacris* from extinction at this stage. Firstly its predators are not specific and concentrate on the most abundant prey; in addition, the inconspicuous appearance of the green, and rather inactive solitary hopper will give it a good chance to survive. Secondly in areas with a high watertable the grass will grow rapidly and will force the females to lay their subsequent egg-pods elsewhere, thus ensuring possibly better egg-pod survival for at least part of their brood.

² One may ask whether Lake Rukwa, which rarely dries up, could not provide adequate breeding opportunity in periods of dry years. However, the Anisoptera species of the Rukwa plains are typical reedy-pool and marshland species and not lacustrine types. In addition, when the lake level is low the water is made strongly alkaline by sodium carbonate and it appears unlikely that many species breed in it. RICARDO (1938) indeed found only one single larva in her samples of the lake fauna.

drastically reduced the multiplication rate in a year in which the lake level was low.

It is self-evident that this story is very hypothetical, although on the grounds of my results it seems to be an acceptable explanation. On several of the aspects a longer series of observations would have been desirable, such as on the exclusiveness of the mortality among young hoppers, and the changes in population levels of both Asilidae and Anisoptera in periods of years of average and of sub-average rainfall. There are other points on which one would like to have more detailed information, such as on the effectiveness of various Anisoptera species as predators on hoppers, and on the duration of the larval life of these predators.

The suggested explanation of the problem of the fluctuations in numbers of *Nomadacris*, if true for North Rukwa, would probably also be applicable to the other outbreak areas; this supposition finds support in GUNN's and SYMMONS' finding (1959) of a correlation between locust population level and rainfall in the Malagarasi, similar to the correlation that is valid for North Rukwa.

8 Differences in Importance of the Outbreak Areas

8.1 Introduction

During my last season in the Rukwa Valley I made some preliminary observations on the third and last problem mentioned in section 1.4. It is the experience of the International Red Locust Control Service that some outbreak areas produce more swarms, swarmlets and dense concentrations of locusts and hoppers than others. Some areas require control almost every year, others only occasionally or hardly ever. These differences in 'productiveness'¹ can be demonstrated by comparing the total amounts of insecticides that were used in each outbreak area, as is done in fig. 19 for the period of 1952 to 1962. DEAN (unpublished) compared the areas by counting the number of swarms and concentrations reported in each area since 1945, and he found the same sequence in productiveness. A third block diagram indicates the frequency of production in each area over a period of eleven years².

For the North and Central Rukwa outbreak areas the apparent difference in productiveness receives confirmation from the reproduction rates, defined as the multiplication from the parent population just before maturation to the filial population just after fledging³. In nine successive years this reproduction rate could be calculated with a varying degree of accuracy (table 34). In some cases the assessed numbers of fledglings had to be corrected for the mortality that resulted from control operations (section 7.1). When in each year the ratio of the multiplication rates in North and in Central Rukwa is taken, the mean of these ratios is about 2.3 to 1. The respective shares in the total amount of insecticides, used between 1953 and 1962 in all outbreak areas, were 60 and 25 %, a ratio of 2.4 to 1. Of the total number of swarms, swarmlets and concentrations reported in all areas since 1945, North Rukwa produced 48 % against Central Rukwa 18 %, which gives a ratio of 2.7 to 1. It appears therefore, that the observed difference in productiveness is real. It also appears that the source of the difference lies somewhere between the maturation of

¹ The term 'productiveness' will be used as a mean of defining both frequency and intensity of appearance of hopper concentrations and adult swarms in an area. It should be realised that the productiveness of an area does not say much about the chance that a plague will start from there, as in this several other factors are involved.

² Too little is known yet about the Kafue flats and the Chilwa area to include these areas in the comparison.

³ 'Reproduction rate' will from here on be used in this sense.

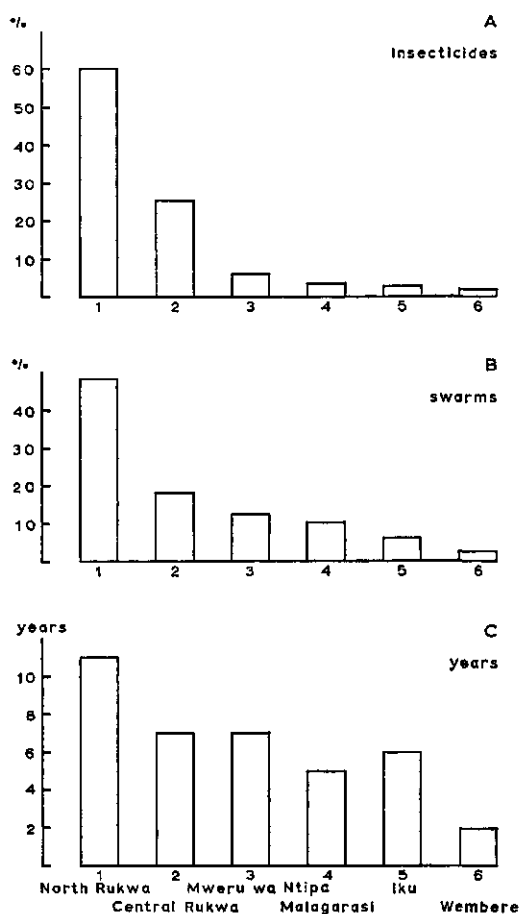


Fig. 19. The sequence of importance of the Red Locust outbreak areas, in respect of amount of insecticide used, and of productivity of swarms and concentrations

Legend:

- A. The total amount of insecticides used between 1952 and 1962, split up for the different areas in % of the total. (All amounts converted to acres covered on the basis of 25 lbs BHC-dust per acre and of 1 gallon DNC, Dieldrin 15% and BHC 15% per acre)
- B. Total number of swarms and sprayable concentrations since 1945, split up for the different areas in % of the total
- C. Number of years with swarms and sprayable concentrations in 17 years between 1945 and 1962

Table 34. Multiplication rates from the parent population at the start of the rains to the appearance of the imagines of the next generation in the North and Central Rukwa outbreak areas

| Breeding season | North Rukwa | Central Rukwa |
|-----------------|--------------------|-------------------|
| 1953/54 | Between 40 and 100 | Between 15 and 40 |
| 1954/55 | about 30 | about 15 |
| 1955/56 | about 5 to 10 | about 1 to 2 |
| 1956/57 | about 3.5 | about 8 |
| 1957/58 | between 20 and 40 | about 7.5 |
| 1958/59 | about 9 | about 9 |
| 1959/60 | about 10 | about 5 |
| 1960/61 | about 3.5 | less than 3 |
| 1961/62 | about 10 | very low |

the parents in November, and the appearance of the imagines of the next generation in February and March.

I did not have time and opportunity to do much research on this problem, but some of the observations I made appear worth recording in view of possible future research, as they may provide some indications for the direction in which the answer could be sought.

8.2 Outbreak Centres in Central Rukwa

In Central Rukwa adult locusts can be found in all grasslands, but the large and dense hopper concentrations are usually found in certain parts of the area. This observation stemmed from Mr R. R. Forrester, then a field officer who had been with the I.R.L.C.S. for more than ten years, most of which he spent in Central Rukwa. Mr Forrester was asked to indicate these 'hopper concentration areas' on a map, and the same was asked independently of Mr J. B. Eyssel, Chief Technical Officer, who also took an active part in the heavy hopper campaigns in the early 1950's. Forrester and Eyssel marked exactly the same parts of the area, with the exception of one small area just west of the Momba river (in fig. 21c indicated with broken lines), which Mr Eyssel did not mention. The two spray pilots Mr T. Malujlo and Dr A. R. W. Crosse Upcott, who both joined the Service after the years of the large hopper campaigns in Central Rukwa, had no experiences of really wide spread infestations, but the few sectors they indicated had also been marked by Forrester and Eyssel. Crosse Upcott also marked a small area just east of Chingoma camp, which had once harboured some dense concentrations.

In the Council minutes and the Annual Reports of the I.R.L.C.S. from 1947 onwards, sectors of Central Rukwa, that harboured dense or very dense concentrations, were mentioned by name in 35 cases. In 29 of these cases the area mentioned falls inside one of the 'hopper concentration areas', and in 3 more cases probably also. In the three remaining cases the mouth of the Kamba river was mentioned twice and the Limangombe sector once.

It should be pointed out that concentrations frequently, but not exclusively, have been found in these 'hopper concentration areas', and that at times dense hopper bands have been reported and controlled elsewhere, but the really large and dense infestations were seen in the sectors indicated in fig. 20c. These sectors will be referred to as 'outbreak centres'.

The apparent existence of outbreak centres in Central Rukwa offers a sharp contrast with the experience from North Rukwa, where hopper concentrations have been found regularly in all sectors, with the exception of some perimeter plains and of a relatively small area of rain grassland in the south-west, known as the 'topi stamping ground', in which area the soil is hard and the grass cropped short by the continuous grazing of large herds of topi, zebra and buffalo.

From the above experiences and observations it appeared worthwhile to have a

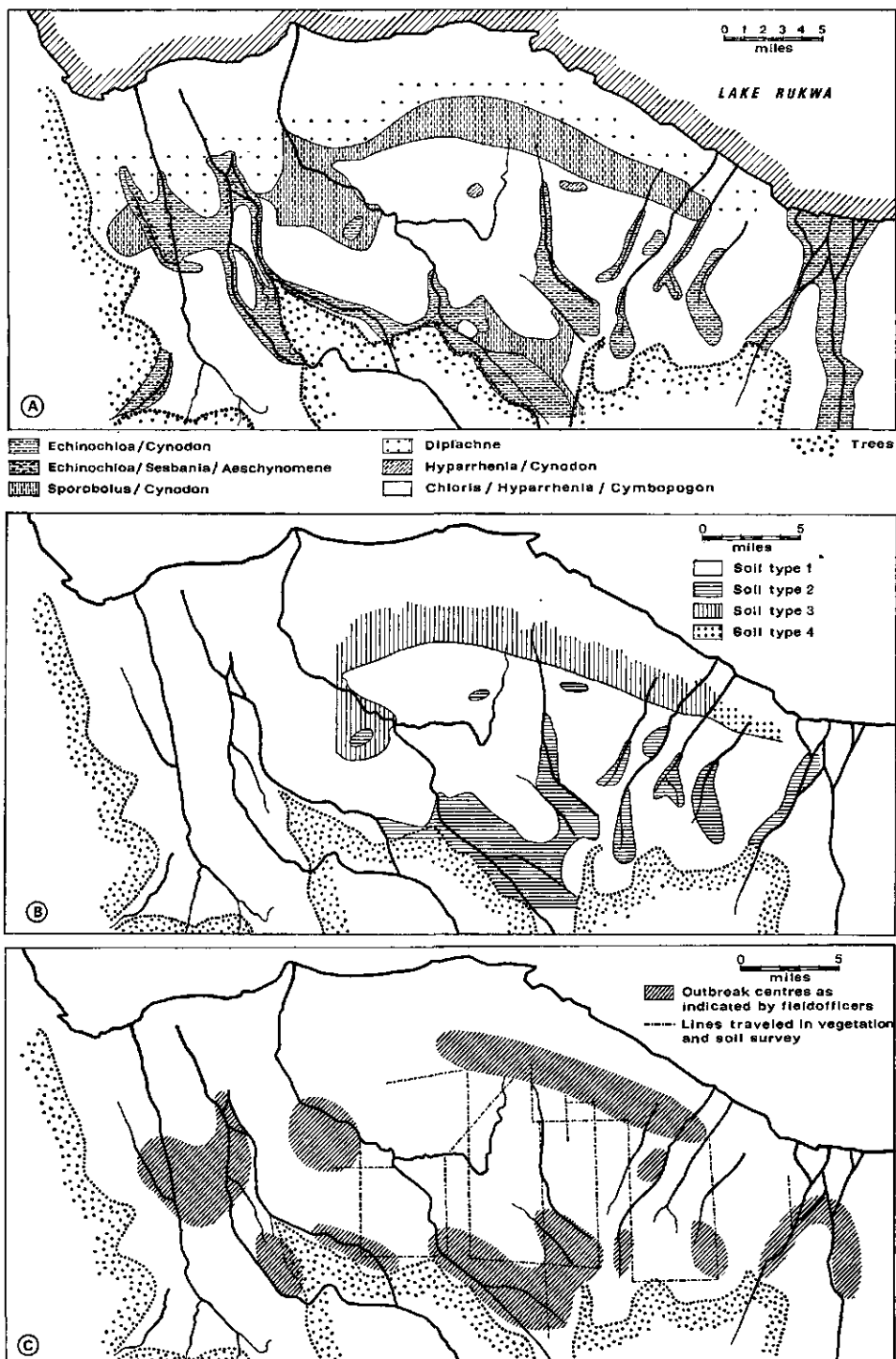


Fig. 20. Vegetation and soil in Central Rukwa, compared with outbreak centres of *Nomadacris*

closer look at various aspects of Central Rukwa, and in particular at the vegetation and the soil.

8.3 Vegetation Zones in Central Rukwa

In September 1962 I carried out a survey of the vegetation and the soil types in that part of Central Rukwa that was accessible. Owing to the unusually high level of the lake at the end of the dry season, the western part of Central Rukwa was still under water and the survey could be carried out only in the eastern half. From personal observations in earlier years, from a vegetation map drawn up by Dean in 1959 and 1960 and from aerial reconnaissance following the 1962 survey, the vegetation map could be made to cover the whole of Central Rukwa.

The survey of the eastern part was carried out along 8 parallel lines, running north/south 2 miles (3.2 km) apart, totalling 54.2 miles (87 km), and 8 lines across with a total length of 31.8 miles (51 km)¹, supplemented with observations made during any travelling about in the plains. At the time of observation most of the grass had been burnt, but recognition of the dominant grasses did not offer any difficulty.

VESEY FITZGERALD (1955a) has given a general description of the types of herbage and of their zonation in Central Rukwa. The results of my more detailed survey (fig. 20 a) agreed with his observations. The following main types of herbage, as characterised by their dominant grasses, were recognised:

- a. Flood-plain grassland, with *Echinochloa pyramidalis* and *Cynodon dactylon*, locally with *Cyperus longus*. *E. pyramidalis* does occur in large pure stands, but usually the two main grasses form a mosaic. This is the common type of vegetation along fresh water drainage lines and in flood basins. In Central Rukwa these flood basins are large shallow depressions, mostly close to the south-western edge of the plains, and usually lying along a river or acting as the source of a river or channel². The basins are drained very slowly and they remain flooded for long periods after each rainy season. *Sporobolus robustus* and rarely *Hyparrhenia rufa* are sometimes found in this herbage, but usually only in zones of transition to other types of grassland. In places that are subject to prolonged and deep flooding often *E. pyramidalis* is found in mosaic with *Sesbania* and *Aeschynomene*.
- b. Lake-shore grassland, in which several zones can be distinguished. First there is a zone of *Sporobolus robustus*, either in pure stands or dominating in a mosaic with *Cynodon dactylon*. Towards the lake there is a broad zone of almost pure *Diplachne fusca*, which at the time of the survey formed the transition to open water. In a few

¹ As indicated in fig. 20 c.

² In North Rukwa there are only two flood basins, which are large, the Bonde la Kavuu, where the Kavuu widens to a large shallow depression on entering the plains, and the Kiboko swamp, a flood basin along the Rungwa river. These areas are of a more swampy nature than the flood basins in Central Rukwa.

places close to the lake shore *Sporobolus spicatus* was found to inhabit small partly bare patches with a very high soda content in the soil¹.

- c. Rain grassland; in usually sharply defined transition zones the vegetation types (a) and (b) merge into the vegetation of the rain grassland, which occupies large parts of Central Rukwa. It is dominated by *Chloris gayana*, *Hyparrhenia rufa* and *Cymbopogon excavatus*. This vegetation is characteristic of areas of higher level. These are not subject to annual flooding, or they are flooded for very short periods only, as a result of local precipitation. In the present period of extraordinary high lake level these areas are still above water.

Usually there are clear transition zones between two types of vegetation. These so-called ecotones are especially distinct in places where there is a sudden drop in level, such as along rivers and channels and along the perimeters of the above mentioned flood basins.

North Rukwa, on the other hand, consists for the major part of virtually continuous flood-plain grassland resembling the Central Rukwa vegetation type (a) with *E. pyramidalis* both in pure stands and in mosaic with *C. dactylon* and *C. longus*; towards the lake shore there is a broad belt of lake-shore grassland, the Central Rukwa type (b). Along the edge of the woodland there are mostly narrow belts of rain grassland in which the mosaic differs somewhat in composition from the corresponding types in Central Rukwa².

8.4 Soil Profiles in Central Rukwa

The soil survey was carried out along the same sample lines that were traversed for the vegetation study. In total 137 samples were taken at irregular distances along the lines, mostly in places where there was a change in vegetation. Examination of the soil was restricted to the top layer of about 8 to 12 in. (20 to 30 cm), which can be considered to be the habitat of the egg-pod. Digging was done with a spade when the soil was moist and with a pick axe where the soil had dried out and was very hard.

There is little doubt that the Central Rukwa plains represent the portion of the original lake bed, on which the river Momba and some smaller rivers deposited their silt³. In the lower lying areas deposition of silt is still taking place. In the course

¹ This grass also colonises the lake bed when the lake recedes.

² At the time of writing (1966) most of the North Rukwa and much of the Central Rukwa plains has been under water for over three years and this has upset the normal pattern of vegetation types. Most submerged parts now have a permanent swamp vegetation with *Echinochloa*, *Sesbania*, *Aeschynomene* and *Vossia*. When the water level goes down the vegetation will no doubt gradually return to the zonation that has been described above.

³ Alluvial deposits along the whole length of the Rukwa trough indicate that previously Lake Rukwa was an extensive and permanent lake (TEALE, 1933) and there is evidence that its water surface reached about 600 ft (185 m) above the present level (GRANTHAM, 1932). It is likely that at that stage Lake Rukwa had an outlet towards Lake Tanganyika. The present valley floor is the former lake bed, which is a 500 ft (150 m) thick layer of silt on the bedrock.

of time the top soil has developed into a black calcareous clay, of the type which in Africa is commonly called 'black cotton soil'. In the elevated areas the underlying soil is a hardly developed white-grey thin-layered soil, which breaks easily into small flakes. It is frequently seen, where it has been brought to the surface by jackals and ant-eaters when they dig their holes. Between this layered subsoil and homogeneous clay there are many intermediate forms. In the flood basins and channels the subsoil is a homogeneous clay, lighter in colour than the topsoil. The toplayer is nowhere less than about 2 in. (5 cm) thick. In the elevated areas it is a grey clay, at the surface often powdery when dry.

The following main types of soil profile could be recognised (fig. 20 b):

1. A-horizon¹: Black or grey-black clay, 3 to 8 in. (8 to 20 cm) thick, often light grey when dry. Few roots from a sparse vegetation, no sod.
B-horizon¹: Brown-black soil with whitish-grey or brown crumbs or flakes, which usually are easy to crumble².
2. A-horizon: Thick layer of black clay, 8 to 24 in. (20 to 60 cm) which is deeply fissured when dry. Usually dense, mainly superficial roots of dense vegetation. Good coherent sod of 2 to 4 in. (5 to 10 cm) thick. Merging into
B-horizon: Fine clay, differing from the A-horizon only in colour, which is more grey.
3. A-horizon: Black or grey-black clay, 5 to 8 in. (12.5 to 20 cm) thick, with superficial roots of medium dense vegetation. Sod, but often less coherent than in 2. Merging into
B-horizon: Mealy, blue-green or yellow-brown, slightly spongy soil. Soils of this type were found only along the lake shore and the difference in appearance with type 2 may be the result of differences in alkalinity, which were found to be considerable (CHALILA, 1959).
4. A-horizon: Grey-white or white powdery soil with a soda crust and little vegetation.
B-horizon: identical to the A-horizon, or similar to the B-horizon of type 3. This soil type is found only in small patches of *Sporobolus spicatus* in the lake-shore grassland.

At the edge of the plains there often is a sharp transition to the more sandy soils of the woodland, a transition which coincides with a sharp increase in level. Distinct transitions between the different soil-profile types were found, and these were clearly associated with changes in ground level.

¹ Most undisturbed soils possess a profile, consisting of definite horizons or layers of soil which differ in their properties. The upper, or A-horizon generally differs appreciably in texture from the B-horizon, which lies below it (KRAMER, 1949). Here only the upper layer of the B-horizon has been examined.

² In places the A-horizon was a grey clay, only 2-4 in. thick (5 to 10 cm), which easily crumbled and pulverised. There the B-horizon was a white soil which fell apart in large flaky crumbs.

In North Rukwa an extensive survey could not be made, but in November and December 1962 I examined the soil profile in several places along the accessible western fringes of the plain. From these and from previous observations it appeared that the major part of North Rukwa has the soil profile type 2, merging into type 3 near the lake. The northern Katwa Makondo and the Lumpungu perimeter plains had a profile which resembled the Central Rukwa type 1, but the vegetation and soil in this area are not very uniform.

8.5 Discussion

A comparison of the distribution of outbreak centres, vegetation types and soil profiles leads to the following conclusions. Firstly, each vegetation type is associated with a particular type of soil profile; the flood-plain grassland with a homogeneous clay profile, the lake-shore grassland with an upper horizon of black clay and a sub-soil of mealy blue-green clay, and the rain grassland with a comparatively thin top layer of grey to black clay and an only partly weathered sub-soil of a flaky or crumbly nature.

Secondly, there were no outbreak centres in the rain grassland. All outbreak centres were either in flood-plain grassland (with *Echinochloa pyramidalis*, *Cynodon dactylon* and *Cyperus longus* as the dominant grasses) or in the *Sporobolus robustus* belt of the lake-shore grassland¹. Both types of grassland are characterised by a thick top layer of alluvial clay over a well-weathered sub-soil, with a dense vegetation of grasses that form a superficial root system which turns the top layer of the soil into a coherent sod.

Thirdly, not only were all outbreak centres in flood-plain grassland, but in Central Rukwa all flood-plain grasslands had been indicated by Forrester and Eyssel as outbreak centres. In North Rukwa, on the other hand, rain grassland is found only in small fringes bordering the woodland and in some perimeter plains, and the main part of the area is occupied by continuous flood-plain grassland; in this area no distinct outbreak centres have been recognised.

In March 1963 an aerial survey was made of the Malagarasi, the Wembere, the Iku and the Mweru wa Ntipa outbreak areas. It confirmed the existence of the zonations of the vegetation as has been described by VESEY FITZGERALD (1955 a) and gave a good impression of the presence and extent of flood-plain grassland in the various sectors. For the Mweru wa Ntipa and the Malagarasi there are I.R.L.C.S. records on incidence and intensity of hopper infestations in the different parts of the area and these records frequently mentioned those sectors that have extensive flood-plain grasslands.

¹ During the dry season in the lake-shore grasslands usually only the *Sporobolus robustus* belt is burnt. At the end of the dry season the unburnt *Diplachne fusca* usually harbours a scattered population which comes to the burnt-off ground after the first rains and probably oviposits mainly along the edge of the unburnt grass. This is probably the explanation of the elongated shape of the outbreak centre in the *Sporobolus* belt.

Thus, there appears to be a close link between hopper incidence and flood-plain grassland. The impression I received from the comparison of the North and Central Rukwa grasslands and the other outbreak areas would certainly suggest a sequence in importance, similar to that given in fig. 20. It could well be, therefore, that the level of productiveness of an outbreak area depends on the relative extent of flood-plain grassland in that area.

The nature of this apparent link between hopper incidence and flood-plain grassland is not at all clear. One could suggest a number of possible explanations, such as a laying preference of females for flood-plain grassland, more successful incubation of eggs in flood-plain soil, or a higher hopper mortality in rain grassland (*e.g.* correlated with distribution of Stork and Egret). From a number of observations and small experiments¹ I would be inclined to think that in the flood-plain grassland soils the moisture conditions during incubation could well be favourable compared to those in the rain grassland soil. Much more detailed research, however, would be required to decide whether this is so.

Assuming then that the basic characteristic of an outbreak area is the existence of large areas of flood-plain grassland, one could use this criterium for recognising potential outbreak areas. VESEY FITZGERALD (in DU PLESSIS, 1962) has drawn up a list of suspected outbreak areas, basing his survey on evidence of impeded drainage, occurrence of irregular flooding and the resulting natural grasslands, and the presence of a resident locust population. Listing all areas with large stands of flood-plain grassland, that can be found on the available soil and vegetation maps², one comes to a list which is almost identical to Vesey FitzGerald's. In my opinion it would be wise to inspect all these areas when the conditions appear to be favourable for upsurges.

Finally considering the original aim of this research programme, it is clear that it will be extremely difficult, if not impossible to develop an ecological method which will effectively control *Nomadacris* in its outbreak areas.

A number of ecological approaches have been tried which have been described by ROBERTSON (1958 b) and GUNN (1960). These trials included the use of cattle to change the grassland, the planting of trees in the plains to reduce the area of grassland, and fire control to reduce the available breeding ground. All these schemes had to be abandoned as they turned out to be either too costly, or impracticable or too unreliable.

It should be realised that a very important feature of the outbreak areas is their ecological instability. The effects of the alternation of a wet and a dry season, and of periods of dry and of wet years, are amplified by the impeded or the closed drainage. The resulting enormous changes in water regime during the year and from year to

¹ Laid down in an unpublished report (I.R.L.C.S. library).

² MILNE, 1936; TRAPNELL, MARTIN and ALLAN, 1950; Atlas of Tanganyika, 1956; Atlas of the Federation of Rhodesia and Nyassaland, 1962.

year create the conditions required for the dramatic fluctuations in numbers which we would like to prevent. When in an outbreak area the water level is high over a period of years (as in the Mweru wa Ntipa since 1957 and in the Rukwa plains since 1962) the locust population remains at a low level and does not require much, if any control. It is, therefore, not surprising that the only ecological method of control that appeared to have success was the stabilisation of the conditions in the Iku plains by the raising of the water level through building the Katuma dam. There is little doubt that stabilising ecological conditions by raising the water to such a level that temporary flooding occurs only over a limited area every year, will drastically reduce the chance of a build-up to swarm density. Not only will the available breeding ground be reduced to the areas of rain grassland, but the predator populations will be stabilised mostly at a high level; in addition the predators will tend to concentrate in the remaining grass margins around the water, which constitute the hopper nursery areas.

It has been said that raising the water level would create new outbreak areas by converting the woodland bordering the plains into grassland. This need not happen if one would succeed in stabilising the water at such a level that the annual alternation of flooding and drying-up in the flat parts of an area is prevented, but this will not be easy. Also, along the perimeters of most outbreak areas the changes in ground level are sharp and a change in water level of several feet will make little difference in the size of the area that is flooded.

A stabilisation scheme can be devised only for outbreak areas the drainage of which is impeded, by impeding the drainage even more. This has been done in the Iku area and a similar solution may be feasible for the Wembere depression by blocking the only outlet through the Sekenke ridge. The Malagarasi region and the Kafue flats could in theory also be eliminated as outbreak areas by building a weir across the rivers, but this will be both difficult and costly.

Outbreak areas that form the bottom of a closed drainage can be flooded only if an additional source of water could be found. For the Rukwa Valley such a source is not available. The Mweru wa Ntipa, however, is bypassed at close range by the Kalungwishi river. It was by building a weir in this river, and when necessary diverting part of its water into the Mweru wa Ntipa (via the Mofwe dambo), that a flooding scheme proposed to stabilise the water at a high level and to prevent the occasional drying up of the area, which when it happens brings the fishing industry to a halt and presents the Red Locust with a sudden expanse of favourable breeding ground.

Such a stabilisation scheme, however, would be very costly and since chemical control has developed into an efficient, relatively cheap and probably reasonably fool-proof method, it remains doubtful whether the savings resulting from a flooding scheme would warrant the costs.

Summary

This paper describes five years of research on the population dynamics of the Red Locust (*Nomadacris septemfasciata*) in its outbreak areas. These areas are extensive flat grasslands on alluvial clay soils, badly drained and consequently flooded annually, in a region of one rainy season per year, and situated in western Tanzania (formerly Tanganyika) and northern Zambia (formerly Northern Rhodesia). The research concentrated on three problems: (1) Which mortality factors affect a Red Locust population during the successive stages of its one year life cycle? (2) How can it be explained, that the observed violent fluctuations in numbers from one generation to the next are inversely correlated with the rainfall total in the last but one rainy season, as it has been demonstrated by SYMMONS (1958)? and (3). Why is it that there are differences in productiveness between the outbreak areas?

The correlation with the rainfall indicated that the crucial reductions take place somewhere between the maturation of the parents and the emergence of the imagines of the filial population. This was confirmed by the data, that were obtained on the numerical reductions as well as on the mortality causes.

It appeared that there can be fairly large variations in fecundity of the parent population from year to year, but it is thought unlikely that these are responsible for the observed fluctuations in multiplication rate. During the incubation egg mortality can be caused by extremes in rainfall, in particular a general and prolonged drought being not uncommon. Both drought and early flooding are able to bring about considerable reductions in numbers, but neither can be anything more than an unpredictable calamity. The really drastic and consistent reductions appeared to take place during the first and second-hopper instars.

Robberflies (Asilidae) and some species of dragonflies (Odonata) were thought to be mainly responsible. The population level of the Asilidae is not correlated with the rainfall in the last but one rainy season. However, both earlier researches on the life cycle of Odonata in the tropics and the authors own observations indicate that the population level of Odonata is likely to be positively correlated with the previous years rainfall, dependent as their larval stages are on the duration of the annual flooding in the outbreak-area grasslands. The Odonata species that prey on the Red Locust hoppers could, therefore, well be the most important agent in the fluctuations in the locust's breeding success.

Normally, mortalities among third to sixth-instar hoppers appeared to be negligible, only Stork and Egret being able to inflict appreciable losses, but rarely doing so.

A close comparison of the two best studied outbreak areas, the North and the

Central Rukwa plains around Lake Rukwa (Tanzania), revealed the probable existence of outbreak centres within the outbreak areas. These outbreak centres appear to be closely linked with flood-plain grassland and with part of the lake-shore grassland. Why this is so, did not become clear, but it is postulated that differences in incubation success, correlated with different moisture conditions, may be responsible.

It is considered unlikely that the research on the ecology of *Nomadacris septemfasciata* will lead to an economically feasible ecological method of control in the outbreak areas.

Samenvatting

Dit artikel beschrijft vijf jaren onderzoek naar de populatiedynamica van de rode sprinkhaan (*Nomadacris septemfasciata*, SERVILLE) in zijn uitzwermgebieden. Deze gebieden liggen in het westelijk deel van Tanzania (vroeger Tanganyika) en in noord Zambia (vroeger Noord-Rhodesia), in een deel van Afrika dat één regenseizoen per jaar heeft, van November tot April. Het zijn zeer uitgestrekte, volkomen vlakke graslanden op alluviale kleigronden, die een zo slechte afwatering hebben dat ze ieder jaar geheel of gedeeltelijk onder water komen te staan.

Het onderzoek concentreerde zich op drie problemen: 1. Welke mortaliteits- en reductiefactoren werken in op een sprinkhanenpopulatie gedurende de opeenvolgende stadia in de eenjarige levenscyclus? 2. Wat is de verklaring van de zeer sterke schommelingen in aantallen van de ene generatie op de andere, die volgens SYMMONS (1958) een negatieve correlatie vertonen met de regenval in het vorige regenseizoen? 3. Hoe komt het dat de uitzwermgebieden zo sterk verschillen in zwermproductie?

De correlatie tussen populatieschommelingen en regenval maakte het waarschijnlijk dat de beslissende aantalsreducties plaatsvinden ergens tussen de geslachtelijke rijping van de ouders in november en het verschijnen van de imagines van de volgende generatie in februari/maart. Dit vond bevestiging in waarnemingen over de aantalsverminderingen in de verschillende levensstadia, alsook in die over de oorzaken van de mortaliteiten.

Het bleek dat de fecunditeit van de ouderpopulatie van jaar tot jaar sterk kan variëren, maar het lijkt onwaarschijnlijk dat deze variaties verantwoordelijk zijn voor de waargenomen verschillen in vermenigvuldiging van één generatie tot de volgende. Gedurende de incubatie van de eieren kan een teveel of een tekort aan neerslag ei-sterfte veroorzaken, met name droogte komt nogal eens voor. In beide gevallen kan een grote reductie in aantallen het gevolg zijn, maar regenval kan hier niet als direct regulerende factor optreden. Aanzienlijke en geregelde verminderingen van aantallen bleken op te treden in de eerste twee larvale stadia. Roofvliegen (*Asilidae*) en een aantal libellesoorten leken de voornaamste veroorzakers van deze mortaliteiten te zijn. Het populatieniveau van de Asiliden kan niet positief gecorreleerd zijn met de regenval in het vorig seizoen, maar zowel vroegere onderzoekingen als eigen observaties over de levenscyclus van de Odonata in de tropen leiden tot de conclusie dat het populatieniveau van deze insecten zeer wel een positieve correlatie met de regenval kan hebben, omdat het voltooien van de larvale stadia afhankelijk is van de duur van de jaarlijkse inundatie der uitzwermgebieden. De Odonata die op *Nomadacris* prederen zouden daarom heel goed de belangrijkste factor kunnen zijn in de aantals-

fluctuaties van deze sprinkhaan.

De mortaliteit gedurende de laatste vier larvale stadia bleek onbelangrijk te zijn, alleen ooievaars en veereigers kunnen lokaal een grote sterfte veroorzaken, maar dit is uitzondering.

Een vergelijkende studie van de twee best bestudeerde uitzwermgebieden, de grasvlakten van Noord en van Centraal Rukwa rondom het Rukwameer (Tanzania), onthulde dat er waarschijnlijk binnen een uitzwermgebied uitzwermcentra bestaan. Deze centra vallen samen met bepaalde vegetatie- en bodemtypen, die gevonden worden in die delen van de grasvlakten die jaarlijks langdurig geïnundeerd zijn. Het werd niet duidelijk waarom dit zo is, maar het is mogelijk dat de oorzaak ligt in verschillen in incubatiesucces van de eieren, samenhangend met verschillen in bodemvochtigheid.

Het lijkt niet waarschijnlijk dat verder onderzoek naar de ecologie van *Nomadacris* zal kunnen leiden tot een economisch verantwoorde vorm van ecologische bestrijding van het insect.

References

- ALBRECHT, F. O. 1956a Limitation des effectifs chez un acridien: influence de la sécheresse sur les oeufs de *Nomadacris septemfasciata* (SERV.). *Locusta* 4: 1-21.
- ALBRECHT, F. O. 1956b The anatomy of the Red Locust. *Anti Locust Bull.* no. 23, 9 pp.
- ALBRECHT, F. O. 1959 Facteurs internes et fluctuations des effectifs chez *Nomadacris septemfasciata* (SERV.). *Bull. biol. France et Belgique* 4: 414-461.
- ATLAS 1956 Atlas of Tanganyika. Depart. of Land and Surveys, Dar es Salaam.
- ATLAS 1962 Atlas of the Federation of Rhodesia and Nyassaland. Federal Depart. of Trigonometrical and Topographical Surveys. Salisbury.
- BACKLUND, H. O. 1955a Small patches with permanent Red Locust population in Northern Tanganyika Territory. *E. Afr. agric. J.* 20: 202-204.
- BACKLUND, H. O. 1955b Red Locusts and vegetation. *Oikos* 6: 124-148.
- BACKLUND, H. O. 1956 Aspects and successions of some grassland vegetation in the Rukwa Valley, a permanent breeding area of the Red Locust. *Oikos*, Suppl. 2, 132 pp.
- BREDO, H. J. (1947) Report on the control measures and their organisation against the Red Locust in the outbreak centres Mweru wa Ntupa and Rukwa since 1938. 60 pp. (Unpublished).
- BURNETT, G. F. 1951 Observations on the life-history of the Red Locust, *Nomadacris septemfasciata*, (SERV.) in the solitary phase. *Bull. ent. Res.* 42: 473-490.
- CANNING, E. 1956 A new Eugregarine of locusts, *Gregarina garnhami* n. sp., parasitic in *Schistocerca gregaria* FORSK. *J. Protozool.* 3: 50-62.
- CASIMIR, M. 1962 History of outbreaks of the Australian plague locust, *Chortoicetes terminifera* (WALK.), between 1933 and 1959, and analysis of the influence of rainfall on these outbreaks. *Austr. J. Agric. Res.* 13: 674-700.
- CHALILA, S. E. (1959) A short report on soil sampling at Kafukola, Central Rukwa. Unpublished report, 3pp.
- CHAPMAN, R. F. 1959 Observations on the flight activity of the Red Locust, *Nomadacris septemfasciata* (SERVILLE). *Behaviour* 14: 300-334.
- CHAPMAN, R. F. 1962 *Ceracia nomadacridis* VAN EMDEN (Diptera: Tachinidae) parasitising *Nomadacris septemfasciata* (SERVILLE) (Orthoptera: Acrididae). *Proc. R. Ent. Soc. Lond. (A)* 37: 69-71.
- CHAPMAN, R. F. (1963) Microclimate in a locust habitat. Unpublished report I.R.L.C.S. library.
- CHAPMAN, R. F. and I. A. D. ROBERTSON 1958 The egg-pods of some tropical African grasshoppers. *J. ent. Soc. S. Africa* 21: 85-112.

- CLAUSEN, C. P. 1940 Entomophagous insects. McGraw-Hill Book Cy, New York, Toronto, London.
- CORBET, P. S. 1962 A biology of dragonflies. Witherby, London.
- DEAN, G. J. W. 1963 Field trials with a persistent stomach insecticide against populations of the Red Locust, *Nomadacris septemfasciata* (SERV.) in an outbreak area. *Bull. ent. Res.* 54: 349-359.
- DEAN, G. J. W. 1964 Stork and egret as predators of the Red Locust in the Rukwa Valley outbreak area. *Ostrich* 35: 95-100.
- DEAN, G. J. W. 1967a Grasslands of the Rukwa Valley. *J. appl. Ecol.*, 4: 45-57.
- DEAN, G. J. W. 1967b Observations on the structure of hopper bands and movement of hoppers of the Red Locust (*Nomadacris septemfasciata* Serville). *J. ent. Soc. S. Africa*, 80: 1-17.
- DU PLESSIS, C. (1959) (1960) (1961) Annual Reports of the Director I.R.L.C.S. Unpublished.
- FAURE, J. C. 1955 The life history of the Red Locust (*Nomadacris septemfasciata* SERVILE) Sci. Bull. Dep. Agric. S. Afr. 144: 32 pp.
- GAMBLES, R. M. 1960 Seasonal distribution and longevity in Nigerian dragonflies. *J. W. Afr. Sci. Ass.* 6: 18-26
- GARDNER, A. E. 1956 The biology of dragonflies. Proc. S. Lond. ent. nat. Hist. Soc. 1954-55: 109-134.
- GRANTHAM, D. R. 1932 The Lupa goldfield. Bull. Geol. Surv. Dept. Tanganyika Territory, 3: 1-34.
- GREATHEAD, D. J. 1966 A brief survey of the effects of biotic factors on populations of the desert locust. *J. Appl. Ecol.* 3: 239-250.
- GUNN, D. L. 1955a Mweru wa Ntipa and the Red Locust. *N. Rhod. J. Livingstone*, 2 (6): 3-15.
- GUNN, D. L. 1956 A history of Lake Rukwa and the Red Locust. Tanganyika Notes, 42: 1-18.
- GUNN, D. L. 1957 The story of the International Red Locust Control Service. *Rhod. agric. J.* 54: 8-24.
- GUNN, D. L. 1960 Nomad encompassed. *J. Ent. Soc. S. Africa*, 23: 65-125.
- GUNN, D. L. a.o. 1948 Locust control by aircraft in Tanganyika. Int. Red Locust Control Org., Abercorn, 153 pp.
- GUNN, D. L. AND P. M. SYMMONS 1959 Forecasting of locust outbreaks. *Nature, Lond.*, 184: 1425.
- HOBBY, B. M. 1935 Rhodesian Asilidae (Diptera) and their prey, collected by C. F. M. Swynnerton. *J. Anim Ecol.* 4: 90-112.
- HODGKIN, E. P. AND J. A. L. WATSON 1958 Breeding of dragonflies in temporary waters. *Nature, Lond.*, 181: 1015-1016.
- HULL, F. M. 1962 Robberflies of the World, the genera of the family Asilidae. Bull. Smithsonian. Inst. no. 224, 907 pp.
- HUSAIN, M. A., T. AHMAD and C. B. MATHUR 1941 Studies on *Schistocerca gregaria* FORSK. X. Role of water in the bionomics of the Desert Locust. *Indian J. agric. Sci.*, 10 (1940): 927-944.
- HUNTER JONES, P. M. 1964 Egg development in the Desert Locust *Schistocerca gregaria* (FORSK), in relation to the availability of water. *Proc. R. ent. Soc. Lond. (A)* 39:
- IMMS, A. D. 1951 A general text book of Entomology. Methuan and Co., London.
- KRAMER, P. J. 1949 Plant and soil water relationships. McGraw-Hill Book Cy, New York, Toronto, London.

- LEA, A. 1958 Recent outbreaks of the Brown locust, *Locustana pardalina* WALK, with special reference to the influence of rainfall. *J. Ent. Soc. S. Afr.* 21: 163-213.
- LEA, A. and D. VAN V. WEBB 1939 Field observations on the Red Locust at Lake Rukwa in 1936 and 1937. *Sci. Bull. Dep. Agric. S. Afr.* 189: 81 pp.
- LER, P. A. 1958 The biology of an Asilid feeding on Acrididae. *Dokl. Kazakh. Akad. Selskokhoz Nauk, Alma Ata* 3: 16-23.
- LLOYD, J. H. 1959 Operational research on preventive control of the Red Locust (*Nomadacris septemfasciata* SERVILE) by insecticides. *Anti-Locust Bull.* 35: 65 pp.
- MC MARTIN, A. 1935a The South African Locust fungus. *Publ. S. Afr. Sugar Ass.*
- MC MARTIN, A. 1935b The Natural Enemies of locusts. *S. Afr. Dep. Agric.*
- MICHELMOORE, A. P. G. (1936) Locust Investigations in Tanganyika. Report no. 4, Confidential report Ec. Adv. Council, Committee on locust control. Unpublished.
- MICHELMOORE, A. P. G. and W. ALLAN 1934 Observations on phases of the Red-winged Locust in Northern Rhodesia. *Bull. ent. Res.* 25: 101-128.
- MILNE, G. 1936 A provisional soil map of East Africa. Crown Agents, London.
- MILNE, G. (1937) Soils from the flood-plain of Lake Rukwa, Tanganyika Territory. Unpublished report I.R.L.C.S. library.
- MORANT, V. 1947 Migrations and breeding of the Red Locust (*Nomadacris septemfasciata*, SERVILE) in Africa, 1927-1945. *Anti-Locust Memoir* 2, 60 pp.
- MORRIS, R. F. 1959 Single factor analysis in population dynamics. *Ecology*, 40: 580-588.
- MOSSOP, M. C. 1951 A patch of Red Locusts persisting in Southern Rhodesia. *Rhod. Agric. J.* 48: 327-329.
- NORRIS, M. J. 1959 The reproduction of the Red Locust (*Nomadacris septemfasciata* SERVILE) in the laboratory. *Anti-Locust Bull.* 36, 46 pp.
- PINHEY, E. C. G. 1961 Dragonflies (Odonata) of Central Africa. *Occas. papers Rhodes-Livingstone Museum* 14, 97 pp.
- PRITCHARD, G. 1966 On the morphology of the compound eyes of dragonflies (Odonata: Anisoptera), with special reference to their role in prey capture. *Proc. R. ent. Soc. Lond. (A)* 41: 1-8.
- RICARDO, C. K. 1938 The fishes of Lake Rukwa. *J. Linnean Soc. London* 40: 625-657.
- ROBERTSON, I.A.D. 1954 The numbers of eggs in pods of the Red Locust *Nomadacris septemfasciata* (SERVILLE) (Orth., Acrididae). *Ent. mon. Mag.* 90: 254-255.
- ROBERTSON, I. A. D. 1958a The reproduction of the Red Locust, *Nomadacris septemfasciata* (SERVILLE), (Orthoptera, Acrididae), in an outbreak area. *Bull. ent. Res.* 49, 479-496.
- ROBERTSON, I. A. D. 1958b Tree-planting trials for the control of the Red Locust (*Nomadacris septemfasciata*) in the Rukwa Valley, Tanganyika. *E. Afr. agric. J.* 23: 172-178.
- SCHAEFER, E. E. 1936 The white fungus disease (*Beauveria bassiana*) among Red Locusts in South Africa and some observations on the grey fungus disease (*Empusa grylli*). *Sci. Bull. Dep. Agric. S. Afr.* 160, 28 pp.

- SCHEEPERS, C. C., and D. L. GUNN 1958 Enumerating populations of adults of the Red Locust, *Nomadacris septemfasciata* (SERVILLE) in its outbreak areas in East and Central Africa. *Bull. ent. Res.* 49: 273-285.
- SCHWERDTFEGER, F. 1958 Is the density of animal populations regulated by mechanisms or by chance? *Proc. 10th Int. Congr. Ent.*, Montreal 1956, 4: 115-122.
- SHULOV, A. and M. P. PENER 1963 Studies on the development of eggs of the Desert Locust (*Schistocerca gregaria* FORSKAL) and its interruption under particular conditions of humidity. *Anti-Locust Bull.* 41, 59 pp.
- SKAIFE, S. 1925 The locust fungus *Empusa grylli*, and its effect on its host. *S. African J. Science*, 22: 298-308.
- SPRADBERY, J. P. (1960) The durations of the instars and the level and distribution of mortality in *Schistocerca gregaria* FORSK. and *Nomadacris septemfasciata* SERV. Unpublished report, 47 pp.
- STORTENBEKER, C. W. (in prep.) *Ceracia nomadacridis* VAN EMDEN (Diptera: Tachinidae) parasitising *Nomadacris septemfasciata* (SERVILLE) (Orthoptera: Acrididae).
- STORTENBEKER, C. W. (in prep.) Morphometrical data on the Red Locust.
- STOWER, W. J., G. B. POPOV and D. J. GREATHEAD 1958 Oviposition behaviour and egg mortality of the Desert Locust (*Schistocerca gregaria* FORSKAL) on the coast of Eritrea. *Anti-Locust Bull.* 30, 33 pp.
- SYMMONS, P. M. 1959 The effect of climate and weather on the numbers of the Red Locust in the Rukwa Valley outbreak area. *Bull. ent. Res.* 50: 507-521.
- SYMMONS, P. M. (1962) The effect of climate and weather on numbers of the Red Locust, *Nomadacris septemfasciata* (SERV.) in its outbreak areas. Unpublished M. Sc. thesis.
- SYMMONS, P. M. (1964) The dynamics of the most recent plague of the Red Locust, *Nomadacris septemfasciata* (SERVILLE), with special reference to the importance of climate and weather. Unpublished Ph. D. thesis.
- SYMMONS, P. M. and A. J. M. CARNEGIE 1959 Some factors affecting breeding and oviposition of the Red Locust, *Nomadacris septemfasciata* (SERV.). *Bull. ent. Res.* 50: 333-353.
- SYMMONS, P. M., G. J. W. DEAN and C. W. STORTENBEKER 1963 The assessment of the size of populations of adults of the Red Locust, *Nomadacris septemfasciata* (SERVILLE) in an outbreak area. *Bull. ent. Res.* 54: 549-569.
- TEALE, E. C. 1933 Provisional geological map of Tanganyika with explanatory notes. *Bull. Geol. Surv. Dep. Tanganyika Territory* 6, 34 pp.
- TRAPNELL, C. G., J. D. MARTIN and W. ALLAN 1950 Vegetation and soil map of Northern Rhodesia.
- UVAROV, B. P. 1928 Locusts and Grasshoppers. A handbook for their study and control. London, Imperial Bureau of Entomology, 352 pp.
- VARLEY, C. G. and G. R. GRADWELL 1960 Key factors in population studies. *J. Anim. Ecol.* 29, 399-401.
- VESEY FITZGERALD, D. F. 1954 Survey of Red Locust habitats and incidence in the Cham-beshi Valley, Northern Rhodesia. Unpublished report I.R.L.C.S. library.

- VESEY FITZGERALD, D. F. 1955a The vegetation of the outbreak areas of the Red Locust (*Nomadacris septemfasciata*, SERVILE) in Tanganyika and Northern Rhodesia. *Anti-Locust Bull.* 20, 31 pp.
- VESEY FITZGERALD, D. F. 1955b Birds as predators of the Red Locust *Nomadacris septemfasciata* (SERVILLE). *Ostrich*, 26: 128-133.
- VESEY FITZGERALD, D. F. 1961 Red Locust reconnaissance in Bechuanaland during March 1961. Unpublished report I.R.L.C.S. library.
- VESEY FITZGERALD, D. F. 1963a Report on a visit to the grasslands in the Kafue flats and around lake Chilwa. Unpublished report I.R.L.C.S. library.
- VESEY FITZGERALD, D. F. 1963b Central African Grasslands. *J. Ecol.* 51, 243-274.
- WALOFF, N. 1954 The number and development of ovarioles of some Acrididae in relation to climate. *Physiol. comp.* 3: 370-390.
- WOODROW, D. F. 1965a Observations on the Red Locust (*Nomadacris septemfasciata* SERV.) in the Rukwa Valley, Tanganyika, during its breeding season. *J. Anim. Ec.* 34, 187-200.
- WOODROW, D. F. 1965b Laboratory analysis of oviposition behaviour in the Red Locust *Nomadacris septemfasciata* (SERV.). *Bull. ent. Res.* 55: 733-745.
- YATES, F. 1949 Sampling methods for censuses and surveys. Griffin, London.
- ZAHNER, R. 1959 Über die Bindung der Mitteleuropäischen Calopteryx - Arten (Odonata-Zygoptera) an den Lebensraum des strömenden Wassers. I. Der Anteil der Larven an der Biotopbindung. *Int. Rev. Hydrobiol.* 44: 51-130.

Invloed van de kopertoestand van de grond op het
kopergehalte van gras en klaver

Verslagen van Landbouwkundige Onderzoeken 695