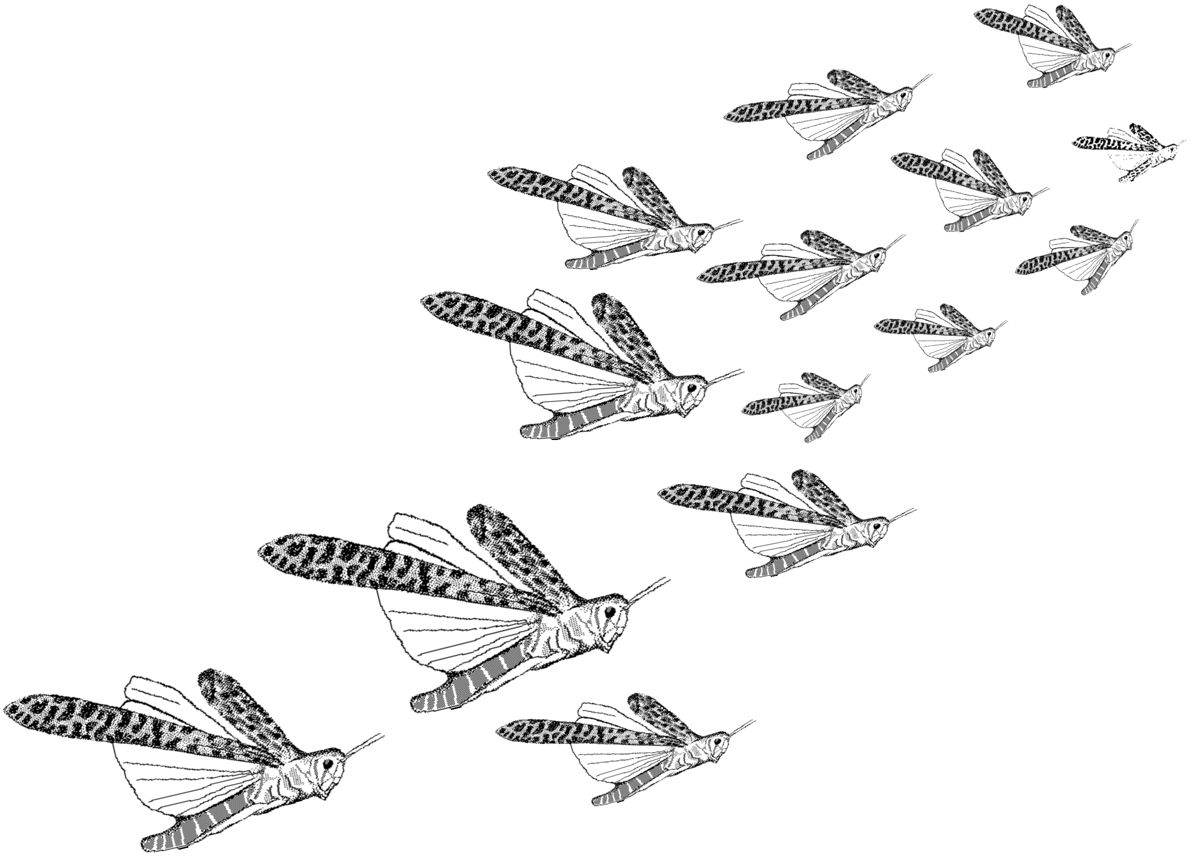
THE DESERT LOCUST GUIDELINES

I. BIOLOGY AND BEHAVIOUR



Food and Agriculture Organization
of the United Nations

THE DESERT LOCUST GUIDELINES

I. BIOLOGY AND BEHAVIOUR

Food and Agriculture Organization of the United Nations
Rome, 1994

Contents

Preface

The most recent Desert Locust plague of 1986-89 demonstrated once again the capacity of this ancient pest to threaten agriculture over large parts of Africa, the Near East and South-West Asia. It emphasized the need for a permanent system of well organised surveys of areas which have recently received rains or have been flooded, and backed up by control forces capable of treating hoppers and adults efficiently, effectively and in an environmentally safe manner.

The events of 1986-89 showed that in many instances the existing strategy of preventive control did not function well, for reasons ranging from the inexperience of the field survey teams and lack of understanding of Ultra Low Volume spraying, insufficient or inappropriate resources and the inaccessibility of some important breeding areas to the inexperience of campaign organisers.

Given the certainty that there will be future Desert Locust upsurges, FAO undertook to produce a series of guidelines primarily for use by National and International organisations and institutes involved in Desert Locust survey and control. The guideline set comprises:

I. Biology and Behaviour

II. Survey

III. Information and Forecasting

IV. Control

V. Campaign Organization and Execution

The guidelines have been largely prepared by P. M. Symmons, a former Head of the Desert Locust Information Service at the Anti-Locust Research Centre in London and the first Director of the Australian Plague Locust Commission, with the assistance of K. Cressman, FAO Locust Survey and Forecasting Officer.

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Acknowledgments

FAO is especially grateful to P. Symmons who produced this Guideline, and to K. Cressman who prepared the text and the illustrations. FAO would also like to thank J. Roffey for his advice and criticism.

1. What are locusts?

Locusts are members of the grasshopper family *Acrididae*, which includes most of the short-horned grasshoppers. Locusts differ from grasshoppers because they have the ability to change their behaviour and physiology, in particular their colour and shape (morphology) in response to changes in density. Adult locusts can form swarms which may contain thousands of millions of individuals and which behave as a unit. The non-flying nymphal or 'hopper' stage can form bands. A band is a cohesive mass of hoppers which persists and moves as a unit. Grasshoppers form neither bands nor true swarms. However, the distinction between locusts and grasshoppers is not clear-cut. There are some species, such as *Oedaleus senegalensis*, which occasionally form small loose swarms. There are 'locusts' such as the Tree Locust which have never been known to form bands. Some species which are undoubtedly locusts, such as the Australian Plague Locust, do not change shape and colour in response to changes in density.

The different states are called phases: the solitarious phase when individuals are at low densities; the gregarious phase when they are at high densities. The transition from the solitarious phase to the gregarious and vice versa is called the 'transient' phase.

The behavioural change can take place rapidly particularly in the case of Desert Locust. In the laboratory locusts which have been reared in isolation try to avoid each other when first put into a cage, but in trying to avoid one locust they come into contact with another. Within approximately half an hour the locusts are found clustered together; they have 'learned' to behave gregariously. Morphological changes, on the other hand, take more time. The full gregarious colour takes one 'crowded' generation to develop and shape takes two or more. The extreme forms found in the field cannot be reproduced in the laboratory.

These differences in the rates of development of the different manifestations of phase often lead to confusion. For example, it is possible to find swarms of solitary (colour) locusts. It is best to restrict the terms gregarious and solitary (or solitarious) to behaviour, and to use gregaricolor (and solitaricolor) for their colours and gregariform (and solitariform) for their shape. Starting with solitary individuals, the capacity to behave gregariously may increase over several generations of crowding since during upsurges swarms and bands become progressively larger and more cohesive.

It is important to remember that phase is essentially a behavioural phenomenon; the colour change and shape change follow the behavioural change. That is, colour and shape are an indication of how the Desert Locusts have been behaving, but not a reliable guide to how the locusts will behave.

There is a progressive difference in shape from the extreme solitariform to the extreme gregariform. This is measured by the ratios of the forewing (elytron, *E*) to the third segment of the rear leg (femur, *F*) and the ratio of the femur to the width of the head (or caput, *C*). The ratios are different for the males and females and can be influenced by the temperature. A measure derived from multiva-

Equation	**Solitarious**	**Gregarious**
males: $0.067002 - 0.004173\,E - 0.057575\,F + 0.224514\,C$	extreme: -0.2	extreme: 0.25
females: $0.031050 - 0.003534\,E - 0.046770\,F + 0.190706\,C$	extreme: -0.2	extreme: 0.25
F / C	male: >3.75	male: <3.15
	female: >3.85	female: <3.15
E / F	male: <2.025	male: >2.225
	female: <2.075	female: >2.272
note: < indicates less than, > indicates greater than.		
female E / male E	1.17 - 1.24	1.07 - 1.12

Figure 1. Three methods for determining phase characteristics of the Desert Locust using morphological measurements.

riate analysis has been worked out using E, F and C but could be derived using any number of variables. Several equations for the sexes are presented in Figure 1.

Each equation gives values ranging from approximately -0.2 for extreme solitary forms to +0.25 for extreme gregarious forms.

In the past, much effort was expended in measuring locusts, but because of the influence of factors other than density, the value of such measurements is limited. Morphometrics can demonstrate the development of an upsurge if samples are available from each generation. A gregariform individual may suggest the presence of swarms in the area recently.

2. The life cycle

The Desert Locust like all other locusts and grasshoppers, passes through three stages: adult, egg, and nymph (hopper).

2.1 Oviposition and incubation

The female lays eggs in batches called egg-pods; the eggs look rather like rice grains and are arranged like a miniature hand of bananas. The female bores into the ground with the valves at the rear of the abdomen and deposits a batch of eggs. She then fills up the hole above the eggs with a plug of froth. The pod is about 5 cm long and is laid with its top 5-10 cm below the surface. This is a surprising depth which requires a great extension of the abdomen (Fig. 2). The Desert Locust lays pods containing less than 80 eggs in the gregarious phase and between 95 and 158 in the solitarious phase.

2.1.1 Oviposition behaviour

The eggs are initially laid in bare ground and often, but not exclusively, in sandy soil. As a rule, the female will not lay unless the soil is moist at about 5-10 cm below the surface. In soft sandy soils, females have been known to lay when soil moisture is only found at

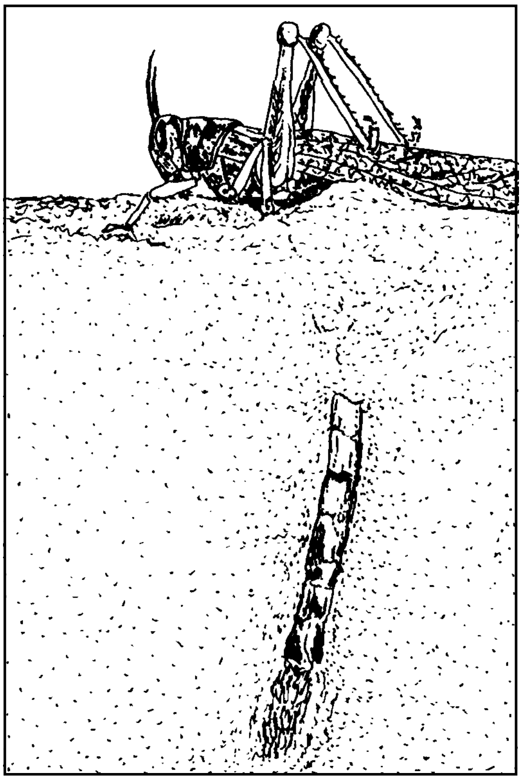

Figure 2. Ovipositing female of the Desert Locust.

depths below 12 cm. Before laying the female often carries out test probing. It is important to realize that laying is not always occurring when the females are seen probing. The only sure test is to dig to check whether pods have been laid.

Experienced Field Officers will know where laying is most likely to have occurred, but these preferred sites will not have exactly the same characteristics in different parts of the infestation area. Moreover, locusts sometimes lay in habitats they usually avoid.

Swarms often lay egg-pods in dense groups, with tens and even hundreds of pods per square metre. The males, together with females which are not ready to lay, may move on. As a result, large swarms split up and males may become separated from females. Laboratory tests show that a laying female leaves a scent which attracts others to lay nearby. In the field, however, it is thought that sight is more important than scent in attracting females to those already laying. This gregarious behaviour means that laying occurs in only a small number of the apparently suitable sites.

2.1.2 Life expectation of mature locusts - number of pods laid by a female

The number of egg-pods a female lays depends on how long it takes for her to develop a pod and how long the female lives. The time between layings in the field has not been studied in detail but it is probably about 10 days. Very little is known from direct observation about life expectation. However, adults become rare some six or seven weeks after the first well synchronized laying except perhaps where temperatures are low. This suggests that nearly all females will lay one pod, about three-quarters will survive to lay a second, and perhaps a quarter to lay a third but very few indeed will manage to lay four pods. That would mean an average of two pods per female. Assuming an average of 70 eggs per pod in the gregarious phase, the potential multiplication rate would then be roughly 70, assuming equal numbers of males and females. In the solitarious phase, where the average number of pods laid by each female is probably rather higher than in the gregarious phase, the potential multiplication rate may be as high as 200. However, these rates are never achieved in practice because of natural mortality.

2.1.3 Maturation and egg development

Under most conditions, the female takes about 10 days to develop eggs to the stage where they are ready to be laid, but the period is probably a little less at high temperatures with lush

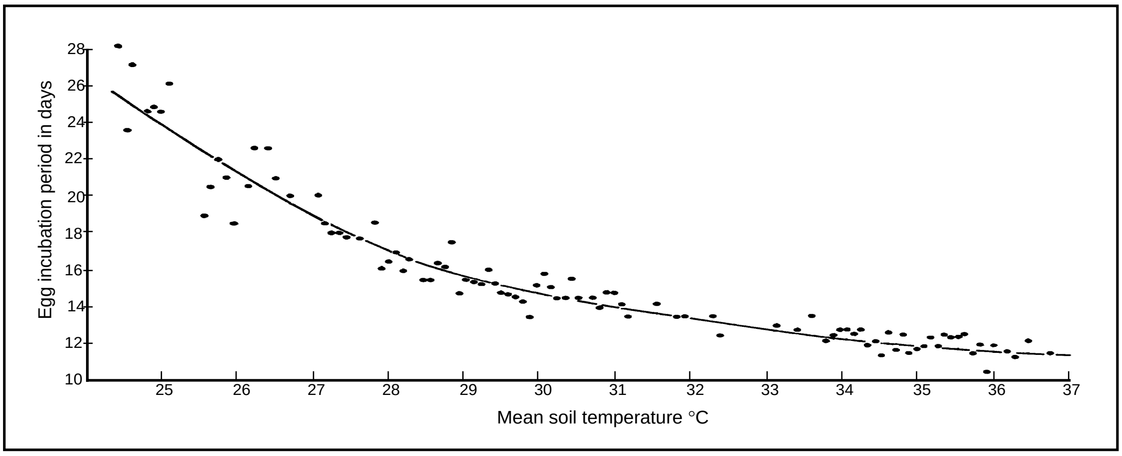

Figure 3. Incubation period and mean soil temperature during egg development (from Wardhaugh et. al., 1969).

vegetation. Egg development within the female is unlikely to occur at temperatures below about 15°C, even with a daily maximum as high as 20°C the adults are likely to remain immature.

The Desert Locust nearly always lays its eggs in soil which is wet enough to allow the eggs to absorb sufficient moisture to complete their development. Eggs are rarely laid in dry or nearly dry soil; if eggs were laid in a dry soil, they would desiccate unless rain fell soon after laying. The rate of development is then exclusively a function of the soil temperature at pod depth (Fig.3). There is a reasonably good relationship between soil temperature and screen temperature so rates of egg development can be predicted satisfactorily from screen temperatures (Fig.4) and indeed from long term means since temperatures do not vary greatly between years for a given place and time of year in most of the breeding areas. However, there can be exceptions to this, notably during the winter; for example, an unusually warm winter occurred in Mauritania during 1987-88 which allowed development to continue.

2.1.4 Egg mortality

A small proportion of eggs are usually not viable. There are a number of egg parasites and predators but their impact is usually small. Eggs can dry up especially if exposed by wind and can be killed by persistent flooding but neither occur often. With rare exceptions, the great majority of the eggs that are laid survive and hatch. This is usually not a vulnerable stage.

2.2 Hopper development and behaviour

2.2.1 Hatching

After hatching, the emerging hoppers work their way up the froth plug to the surface. They immediately moult to the first instar. The hoppers then pass through five instars (sometimes six in the solitary phase) shedding a skin (moulting) between each. At the final moult (called **fledging**) the young adult, known as a **fledgling**, emerges.

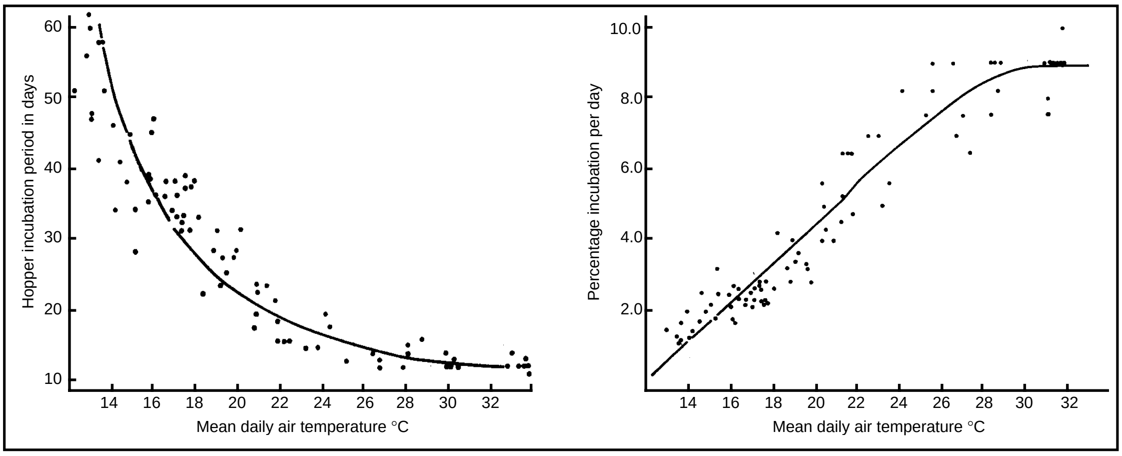

Figure 4. (a) The relationship between mean daily air temperature and incubation (field records); (b) the percentage of development undergone by an egg in one day at different temperatures (from Symmons et. al., 1973).

The rate of hopper development, as with the rate of egg development, is a function of temperature (Fig. 5). The correlation with screen temperatures, however, is less clear than with eggs because the hoppers can to a conisderable extent control their body temperature by basking or seeking shade. There is no evidence that hoppers in relatively dry vegetation develop more slowly.

2.2.2 Hopper survival

The rain associated with egg laying usually produces sufficient vegetation for the hoppers to live on. Hopper populations can die from lack of food but that is unusual. Nevertheless, only a fraction of the hoppers which emerge from the egg survive to fledge. Only two attempts have been made to estimate the change in numbers from parents to fledgling progeny. In both cases, there were fewer fledgling progeny than parents. There was very large mortality in the first instar stage and this seems to be very common both in the laboratory where it has been called perinatal mortality and seems to be associated with inadequate water reserves, and in the field, where cannibalism and predation by ants are frequently recorded. Cannibalism as well as parasitism and predation also causes numbers to decline later on.

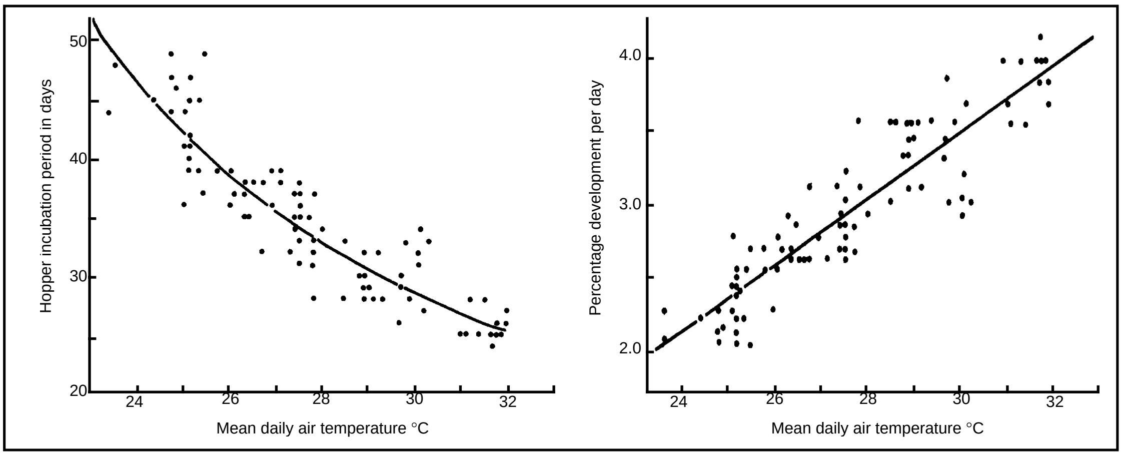

Figure 5. (a) The relationship between mean daily air temperature and hopper development period (field records); (b) the percentage of development undergone by a hopper in one day at different temperatures (from Symmons et. al., 1973).

Time of day	Activity	Duration of Activity	Air temperature
early morning, before dawn	roosting in bushes	from 1 hr. before sunset to 20 min. before sunrise	below 17°C
20 min. before sunrise	descent from bushes; slow dense marching	up to 2.5 hr.	17.5 - 25°C
45 min. to 2 hr. after sunrise	ground grouping	40 - 90 min.	22.5 - 28°C
1.5 hr. after sunrise to midday	marching	4 - 5 hr.	17 - 36°C
middle of the day	roosting	up to 4 hr. if hot	above 36°C
afternoon	marching	up to 1 hr before sunset	36 - 24°C
evening; 80 min. before to 5 min. after sunset	ground grouping	up to 2 hr.	
night	marching	does not always occur but can go on for several hours	
night	roosting	usually for most of the night	below 24°C

Figure 6. Daily behavioural pattern of hoppers in bands (after ALRC, 1966).

2.2.3 Band behaviour

Hatching usually occurs at dawn or shorthly thereafter and the hatchlings move to the nearest clump of vegetation. Within a few hours of hatching, the hoppers turn black. Usually they do not feed or move much for the first day. As a mass, they may cover no more than a few tens of square centimetres, but contain several thousand insects per square metre, forming small dense black patches.

During warm and sunny days, hopper bands follow a pattern of behaviour alternating between roosting and marching throughout the day (Fig. 6). On overcast days, bands usually do not move very far.

Band densities will vary a great deal according to band behaviour and instar as well as the habitat and the weather. For example, ground groups are denser than those roosting which are denser than those marching (Fig. 7). Measurements of maximum densities for hoppers in ground groups range from over 30,000 per m^2 for first instars to just over 1,000 per m^2 for the fifth instar, but average densities are much lower. In late instar bands, the average probably lies between 50 and 100/m^2 as a rule. The relative densities of the different instars mean little since the locusts themselves are increasing in size.

As the hoppers develop, much larger bands form through merging. This process continues into the fourth instar. First, second, and third instar hoppers sometimes get caught up in older instar bands. The increase in size of hopper bands with age can be even greater than the decrease in density (Fig. 8). In the final instar, however, the bands tend to spread out and become less cohesive.

The rate of band movement varies enormously with the temperature, the vegetation cover, and perhaps with the size and coherence of the band. For example, measurements for predominantly fourth instar bands range from 193 to 1,667 m in a day.

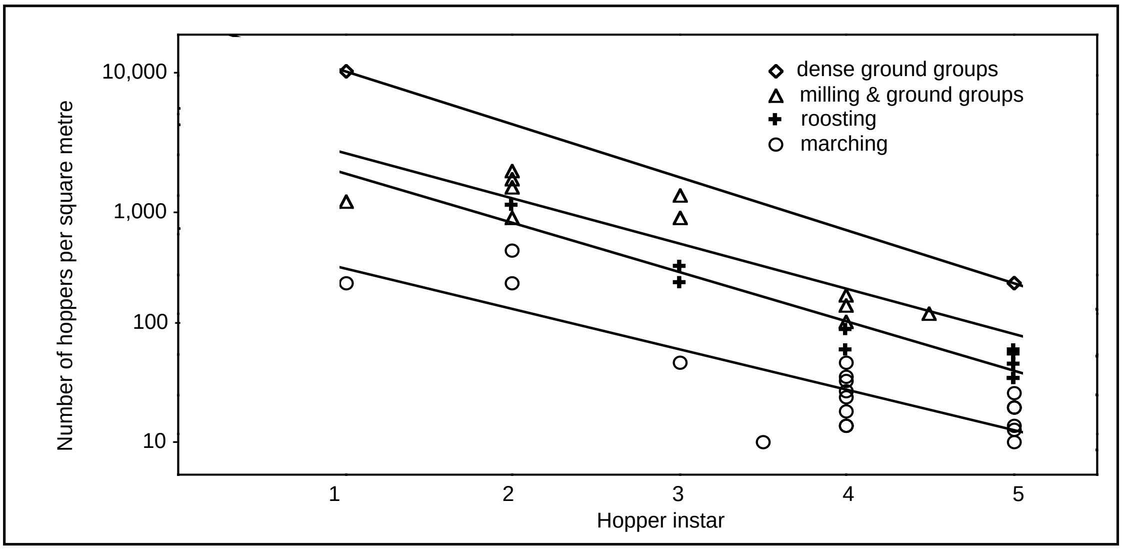

Figure 7. Average density of Desert Locust hopper bands displaying various behaviours (after Pedgley, D., 1981).

Generally, bands move only during the day and usually only from 2-3 hours after dawn to about an hour before sunset. However, there are records of bands moving by night under exceptional high temperatures or when the moon is full. If the vegetation is very dry, bands may continue moving at night in search of green vegetation. The band usually maintains a constant heading during a day; even a major obstruction, such as a river, is not always sufficient to change its path. The heading is often, but by no means always, downwind. At midday, bands usually roost in the vegetation.

Hoppers of every instar can be found in the same area at the same time. This is partly because laying occurs at intervals, and partly because eggs in the same bed, and even in the same pod, do not all hatch at exactly the same time. As a result, most bands contain a mixture of instars, although one or two are usually clearly dominant.

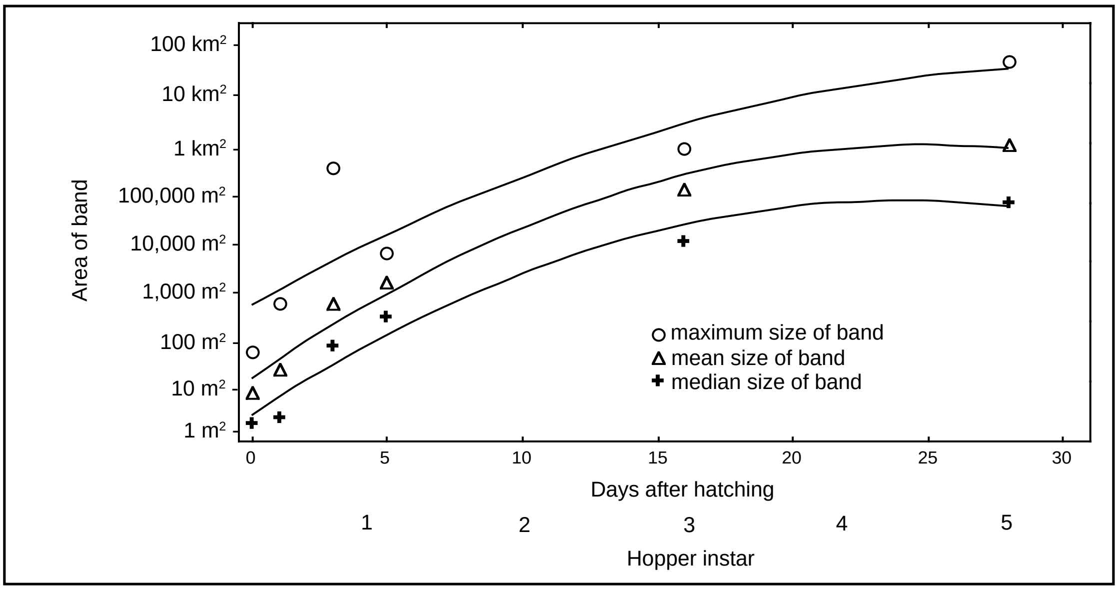

Figure 8. Increase in area of hopper bands with age (after Pedgley, D., 1981).

2.3 Adult development and behaviour

It takes about ten days after fledging for the adult's wings to become hard so that it is capable of sustained flight. The adults then remain immature until they encounter conditions which stimulate maturation. There is, however, a minimum immature period. Adults in an area of lush vegetation with maximum day temperatures of 35°C or more, and with rain to maintain the vegetation growth, can probably lay within three weeks of fledging. At the other extreme, immature adults can survive for six months or more under dry conditions. Adults cannot survive long under hot dry conditions with little to eat; migration to areas where the rains fail is one way in which plagues collapse. Adults can also survive during the winter in West Africa south of the Sahara where it is relatively warm, but these adults do not breed.

2.3.1 Diurnal swarm behaviour

Generally, morning swarm activity starts with descent from the vegetation on which the swarms roost overnight. The locusts often bask on bare ground with their bodies sideways to the sun in order to get the greatest warming effect. As the temperature increases, groups of locusts take off and then land. Eventually, by mid-morning or earlier if the temperature is warm enough for sustained flight, the whole swarm takes to the air. Sustained flight is rare if temperatures are below about 20°C. This limiting temperature is higher under overcast conditions (about 23°C). Photographic and radar estimates of volume densities in flying swarms range from one locust per thousand m^3 to ten locusts per m^3.

Young immature swarms occasionally continue flying after dark on warm evenings but, as a rule, swarms start to settle about an hour before sunset as convection dies away. Very high air-borne densities can occur then.

2.3.2 Swarm behaviour

The first swarms usually form some tens or even hundreds of kilometres downwind from the main area of laying. The young adults drift away from the breeding area; aggregations then form which collect other locusts around them.

All major swarm displacements are downwind, although mature swarms may sometimes move a short distance upwind if the wind is light. A swarm is displaced at some fraction of the wind speed. The behaviour of the locusts in the lowest 400 m or so of a swarm has been studied by taking a series of multiple exposure vertical photographs as the swarm passes. These show that the locusts occur in streams, but that the streams can take any heading within the swarm. The result would then be downwind displacement at the wind speed; however with many swarms, a considerable proportion of the locusts spend some of the time on the ground, so the swarm nearly always moves at less than the wind speed and often a great deal less (Fig. 9).

Very little is known about the behaviour of locusts at higher levels within a swarm, but it seems likely that they also form randomly oriented streams or swirling sheets.

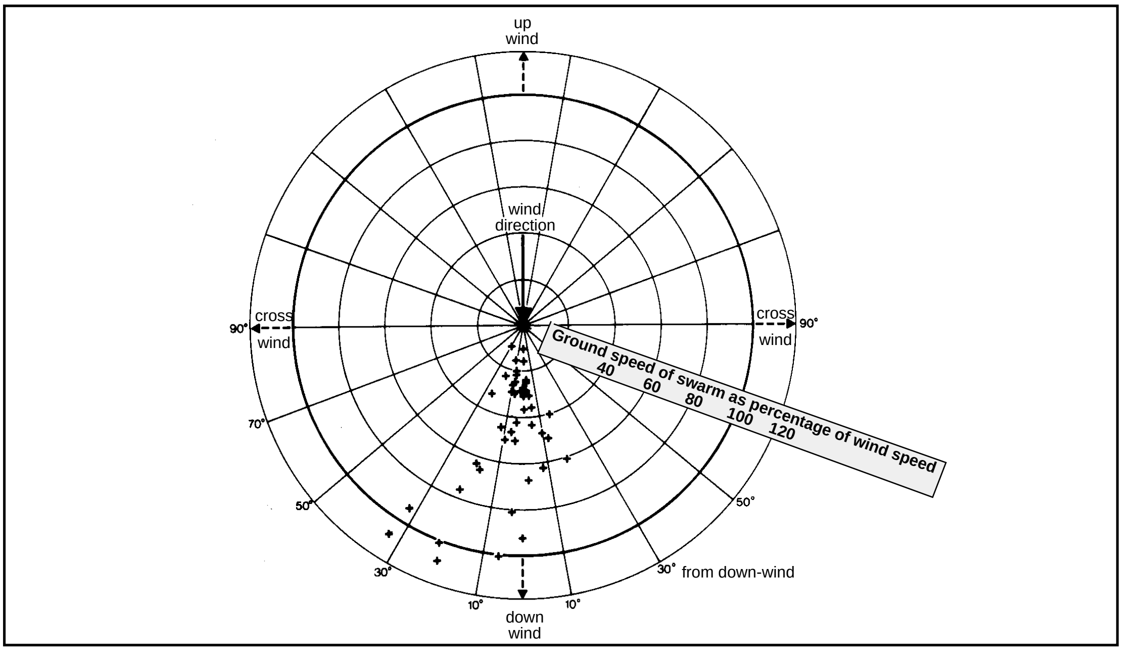

Figure 9. Direction and speed of displacement of individual Desert Locust swarms in relation to the wind in eastern Africa 1951-57. Out of the best documented observations, 26 swarm displacements were within 10° of downwind (from Rainey, R.C., 1963).

At the leading edge of the swarm, locusts descend as a mass turning into the wind to land. At the trailing edge locusts take off, once again into wind, as the swarm clears overhead and then turn to catch up to the departing swarm. The locust, like any other flying machine, lands and takes off into wind.

The means by which the streams maintain their cohesion to form a swarm is not understood. Streams which emerge from the swarm ‘turn back’ into the swarm.

Swarms can occur as low flying sheets (stratiform) or the locusts may pile high in the air, similar to hanging curtains, with the top level as much as 1,500 m above ground (cumuliform) (Fig. 10). Cumuliform swarms are associated with convective updrafts on hot afternoons. It is not clear with cumuliform swarms which wind level determines displacement. Swarms may be ‘towed along’ by winds

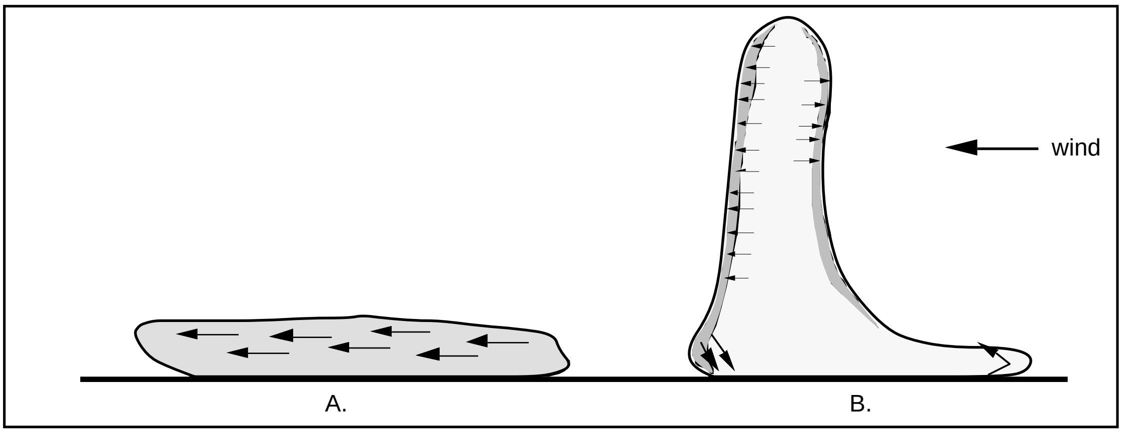

Figure 10. (a) stratiform and (b) cumuliform Desert Locust swarm.

aloft or they may be held back by winds near the surface which are usually slower and often blow from a different direction. Swarms can easily be displaced 100 km or more in a day.

Most estimates of the flying speed of the Desert Locust are in the range of 3-4 m/s; a reasonable figure for locusts in sustained flight is 3 m/s. This would not affect total displacement greatly even if the locusts all flew in the same direction. It is, however, an important fact in air-to-air spraying since it means the locust will be moving relatively rapidly through the spray cloud; even in the strongest winds the air close to vegetation and to hoppers will be moving more slowly than this, so the flying locust will be a better insecticide collector than one on the ground.

Swarm densities vary considerably. There are many estimates for settled swarms giving an average of about 50million/km ^{2} (50/m^2); this is the usually accepted figure for medium density swarms. Swarms generally spread out when flying, typically covering between two and three times the area they occupy when roosting.

2.3.3 Solitary behaviour

Very little is known about solitary hopper behaviour and survival, and not a great deal about solitary adult behaviour either. It is probable, however, that the development rates of eggs and hoppers are the same as those for gregarious hoppers and eggs laid by gregarious females.

Solitary adults migrate at night; individuals have been detected by radar up to heights of 1,800 m. It is not known whether all locusts capable of flight migrate, how long they stay airborne during the night, and whether they fly on a sequence of nights. It is possible that there are both brief low-level flights, leading to short range displacements, as well as sustained higher-level flights, resulting in migration. Indeed, it may well be that some solitary locusts do not migrate at all but merely move locally.

The limiting temperature for night flight would seem to be about the same as for day flight, namely 20°C. This is unexpected since, at the limiting ambient temperature, the body temperature of night fliers must be substantially less than for day-fliers in bright sunshine.

Night flying locusts are able to locate areas of vegetation in which to land, even where these occur only as a few isolated patches. How they do this is not known.

2.4 Maturation

Maturation is the process by which immature adults become sexually mature. This initially occurs in the Desert Locust when the immature adult reaches an area where rain has recently fallen. This, in most cases, means rain in sufficient amounts to allow eggs and hoppers to survive. Although maturation is associated with rain, the connection is not a simple one and is not well understood. It has been suggested that the scent which plants such as myrrh (*Commiphora* spp.) give off **before** the onset of rains may trigger maturation, but the evidence is weak.

Maturation may be associated with rain in an already infested area, or by locusts invading an area where it has recently rained. A mature locust will cause others to mature which is probably the reason why maturation is well synchronized in swarms.

Maturation is not an easily defined state. Males usually become sexually mature before females. The only satisfactory guide to female maturation is egg development within the female.

3. Recessions, upsurges and plagues

With the Desert Locust there are periods, which in the past have often lasted a number of years, during which there are many bands and many swarms. These **plagues** are separated by **recessions**, or periods during which bands and swarms are rare, with most of the locusts at low densities (Fig. 11).

The transition from a recession situation to one of plague is called an **upsurge**. This transition takes place over a number of generations, during which the size of the total gregarious population, and the size of the bands and swarms which make up that population, both increase. Most upsurges die out without leading to a major plague.

Regional upsurges may occur during plague periods. Indeed, what appear as long plagues in Figure 11 are in fact an overlapping series of plagues.

The definitions of plagues and recessions are somewhat imprecise. A plague is said to occur when there are many swarms and very many bands. During a recession, bands and swarms are small and few in number, and may be completely absent. The distinction between plagues and recessions is normally so clear that a precise definition is not necessary. Moreover, a precise definition would exclude upsurges. The upsurge concept, although vague, is both biologically and practically useful.

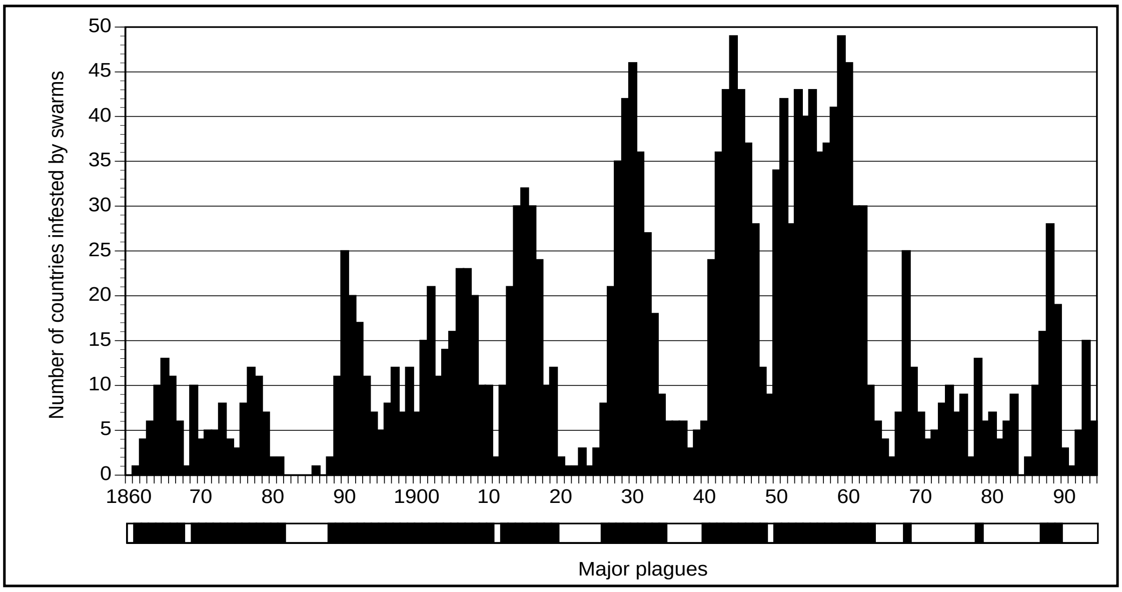

Figure 11. Plague and recession periods of the Desert Locust, January 1860 to March 1994.

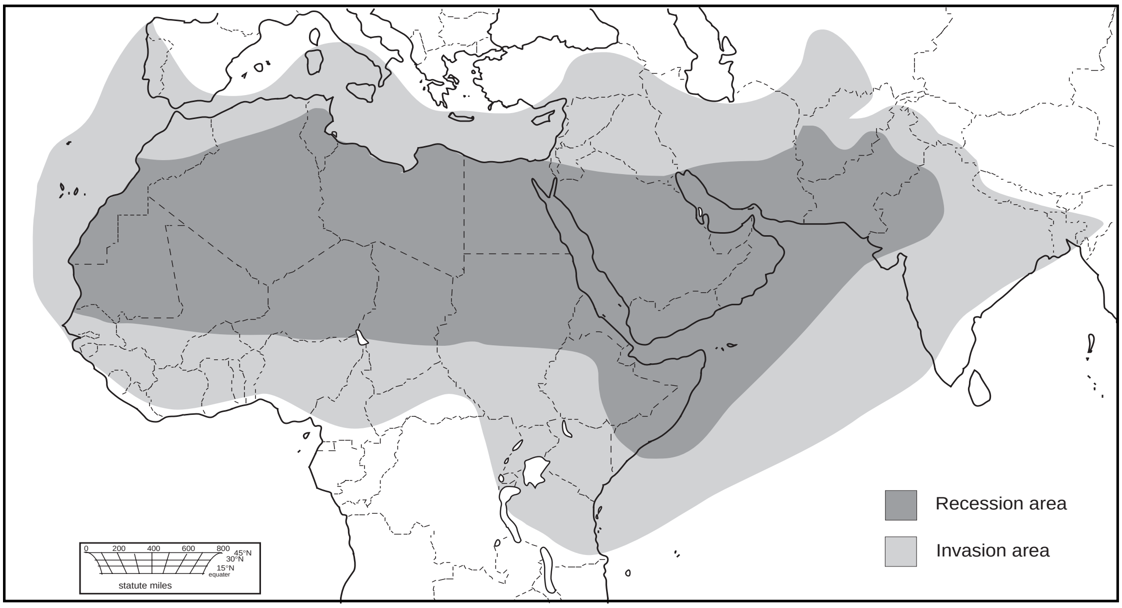

Figure 12. Plague and recession areas of the Desert Locust.

4. Migration and seasonal distributions

Since both day-flying swarms and night-flying solitary individuals are displaced downwind, the seasonal changes in the mean wind flow bring locusts into particular zones during particular seasons. The lower temperatures at night are the reason for the observed smaller north-south shift of the seasonal infestation areas for the night-flying solitaries, compared with day-flying swarms. The infestation areas of the swarming and non-swarming phases are shown in Figure 12.

Downwind displacement tends to bring locusts into an area during the season when rain is most likely. The migrating locusts will often then breed, and by the time the new generation of adults

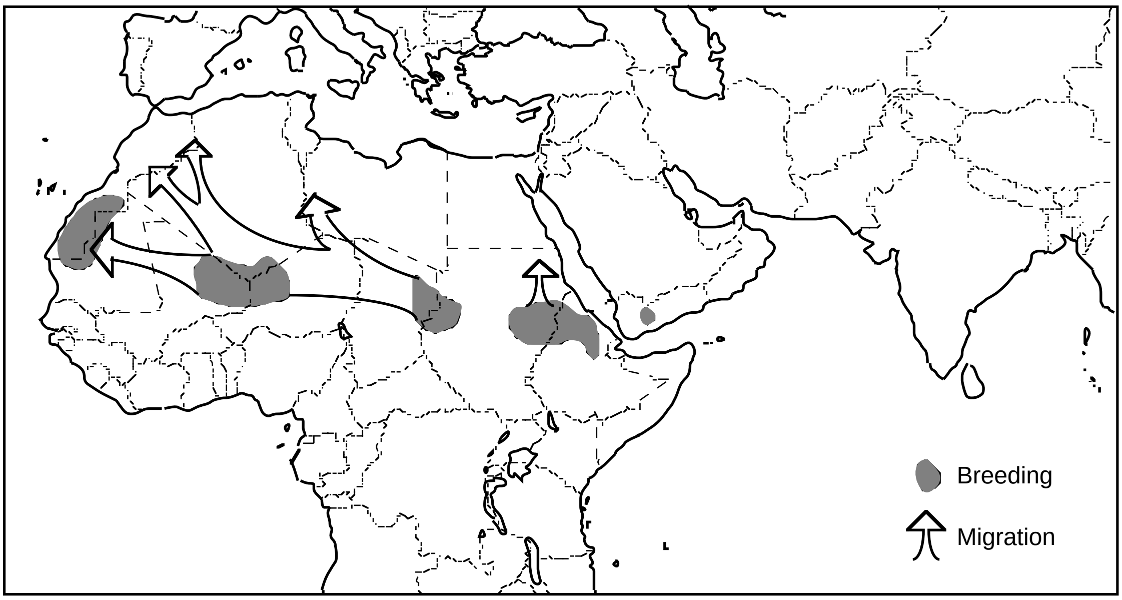

Figure 13. Breeding areas and migration routes during July to December 1987.

is capable of sustained flight, the seasonal wind pattern may well have changed. The locusts will then migrate rapidly, often over very great distances (Fig. 13).

All this is true only in a very general way. Average winds comprise a range of particular winds, and it is the particular winds on which the locusts move. Often there are swarm movements which take place that do not coincide with the average wind flow; moreover, rare and even unprecedented movements continue to occur. This is one reason why, in any particular year, only part of the seasonal breeding area will be infested (Fig. 14). The other major reason will be failure of the seasonal rains and consequent unsuccessful breeding.

4.1 Factors controlling swarm migration

It is always possible to find a warm enough wind from approximately the right direction, to explain why a particular swarm migration has occurred. However, there are often other winds that the swarms could have moved with, but apparently did not. For example, swarms have crossed from central Saudi Arabia to central Sudan in the early summer on many occasions, but to do so they must take advantage of the relatively few days when there are winds from the northeast, and even then the swarms apparently ‘select’ a particular height band. Swarms in West Africa frequently move northwards across the Sahara desert in the autumn, transported by warm southerlies associated with depressions in the western Mediterranean (Fig. 15). The more common northeasterlies are often warm enough to move the swarms back again but that probably does not happen. On the basis of winds and temperatures alone, swarms should move southwards not northwards from the Sahelian belt of West Africa. Indeed, some Desert Locust swarms do move in that direction - the ‘southern circuit’ - as do plague swarms of African Migratory Locust. It would seem there must be either physiological or environmental requirements for migration of which we are at present unaware.

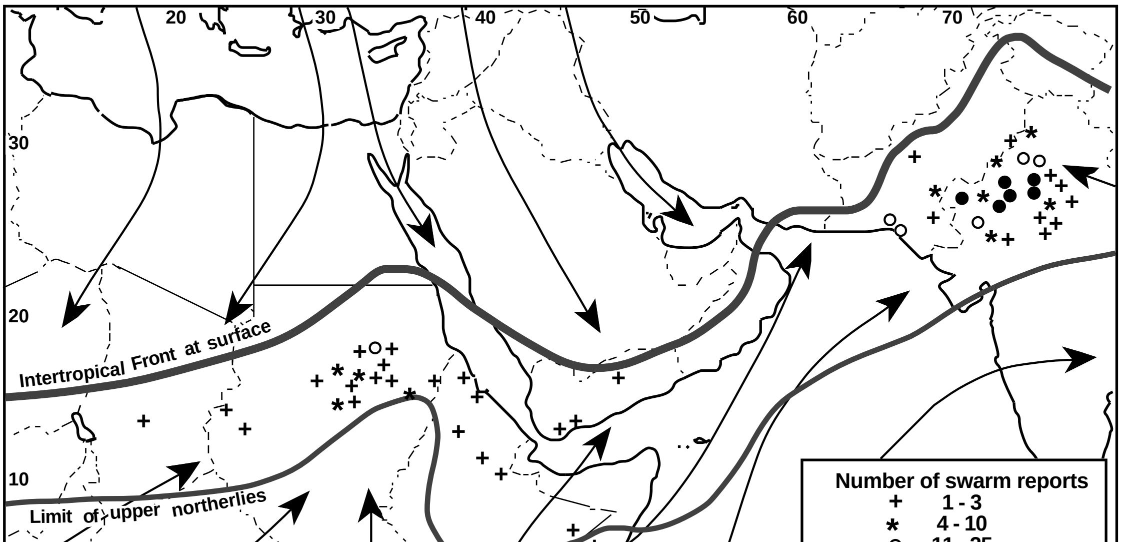

Figure 14. The Intertropical Convergence Zone and the distribution of Desert Locust swarms, July 12-31, 1950 (after Rainey, R. C.,1951).

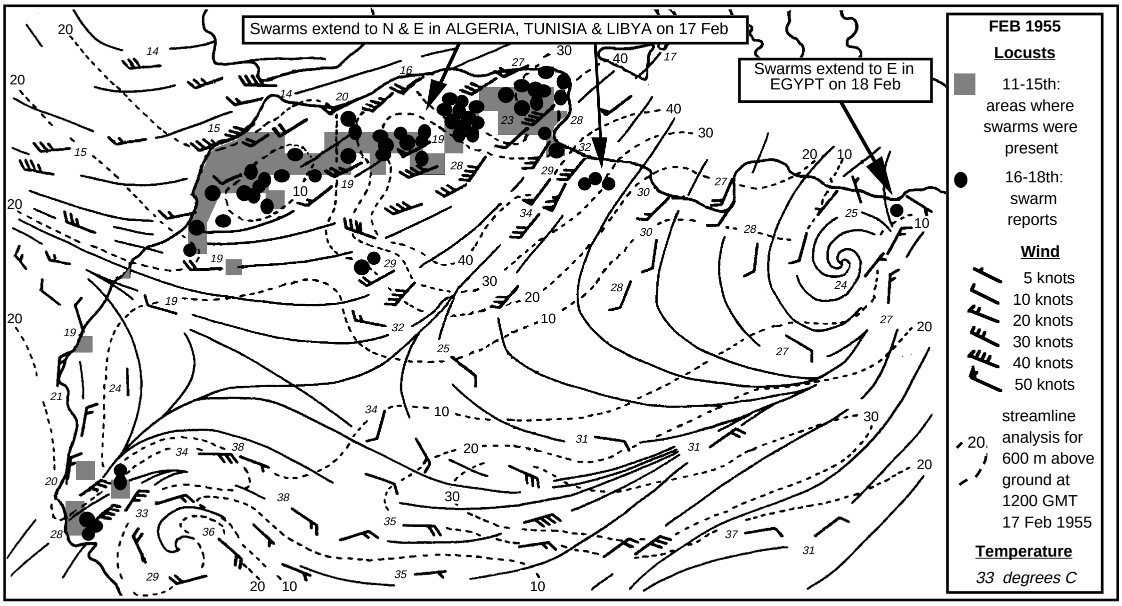

Figure 15. The effects of a central Mediterranean depression, showing winds at 600 m above ground (after Rainey, R. C., 1963).

4.2 Factors controlling solitary migration

Solitarious locusts, like swarms, persist if there is lush green vegetation. When emigration does occur, it may take place over a series of nights. Hence, displacements do not occur in well defined movements but tend to reflect the mean wind pattern more closely than is the case with swarms. It was once believed that solitarious adults did not migrate and it is possible that at least on some occasions part of the population persists.

5. Characteristics of upsurges

Upsurges result from successful breeding over a number of generations by an initially small population. This requires a series of substantial and widespread rains of which at least the earliest ones in the sequence occur in the normally arid recession area. As the upsurge develops, there will be migration taking adults from one breeding area to the next one in the chain.

The few upsurges that have been analysed carefully have been ones which led to plagues, even if short-lived ones. Figure 16 is an example of a sequence from the recent 1992-94 upsurge. For these few upsurges, every sequence of movements has been different. Moreover, several seem to have started from areas where recession breeding occurs very rarely. The most commonly infested recession areas may not be the most important ones.

It is often difficult to decide which is the source of the first parents of an upsurge. Adults may be present in such small numbers that few, if any, are found during normal survey. Alternatively, adults may be brought in from a wide area by the low level convergent wind flow, which is likely to be associated with the rain required for the first successful breeding of the upsurge sequence.

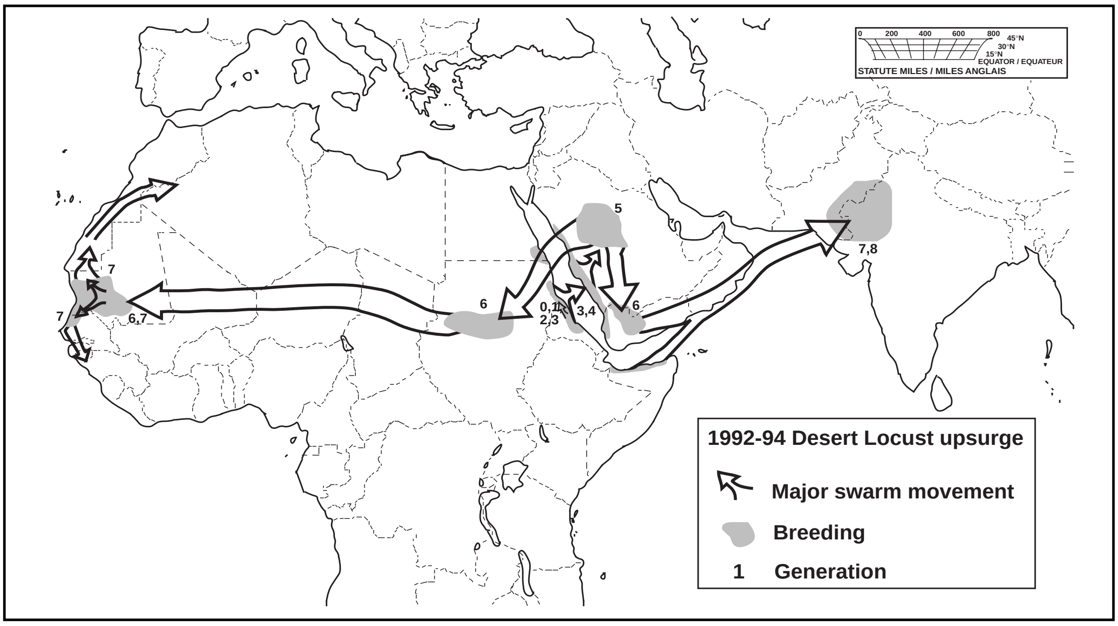

Figure 16. A sequence of breeding by Desert locusts during an upsurge (from FAO/ECLO information up to March 1994).

During the early stages of an upsurge, much of the population is often dispersed widely at well below gregarious densities. Small 'patches' of hoppers then occur and small low density swarms. The swarms often disperse and re-form. At this stage, a large part of the population may still not be in gregariously behaving groups. With successive generations, the proportion of the total population in bands and swarms increases until few scattered locusts remain; the total number of locusts increases as does the size and coherence of the bands and swarms.

There has been much discussion concerning the process of gregarisation. Clearly, gregarisation is more likely to occur where average densities are relatively high, by solitary standards, over a substantial area. Gregarisation will be accelerated in areas where the favourable habitat is localised thus forcing the locusts to come together. In the past, gregarisation has occurred, or can be reliably inferred to have occurred, only in some parts of the Desert Locust recession area (Fig. 17). These are mostly areas where two generations of breeding can occur in rapid succession.

6. Plague declines

Less attention has been paid to the decline of plagues than to their initiation. There is an understandable desire to attribute plague termination to control, although it is likely that control has never been more than a contributory factor. The impact of control is, in any case, difficult to assess.

The most obvious natural cause of plague decline is migration to areas from where either the adults or their progeny cannot return. Another cause is failure of the rains in an area where successful breeding usually occurs. A spectacular example of the former is the trans-Atlantic swarm migrations of October and November 1988.

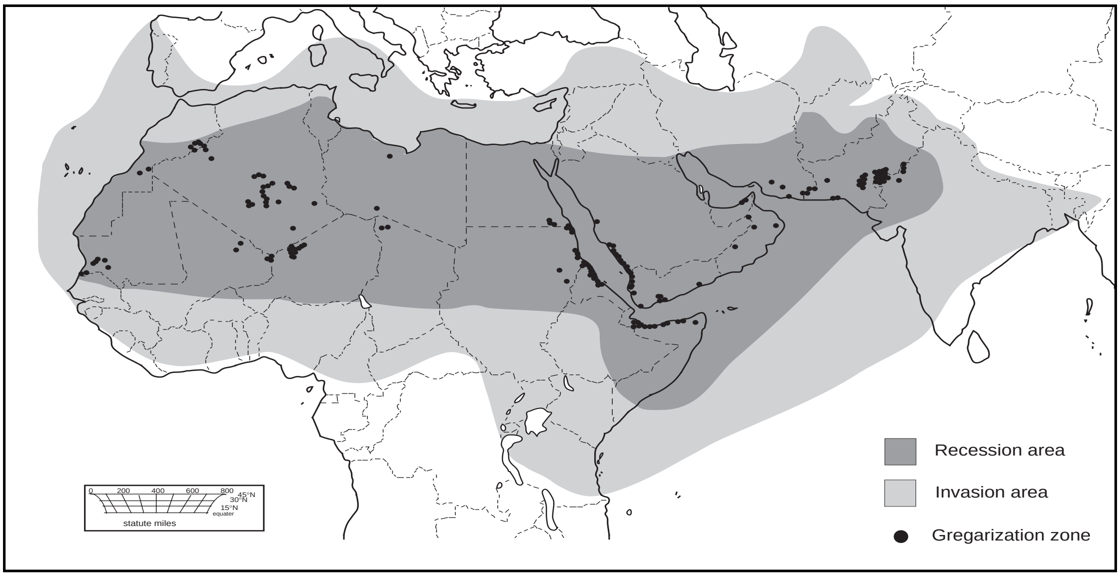

Figure 17. The primary areas of Desert Locust gregarisation (after Waloff, Z., 1972).

An example of the latter is the failure of the Short Rains in the Horn of Africa in 1955 which led to the first break in gregarious populations since 1950.

What is known about plague upsurges and declines does not constitute a wholly convincing explanation of past events. During upsurges, breeding appears to be spectacularly successful; during declines, infestations have in some cases disappeared, and neither control nor lack of rain could have been the cause. For example, in 1968 swarms disappeared into the Harrar highlands of Ethiopia and were never seen again. This has occurred in other years. During late 1988, swarms moved south in West Africa, reappearing during May in Mali, Niger and Burkina Faso. They then disappeared completely and clearly failed to lay. Predation and parasitism may be significant with solitary populations but are unlikely to have a major impact on gregarising populations of or on gregarious populations, except perhaps towards the end of plagues. The main parasites and predators of the Desert Locust are known, and are described in a publication listed in the Appendix.

7. Upsurge and plague ‘forecasting’

The first task of Locust Units during a recession is to detect, as early as possible, where upsurges may be occurring. Clearly, breeding requires both locusts and rain within a seasonal breeding area, but of these, rain is the more variable. Moreover, it is unlikely that the distribution of the solitarious population will be sufficiently well known. This means that any area where substantial rain has fallen at the right season must be regarded as a possible site for breeding. The estimation of the occurrence of rain, not the forecasting of migration, is therefore the main concern. As has been suggested already, when rain occurs in the right quantity at the right time, some solitarious locusts usually appear to take advantage of the conditions. By contrast, during plagues, the seasonally infested areas normally receive enough rain for successful breeding, and the forecasting of swarm migration then becomes the critical activity. Swarms can cross a continent within a few weeks, so forecasting migration is essentially a task for a central service.

8. Control strategies

It had been hoped that plagues could be prevented by limited ground control at the start of upsurges. This clearly failed in parts of the recession area in 1967-68, in 1977-78 and again in 1986-87. On some occasions, the policy will inevitably fail in the future. Failure is inevitable if an upsurge starts in a region where survey and control cannot be carried out either because of remoteness or for security reasons. Failure is likely if an upsurge starts in a country where the resources to maintain a Locust Unit are not forthcoming. Thus, it is necessary to study control methods, and campaign organization and execution, and also why contingency plans are required.

However, the very nature of upsurge populations may make preventive control impracticable in many cases. In practice, control is always restricted to ‘targets’. During the early stages of upsurges, these are numerous, difficult to find and often transitory. Even if these ‘targets’ were eliminated, the major portion of the population might still survive in non-gregariously behaving infestations which were not attacked. In order to be sure of elimination of an upsurge, it might prove necessary to treat the whole of the area which might be infested. Such widespread indiscriminate control would be difficult to organize and difficult to justify. Early upsurge control is most certainly worth attempting. It may prevent some plagues and it must reduce the scale of upsurges it fails to contain, but it cannot be relied upon to prevent all plagues.

There may be a better chance of containing an upsurge that is under way but has not yet developed into a plague. That would require the same organisation and methods as combating a plague. Containing upsurges, and indeed combating plagues, depends on the existence of locust units during the recession, on training and on contingency planning.

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