

DESERT LOCUST TECHNICAL SERIES

Desert Locust population dynamics parameters



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by

J Roffey
1, Saville Close, Cheltenham, UK

and

J I Magor
Natural Resources Institute,
University of Greenwich, Chatham Maritime, UK

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Introduction

Interest in the cost and economics of Desert Locust management increases periodically (Uvarov and Bowman, 1938; FAO, 1958; Joffe, 1995). Currently it stems from high expenditure between 1986 and 1989 to suppress a Desert Locust plague and concurrent grasshopper outbreaks. Simultaneously, an awareness grew of the need to review management strategies and to develop environmentally safer control methods. Developing rational control strategies requires a sound knowledge of the pest's population dynamics because they provide the key to predicting when and where the pest will cause damage, and when and where intervention will be effective.

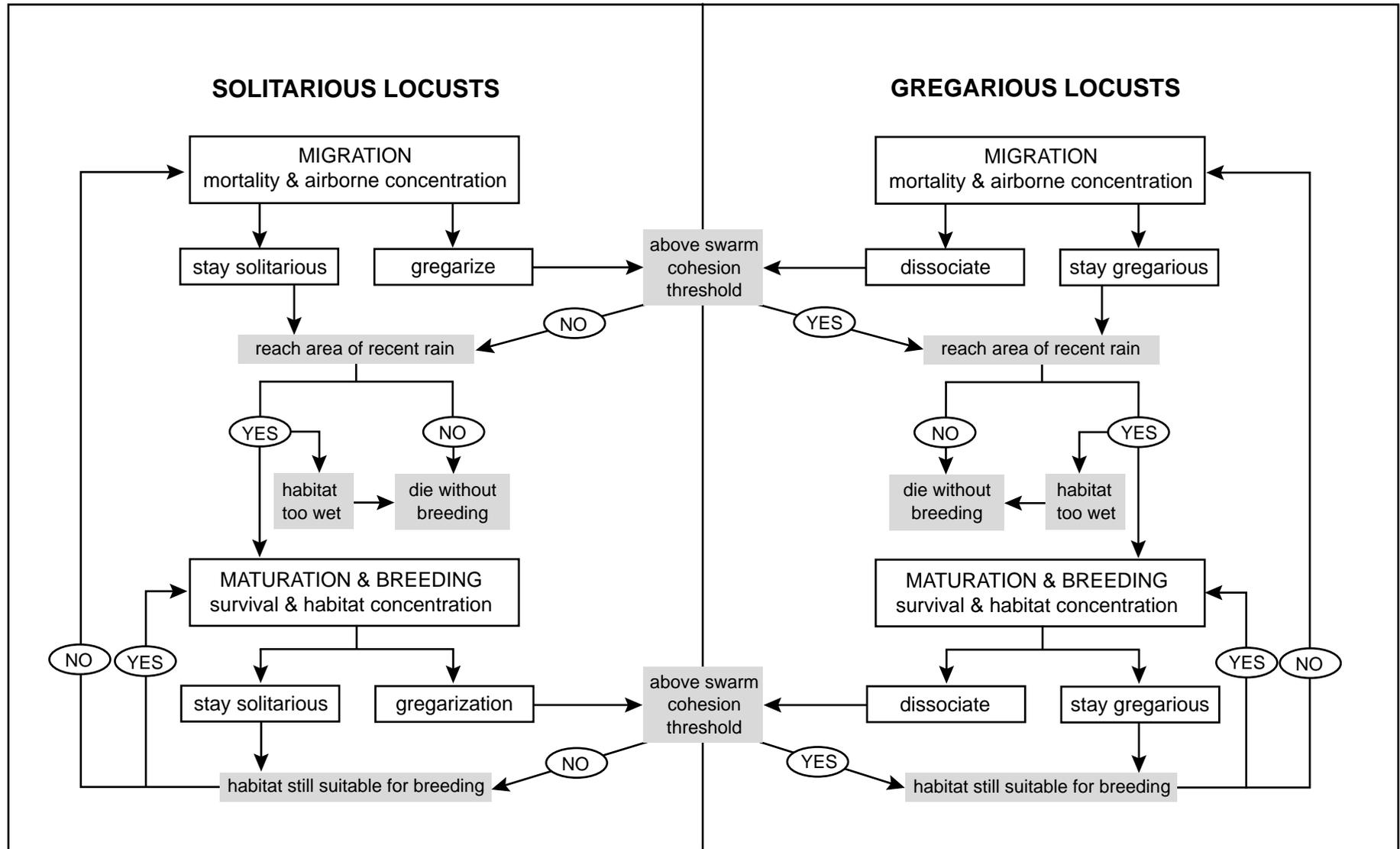
Many authors have described the main processes of Desert Locust population dynamics (Uvarov, 1977; Waloff, 1966; Magor, 1994). Desert Locust plagues are an intermittent problem for about 50 countries in Africa, the Middle East and southwest Asia that are at risk from swarm invasion and breeding. At other times, they move between the 25 countries in the drier, central part of the distribution area that extends from Mauritania to northwestern India and is known as the Recession Area. Numbers and densities are low in this area during recessions but increase during outbreaks and upsurges when swarms form and if unchecked may lead to a plague. Desert Locusts breed in areas that have received enough rain (usually at least 25-50 mm) to provide moisture for egg development and for vegetation to germinate or regenerate and provide food and shelter for hopper development. Waloff (1966) concluded that locust outbreaks (a marked increase in numbers leading to the formation of bands and swarms) occur when rains are sufficiently heavy and prolonged for two generations to breed. This allows a rapid rise in numbers and density followed by the onset of gregarious behaviour. She found that plagues (periods of widespread and heavy infestations, the majority of which are bands and swarms) occur only when locusts breed frequently and successfully over a period of one or more years. The rains must be widespread and heavy in two or more successive seasonal breeding areas that allow the locusts during this upsurge period to continue multiplying and gregarizing to form many swarms. The great mobility of swarms takes them beyond the recession area into major agricultural areas where they may cause rapid and locally devastating crop losses.

This paper summarises information on the parameters required to build the population simulation models needed for making economic evaluations of Desert Locust impacts and for testing strategies and tactics of control interventions. It is based on an unpublished paper by Roffey (1991) and incorporates many amendments suggested by colleagues to whom it was circulated. It will be readily apparent that some parameters are better documented than others. For example, sufficient quantitative data exist for swarm migration and egg and hopper development to be well understood and models of these processes already exist (Reus and Symmons, 1992; Meteo Consult, 1994). Where information is unavailable or insufficient, we have suggested values that may be used and cited data sources so that modellers can evaluate and modify our values.

Population parameters

The basic concept of any model (Figure 1) is to follow locust populations in time and space as they migrate, reach areas of recent rainfall, mature, breed and fledge. The immature adults may then migrate, or they may remain, become mature and breed in the same seasonal breeding area. Emigrants die if they fail to find a suitable breeding area. If the populations are initially solitary, they may become gregarious if certain conditions are met. Once gregarious, populations may dissociate. In this paper, the term 'solitary' includes the solitary end of the *transiens* phase and the term 'gregarious' includes the gregarious end of the *transiens* phase.

Figure 1 Desert Locust population dynamics



Seasonal migration between breeding areas

Migration is a striking feature of Desert Locust biology that takes mainly immature solitary and swarming populations between seasonally distinct breeding areas by a succession of daily downwind displacements. Mature adults also migrate between successive cycles of mating and laying. Usually but not invariably, they move over shorter distances than when immature. Normally, a single generation is produced but if an area remains suitable for breeding, young solitary and swarming adults mature rapidly and do not move far before breeding. When this happens, two or even three generations may be produced in succession in a seasonal breeding area.

Successful breeding requires a high degree of coincidence in space and time between adult locusts and rain. This is achieved by downwind migration that takes locusts towards areas of horizontal wind convergence and rainfall (Rainey, 1951). Swarms breed on spring and summer rains in two major belts lying east-west across the Desert Locust area. Between and partly overlapping these belts, lies an area of winter rainfall. Breeding on these rains is particularly important on the Somali Peninsula and around the Red Sea. (Figure 2). Table 1 contains the normal months for each breeding season. These may overlap when rains are prolonged and fledging populations mature rapidly and breed again without migrating to a new breeding area. Generations are traditionally named after the rainy season in which they were bred. The second summer generation coincides with winter breeding, hence the similarity between summer and winter swarm distribution in India and Pakistan in Figure 2. In Somalia and eastern Africa, the Short Rains coincide with winter rains and the Long Rains coincide with spring rains. Swarms sometimes migrate to areas where breeding does not occur. Such displacements are more common towards the end of a plague and can lead to the disappearance of a regional population.

TABLE 1. Normal duration of Desert Locust breeding seasons

LOCUST SEASON	RAINFALL SEASON	HATCHING	FLEDGING
Spring (Long Rains)	February-May	March-June	May-August
Summer	June-September	July-September	August-October
Winter (Short Rains)	October-January	October-January	November-February

Waloff (1966) and Pedgley (1981) outline the Desert Locust breeding and migration circuits for swarms. Usually, swarm migration continues for two to four months but in certain cases, in West Africa and the Somali Peninsula, it lasts six or more months. Many, if not most, swarms achieve net displacements of at least 1 000 km as a result of their cumulative daily displacements. Displacements of 2 000-3 000 km between breeding areas are not uncommon. The tracks of individual swarms or groups of migrating swarms vary, because wind direction and speed change with time. Tracks vary from almost straight lines for periods of days, to sharp bends or even loops over one or two days. Swarms have rarely been tracked for longer than a month (Gunn, Perry *et al.*, 1948; Rainey, 1963). Consequently, the rates of net displacement during long-range migrations, that may last for two to four months, come from analyses of swarm sightings. The numbers of examples of migrations within and between regions, presented by Pedgley (1981), are neither exhaustive nor do they represent the frequency of such migrations. To date, too few analyses exist to establish migration frequencies but the general pattern is given below.

Solitary populations are presumed to have similar seasonal migration patterns to swarms but to achieve less extensive displacements that are confined to the recession area. Although, the average duration of flight may be low, rapidly changing distributions suggest that non-swarming locusts can make rapid long-range movements of about 1 000 km in a few days.

Swarm migration after spring breeding

Spring breeding affects a belt running from Northwest Africa through the Middle East to Pakistan and northwestern India. It varies in area between years but on average affects more degree squares (1° latitude x 1° longitude) than other seasons. Spring breeding in Northwest Africa may begin from January in northern Mauritania and in southwestern Morocco. It extends throughout the region as the season becomes warmer. Hoppers appear from March until June, or up to August if a second generation occurs. Similarly, spring laying and hatching may occur from February in the coastal areas of around the Red Sea, the Gulf of Aden and Persian Gulf. This means that winter and spring breeding may continue without a break. In the interior of Arabia, in eastern Arabia and in the coastal areas of Iran, egg laying begins in winter. As temperatures rise in spring, it extends northwards through the Middle

East, Iran, Afghanistan and Pakistan. Laying in the northern parts of these countries and in Turkey sometimes continue until June-July. Hopper infestations become increasingly widespread from March and continue into July or early August.

Spring generation swarms form between March-April and June-July occasionally continuing into August in the far north of the area. The earliest swarms may follow the summer and winter swarms in a generally northern direction and may mature and breed in the later stages of spring breeding. Most spring swarms move between May and July to summer breeding areas. Swarms originating in Northwest Africa, move south to the Sahel and may spread eastwards into Chad and the Sudan. Many in the Middle East and on the Arabian Peninsula move south and southwest to Yemen and to African countries bordering the Red sea and Gulf of Aden. During the same period, the remaining swarms from Arabia and the Middle East move southeastward into the Indo-Pakistan summer breeding areas with swarms from Iran, Afghanistan and Pakistan.

The spring or Long Rains generation produced in East Africa and on the Somali Peninsula moves northwards either to the escarpment in northern Somalia or to northeastern Ethiopia where they join invading swarms from Arabia. These movements clear the spring breeding areas and swarms become concentrated into the summer breeding belt. They mature and lay eggs from July or August, usually dying by the end of October. The Somali Peninsula remains dry, however, and swarms there become concentrated along the convergence zone in northern Somalia and remain without breeding until October when Short Rains fall.

Swarm migration after summer breeding

Summer breeding occurs from Senegal through southern Arabia to India on rains associated with the Inter-Tropical Convergence Zone (ITCZ). The summer generation may fledge from late August but more often appears from September until October, continuing into November and even early December if protracted breeding results in two or three summer generations. Some swarms move to winter breeding areas but many continue to spring breeding areas where they remain without maturing until temperatures rise.

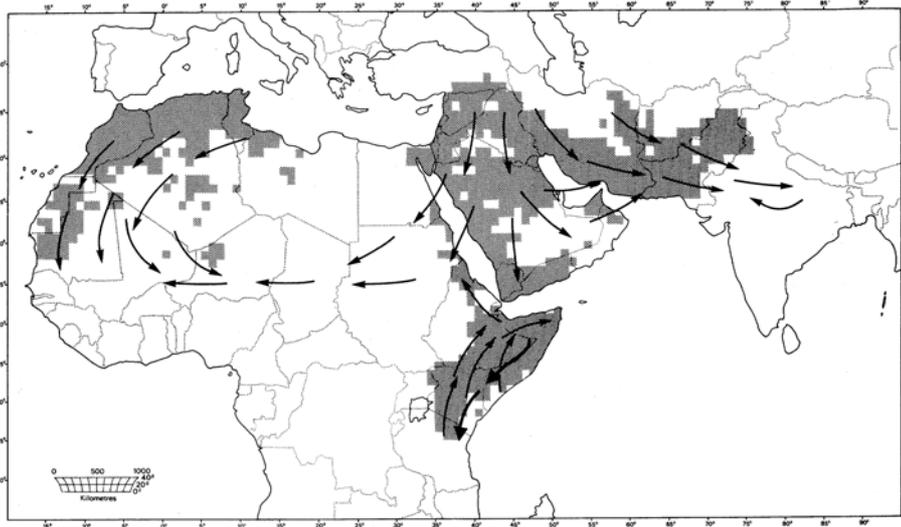
From late September or early October, most swarms from India and Pakistan move westward. Some stay in Pakistan and others reach Iran and Arabia. Sometimes, they then spread southwestward onto the Somali Peninsula. Other swarms may move northwestward through northern India to Afghanistan. Swarms that move eastwards or southwards at this time die without breeding.

Swarms produced in the Sudan, Eritrea and Ethiopia move in two directions during autumn and early winter. Some go northeastward or eastward to the Red Sea coastal plains of Eritrea, the Sudan, Saudi Arabia and Yemen, from where they may move northwards during intermittent spells of southerly winds. Some may reach the Middle East and occasionally move as far east as Iran. Other summer swarms may move southeastwards to augment those which arrived in northern Somalia in June or July and remained there without maturing.

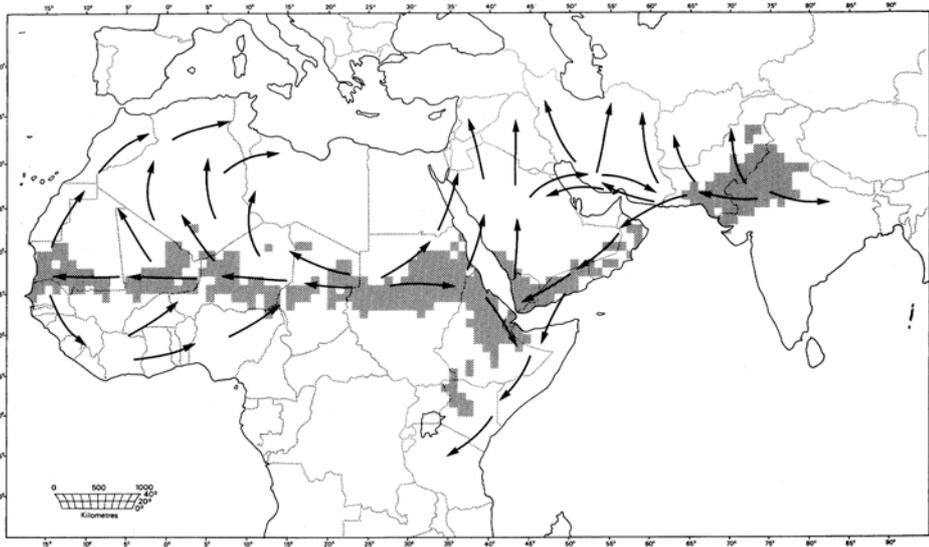
Most swarms originating in West Africa during the autumn move northwards towards Northwest Africa. They may arrive almost simultaneously across a wide front between southwestern Morocco and Libya. More frequently, however, the heaviest infestations at the beginning of the invasion are in southwest Morocco and the adjacent parts of Algeria. The invasion of Northwest Africa becomes more widespread with the onset of northeastward and eastward movements in late winter and spring. There is no clear division between sources of swarms invading Northwest Africa and Arabia. Swarms from western Sudan sometimes reach Northwest Africa, while in other years, swarms from Chad and the Sudan move eastward to the Red Sea and Arabia.

In many plague years, some summer swarms stay south of the Sahara. Those in the east enter Nigeria and move westward across the country. Those in the west move southwest into the Gulf of Guinea countries and then move eastwards. Both groups, finally turn northeastwards during the spring and early summer. Swarms remain immature throughout this southern circuit that may last from October or November until they return to the summer breeding area in the following May or June. They may then mature and lay in July and August with the spring generation swarms arriving from the north. No field observations exist on this point but there is some evidence that fewer eggs are laid after a delay in maturation (Ashall and Ellis, 1962). The absence of breeding in 1989, when few or no swarms arrived from the north, suggests that southern circuit swarms may fail to breed.

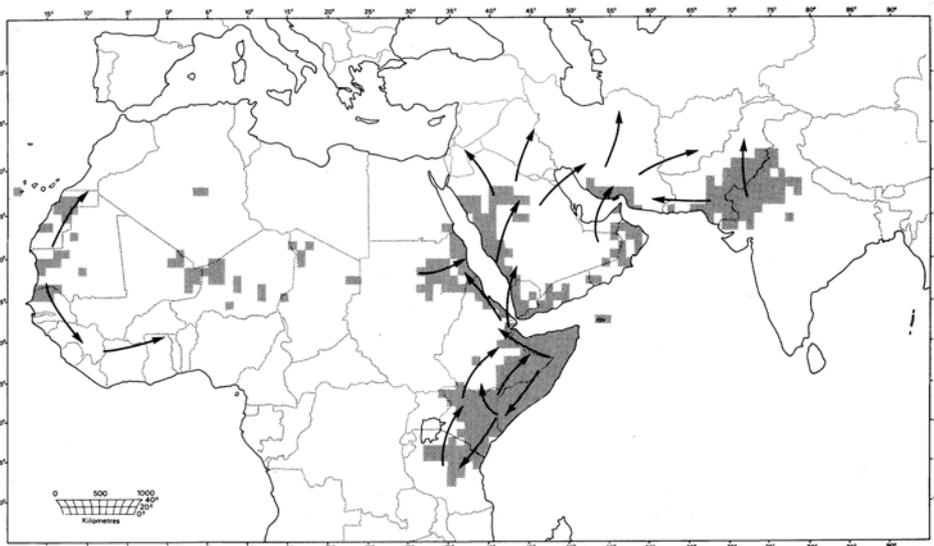
Figure 2 Seasonal breeding areas during plagues and major movements of resulting swarms



Spring breeding areas of the Desert Locust.



Summer breeding areas of the Desert Locust.



Winter breeding areas of the Desert Locust.

Swarm migration after winter breeding

Winter breeding occurs from October in three main areas. Southwest Asia, where summer swarms may either remain and breed in India and Pakistan or move westward and breed after reaching coastal areas of Iran and western Pakistan. A second is the coastal plains of the Red Sea Basin, where some of the northward-moving summer generation swarms remain to breed on rains associated with the Red Sea Convergence Zone. The third is the Somali Peninsula and East Africa. Swarms in this third region may be of several origins. Many will have been produced within the area between March and June during the previous Long Rains or in Arabia during the previous spring. These swarms, which remain immature, become concentrated from June to September in northern Somalia, along a narrow semi-permanent convergence zone between northerly and strong southwesterly winds. From October, they may be joined by summer generation swarms from the Sudan, Ethiopia and from Indo-Pakistan. All of these swarms then move southwards over the Somali Peninsula migrating with or behind the southward moving ITCZ. They mature and breed between October and January in Somalia and in some years in Kenya and northern Tanzania on the Short Rains.

New swarms of the winter generation appear from late November to January. Swarms from the Somali Peninsula frequently move southwestwards initially into Kenya, sometimes continuing into Tanzania. They return later with the ITCZ in a northerly direction, and breed on the Long Rains in Kenya and the Somali Peninsula from March.

Winter generation swarms from the Red Sea basin often join the northward migration of summer generation swarms and breed with them as they move through Arabia, the Middle East and Iran. Late in the spring, they may spread farther north sometimes reaching Turkey. More usually, the swarms move northeastwards into central and northern Iran and Pakistan, sometimes reaching western Afghanistan and occasionally Turkmenistan and Uzbekistan.

Winter breeding also occurs in Western Africa, but more often among recession and upsurge than plague populations. It occurs in countries bordering the Atlantic, around the mountains in southern Algeria, northeastern Mali and northwestern Niger and in northern Chad. Fledging occurs from November to January, extending to February in the north. Second generation summer swarms from Senegal move southwards. The other locusts move northwards to join summer generation swarms and that they mature and breed with them during the spring.

Migration parameters

All major Desert Locust migratory displacements are downwind (Rainey, 1963; Pedgley, 1981). Consequently, locusts can be regarded as parcels of air and their tracks can be simulated by trajectory models (Waloff, 1946; Cochemé, 1966). We have summarized parameters that will enable modellers to estimate when migration will begin. We also give parameters for the time, duration and height of locust flight (Tables 2a & b) because wind speed and direction and, therefore, trajectories change with time and altitude. Further details are available from Pedgley (1981) who summarized the basic information on migration and who cited the original sources.

Rainey (1963) made the most complete series of observations on swarm displacement in relation to wind direction. He obtained a succession of fixes on the swarms, usually from light aircraft, and compared their displacement with the mean wind direction from the surface to the height of the topmost locusts. Draper (in Pedgley, 1981), using these data, showed that the speed of swarm displacement (D km/h) was correlated with wind speed (W km/h) and the maximum height of flight (H m):

$$D = 0.9071W - 0.0199W^2 + 0.0049H - 3.7373$$

He then examined the potential effect of vegetation on the speed of displacement of swarms, by comparing two sets of trajectories simulating the 1968 emigration of swarms from the Sudan to Northwest Africa. He calculated one set using wind speed and direction at 900 metres above ground level. For the other, he used his multiple regression equation. He concluded that the regression equation gave plausible results in areas where swarms would have settled to feed (probably the case for swarms observed by Rainey) but that displacement at wind speed gave better results for areas with little or no vegetation.

TABLES 2a & b. Desert Locust migration parameters and thresholds

TABLE 2a. Migration characteristics

MIGRATION CHARACTERISTICS	
SOLITARIOUS POPULATIONS	GREGARIOUS POPULATIONS
AIR-SPEED	
13-15 km/h (3.8-4.3 m/s)	
ORIENTATION AND GROUND SPEED	
Orientation and vegetation affect ground speed	
<p>Because solitary adults orientate downwind use:</p> <p>Wind speed at height of flight + flight speed (4 m/s)</p>	<p>Swarms drift downwind because of the variation in orientation between the component streams of locusts.</p> <p>Vegetated areas Ground speed (D km/h) correlates with wind speed (W km/h) and maximum height of flight (H metres): $D = 0.9071W - 0.0199W^2 + 0.0049H - 3.7373$</p> <p>Little or no vegetation Assume: ground speed = wind speed (Draper in Pedgley, 1981)</p>
DIRECTION OF FLIGHT	
Downwind	<p>Down the mean wind direction from the surface to the height of the topmost locust (Rainey, 1963).</p> <p><i>Note:</i> If only surface winds known, then displacements will be 10°-20° to the right of the surface wind in the northern hemisphere and to the left in the southern hemisphere.</p>
HEIGHT OF FLIGHT	
Assume related to temperature threshold, often taken to be 20°C Heights are in metres above ground level	
<p>Radar observations (Schaefer, 1976)</p> <p>Average height 400 m (one observation)</p> <p>Maximum height 1 800 m (seen September) 1 000 m (seen October)</p>	<p>Heights of topmost locusts (Rainey, 1963)</p> <p>Minimum 15 m</p> <p>Maximum 1 700 m</p> <p>Anecdotes suggest that immature swarm tracks correlate well with 850 mb winds and mature swarm tracks with 900 mb winds</p>

TABLE 2b. Duration of migration

DURATION OF DAILY AND SEASONAL MIGRATION													
SOLITARIOUS POPULATIONS	GREGARIOUS POPULATIONS												
TAKE-OFF TIME													
<p>Starts sunset + 20-30 minutes (seen visually by Waloff, 1963; Roffey, 1963) Peaks sunset + 70 minutes (peaks seen on radar 15 minutes after darkness prevented visual sighting, Roffey, 1963; Schaefer 1976).</p>	<p>Summer sun-rise + 3-4 h.</p> <p>Cool season & highlands sun-rise + 4-6 h.</p>												
TAKE-OFF THRESHOLDS													
a) Low temperature inhibits take-off													
<p>Assume that take off is related to evening air temperatures and, of those ready to migrate, these percentages will take off</p> <table border="0"> <tr> <td><20°C = 0%</td> <td>25-26°C = 40%</td> </tr> <tr> <td>22-23°C = 5%</td> <td>26-27°C = 80%</td> </tr> <tr> <td>23-34°C = 10%</td> <td>27->28°C = 100%</td> </tr> <tr> <td>24-25°C = 20%</td> <td></td> </tr> </table>	<20°C = 0%	25-26°C = 40%	22-23°C = 5%	26-27°C = 80%	23-34°C = 10%	27->28°C = 100%	24-25°C = 20%		<p>Without sun >23-24°C if immature >26°C if mature</p> <p>With sun >15-17°C</p>				
<20°C = 0%	25-26°C = 40%												
22-23°C = 5%	26-27°C = 80%												
23-34°C = 10%	27->28°C = 100%												
24-25°C = 20%													
b) High temperature inhibits take off and may interrupt flight													
	<p>If morning temperatures high (39°C), immature swarms may delay take-off until evening (26-29°C) and fly at night or may settle around midday and take-off again as afternoon temperatures fall</p>												
c) Strong winds inhibit take-off													
<p>Note that values obtained in field (Roffey, 1963) refer to winds at 2m, whereas, meteorological stations measure surface winds at 10 m where wind speed is higher</p>													
<table border="0"> <tr> <td>2 m</td> <td>take-off</td> </tr> <tr> <td><6 m/s</td> <td>100%</td> </tr> <tr> <td>6-8 m/s</td> <td>50%</td> </tr> <tr> <td>>8 m/s</td> <td>0%</td> </tr> </table>	2 m	take-off	<6 m/s	100%	6-8 m/s	50%	>8 m/s	0%	<table border="0"> <tr> <td>2 m</td> <td>take-off</td> </tr> <tr> <td>>4 m/s</td> <td>swarms may take off during lulls</td> </tr> </table>	2 m	take-off	>4 m/s	swarms may take off during lulls
2 m	take-off												
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6-8 m/s	50%												
>8 m/s	0%												
2 m	take-off												
>4 m/s	swarms may take off during lulls												
d) Effects of food quality and phase of moon insufficiently known to suggest parameters.													
TIME OF SETTLING													
see duration of flight below	Range: -2h to +5h from sunset, see also duration of flight below												
DURATION OF DAILY FLIGHTS													
<p>Average nightly flight = 2h Percentage continuing to fly during night if density halves every 1.5h (Schaefer, 1976) is:</p> <table border="0"> <tr> <td>take-off + 1h</td> <td>= 100%</td> </tr> <tr> <td>take-off + 2.5 h</td> <td>= 50%</td> </tr> <tr> <td>take-off + 4.0 h</td> <td>= 25% to ...</td> </tr> <tr> <td>take-off + 10.0h</td> <td>= 2%</td> </tr> </table>	take-off + 1h	= 100%	take-off + 2.5 h	= 50%	take-off + 4.0 h	= 25% to ...	take-off + 10.0h	= 2%	<p>Daily duration varies with weather:</p> <p>on warm sunny days (sunrise + 2-3h to sunset) 9-10 h (08h to 09h - 18h) in moist air 7 h (10h - 17h) because when Tmax is 30°C then Tmin will be about 20°C in dry air 4 h (12h - 16h) because when Tmax is 30°C then Tmin will be about 10°C</p>				
take-off + 1h	= 100%												
take-off + 2.5 h	= 50%												
take-off + 4.0 h	= 25% to ...												
take-off + 10.0h	= 2%												
MORTALITY DURING MIGRATION													
<p>No field data available. See below for examples of daily losses over time: 2%/day would give a 90% loss in 114 days 5%/day would give a 90% loss in 45 days</p>	<p>Over land assume if warm (>20°C) swarms fly and lose 0.5% a day if cool (<20°C) settled swarms lose 1% a day because predation increases Over water higher rates possible.</p>												
MIGRATION PERIOD ENDS													
<p>End migration a) When locusts fly over area suitable for breeding (See Table 3a below). b) When migrating population dies out</p>	<p>End migration a) when swarms reach area where widespread seasonal rains have begun and maturation begins (See Table 3a below). b) When migrating population dies out</p>												

Breeding

Breeding takes place during wet seasons because rainfall, directly or indirectly, provides the ecological requirements for maturation, laying and the development of eggs and hoppers. Topography also influences when and where breeding occurs because highlands often receive more rain than lowlands and run-off can lead to suitable breeding conditions in wadis tens of kilometres downstream from where the rain fell.

Maturation

Solitarious and gregarious Desert Locusts mature under rather different conditions. Swarms fly over the small areas of green vegetation where solitarious adults land and breed. Immature swarms continue migrating until they reach an area where widespread and heavy seasonal rains have begun. Then, they mature and start to lay within a week, unless it is too cool (air temperatures at 1 m <17°C) (Popov, 1954). Maturation and laying are frequently synchronised over wide areas because the widespread rains marking the onset of a rainy season are also often concurrent. Rainey (1963), for example, noted that swarms matured and laid in widely separated areas between Mauritania and India on very similar dates in July 1954 as rains associated with the ITCZ began. Carlisle, Ellis and Betts (1965) gave examples of synchronicity for most major breeding areas and months. Maturation is delayed in some areas. Swarms often reach summer breeding areas up to two months before the main seasonal rains begin but only occasionally mature and lay on the early rains. In Northwest Africa and the Middle East, swarms arrive in October and November, at the beginning of the rainy season but do not mature and lay until temperatures rise in the spring (Table 3a).

A characteristic feature of solitarious breeding is that individuals are at all stages of development simultaneously. Migrating solitarious adults settle selectively in green areas that they encounter and then mature rapidly. The mechanism by which these night-flying adults detect such areas is unknown, as is the range at which they can locate green vegetation. Concentration into green areas can, however, be an important precursor of gregarization as can the concentration of females during laying (Roffey and Popov, 1968). There is little direct information on the rate at which solitarious adults mature in the field. Indirect evidence of the interval between fledging and subsequent reports of laying in the same breeding area, suggest a minimum of about three weeks. The interval between solitarious adults arriving in an area that promotes maturation and the onset of laying is unknown. By analogy with swarms, it is likely to be about one week in warm weather ($T_{max} >25^{\circ}\text{C}$) or longer if the weather is cool.

Laying

Swarms change from migratory flight to reproductive activities over several days. As the number of fully mature adults increases, they form numerous feeding, marching, copulating and later laying groups whilst the less mature individuals continue to migrate. Swarms often break up as they mature but frequently rejoin when they resume migratory flights between laying cycles. Laying parameters and thresholds are given in Table 3b.

The basic requirement for laying is moist soil at a depth of approximately 5-15 cm. Unless the locust can embed the whole egg-pod in moist soil, she will not lay at that site (Popov, 1958). Female locusts also do not lay in very clayey, stony or saline soils. If females find no suitable sites, they are able to retain fully developed eggs for about three days, after which they will lay on the ground or on trees and bushes (Popov, 1958). Popov found that the equivalent of 15-20 mm of rain 24-48 hours before laying provided the most acceptable sites for laying. In seasons of poor rains, mature adults may reach areas where rain is insufficient for laying and jettison their eggs. This happened over a large part of the Somali Peninsula in late 1955 and contributed to the disappearance of a large swarming population.

The total period for laying by a swarm ranges from 7-30 hours (Popov, 1958). At the end of laying, the pairs separate and the swarm usually leaves the laying site. Because a swarm tends to split up as it matures and lays, it is normal for it to lay several eggfields. All are laid within a day or two and usually within a few kilometres of one another. Other swarms in the migrating group also lay nearby at about the same time. After laying, the swarms reform, continue migrating and lay again about ten days later (Table 3b). Locusts lay egg-pods in groups at the most favourable sites within the eggfield. This behaviour strongly influences the distribution of hoppers and has implications for survey and control

tactics (see section on population sizes). Laying density among solitarious females also affects phase change (Simpson et al., 1999, see section on phase change).

TABLE 3a-d. **Desert Locust breeding parameters and thresholds**

TABLE 3a. **Maturation parameters**

MATURATION PARAMETERS AND THRESHOLDS	
SOLITARIOUS POPULATIONS	GREGARIOUS POPULATIONS
RAINFALL THRESHOLD FOR INDUCING MATURATION AND LAYING	
<p>Locusts mature if they reach green areas. Assume area is green if: 25 mm rain fell in previous month or 50 mm rain fell in previous two months</p> <p>Higher values (30 mm) may be necessary to ensure hopper survival in early summer when high temperatures and low humidities cause high evaporation (Bennett, 1976)</p> <p>Run off important source of moisture in: Saharan Massifs; Red Sea coastal plains; Gulf of Aden coastal plains.</p>	<p>Swarms mature as main rains begin. Assume this occurs if: 25 mm rain fell in previous week or 50 mm rain fell in previous two weeks</p> <p><i>Note:</i> immature swarms fly over desert habitats around mountains where solitarious adults breed to areas of higher rainfall (80-400 mm a year)</p>
DURATION OF MATURATION TO LAYING	
Unknown; use swarm data	about 1 week if warm (Tmax >25°C) longer if cooler
DELAYED SWARM MATURATION	
a) Until widespread seasonal rains begin	
Assume non-swarving populations similarly affected.	<p>1. South of Sahara, and in India maturation and laying usually not induced by rains in May or June that locally may exceed the threshold. Breeding starts in July with the onset of summer rains.</p> <p>2. Northern Somalia, immature and partly mature swarms concentrated along the windshift line from May to September do not mature and lay even though engulfed in heavy afternoon showers. They migrate, mature and lay from October when the Short Rains fall on the Somali Peninsula</p>
b) until spring temperatures rise	
Not applicable as these areas are outside the recession area.	<p>Northwest Africa, Egypt, the Middle East, northern Arabia the Mekran of Iran and Pakistan and northwestern India Swarms arriving between October and January normally remain immature until temperatures rise in late January or early February</p>

TABLE 3b. Laying parameters

LAYING PARAMETERS AND THRESHOLDS																																																																
SOLITARIOUS POPULATIONS	GREGARIOUS POPULATIONS																																																															
EGG-POD DENSITIES Vary with habitat																																																																
<p>Too few field values recorded to give values</p> <p>Note: in restricted habitats individuals form groups whilst laying and also lay over a period. Example given was several hundred pods of varying ages with maximum density of 71 pods in 900cm² (Roffey and Popov, 1968) In addition, this crowding promotes gregarization whereas females laying in isolation solitarize their offspring (Simpson et al. 1999)</p>	<p>Usual distribution 200-500/m² in groups of tens to hundreds</p> <p>Stower Popov and Greathead (1958) found pods grouped so that 99% of pods were in 4% of an eggfield where: Average density was 5/m²</p> <p>Ellis and Ashall (1957) found groupings: In uniform habitats of 1-2/m² In restricted habitats of <1 000/m²</p> <p>Effects on band survival Bands dissociated when average egg-pod density was 0.14-1.4/m²</p>																																																															
NUMBER OF EGGS PER POD																																																																
Varies with female age, rainfall and vegetation (Ashall and Ellis 1962) Solitarious adults produce more eggs per pod than gregarious locusts																																																																
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<p>No direct field observations but Tamesna dissections suggest: 3 pods/female in an upsurge (Roffey and Popov, 1968)</p> <p>Interval use swarm values (6-11 days)</p>	<p>Analysis of East African field reports shows three layings by swarming populations</p> <p>First and second layings of equal scale as most females participate</p> <p>Third laying smaller as most females die before third laying (Popov, 1958a)</p> <p>Analysis of 3 years laying in Somalia indicates 50% pods laid are in eggfields found during first laying (Joyce, 1962)</p> <p>Interval 6-11 days depending on temperature</p>																																																															

TABLE 3c. Incubation and hopper development rates

SOLITARIOUS POPULATIONS	GREGARIOUS POPULATIONS																												
DURATION OF INCUBATION																													
Use values for swarms	<p>Egg development is dependent upon soil temperature around the egg-pod but mean daily percentage development (y) is almost as reliably estimated by mean daily air temperature as by soil temperature</p> $y = 9.416e^{-0.00357(35.019t)^2}$ <p>where y is mean daily percentage development t is mean of maximum and minimum screen temperature for a day (°C) e is the Napierian constant, 2.718</p>																												
HOPPER DEVELOPMENT																													
a) number of instars																													
<p>5 and 6 instars occur</p> <p>Stower and Greathead (1969) observed 20% of field population with 6 instars.</p> <p>Rao's (1960) data on scattered populations in Indo-Pakistan, 1931-39 showed that the proportion of hoppers with 6 instars in 63 samples was inversely related to breeding success.</p> <p>During plague decline (1931-33) proportion of hoppers with 6 instar hoppers rose from 6% to 94%.</p> <p>During recession (1933-39) proportion with 6 instars varied from 7-71% mean 38%</p>	<p>5 instars</p>																												
HOPPER DEVELOPMENT																													
b Duration of development depends upon air temperature																													
<p>Assume hoppers with 5 instars take same time as swarms. Hoppers with 6 instar take an extra 7-10 days to develop.</p> <p>Note: Data are sparse and contradictory. Hoppers with 6 instars took an extra 5 days to develop (Stower and Greathead, 1969) but Uvarov (1966 p. 337-338) notes that this is not invariably so. In laboratory studies, they took 3.5 days less than those with 5 instars.</p>	<p>Reus and Symmons (1992) based their hopper development rates on graphs in Wardhaugh, Ashour <i>et al.</i> (1969).</p> <p>If temperature between 20°-33°C $y = a*t - c$ where y is the mean daily percentage development t is the mean of the maximum and minimum screen temperature for a day (°C) a & c are constants varying with instar</p> <table border="1"> <thead> <tr> <th>Instar</th> <th>a</th> <th>c</th> </tr> </thead> <tbody> <tr> <td>1st</td> <td>0.22</td> <td>3.16</td> </tr> <tr> <td>2nd</td> <td>0.32</td> <td>5.12</td> </tr> <tr> <td>3rd</td> <td>0.41</td> <td>6.87</td> </tr> <tr> <td>4th</td> <td>0.55</td> <td>9.03</td> </tr> <tr> <td>5th</td> <td>0.86</td> <td>13.52</td> </tr> </tbody> </table> <p>If temperature between 10-20°C $y = 100e^{(t-10)*a} - 100$ where y is the mean daily percentage development t is the mean of the maximum and minimum screen temperature for a day (°C) a is a constant which changes with instar e is the Napierian constant 2.718</p> <p>Values for 'a' are:</p> <table border="1"> <tbody> <tr> <td>1st instar</td> <td>0.00127</td> </tr> <tr> <td>2nd instar</td> <td>0.00120</td> </tr> <tr> <td>3rd instar</td> <td>0.00135</td> </tr> <tr> <td>4th instar</td> <td>0.00187</td> </tr> <tr> <td>5th instar</td> <td>0.00361</td> </tr> </tbody> </table>	Instar	a	c	1st	0.22	3.16	2nd	0.32	5.12	3rd	0.41	6.87	4th	0.55	9.03	5th	0.86	13.52	1st instar	0.00127	2nd instar	0.00120	3rd instar	0.00135	4th instar	0.00187	5th instar	0.00361
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TABLE 3d. Mortality between laying and fledging

SOLITARIOUS POPULATIONS	GREGARIOUS POPULATIONS																																										
NUMBER OF EGGS PER GENERATION																																											
400 average number/female (Roffey and Popov, 1968)	140 average number/female (Joyce, 1962) Mean/pod = 85.82 - 12.02x where x = oviposition number (Cheke, 1978)																																										
EGG MORTALITY																																											
<p>Only two quantitative studies exist.</p> <p>No egg parasitism or predation recorded in Tamesna (Roffey and Popov, 1968)</p> <p>Greathead (1966) suggested parasitism by <i>Scelio</i> would prove important but, to date, no data support this suggestion.</p> <p>Use Greathead's (1966) suggestion that the average loss to eggs is: 10% inviability 3% hatching failure</p>	<p>Greathead (1966) and Joyce (1962) summarised the few field studies. All are from the Central Region.</p> <p>High mortality if soil temperature >35°C</p> <p>Total losses noted vary from about 5-65% <10% inviability 3-4% fail to hatch <40% from predation <10% from mould, bacteria, desiccation</p> <p>Assume the average loss to eggs is: 20% mortality 10% inviability 3% hatching failure</p>																																										
HOPPER MORTALITY																																											
<p>Only two complete studies exist and both are from the Eritrean coast.</p> <p>Stower & Greathead (1969) found: 40% parasitised by <i>Blaesoxipha filipjevi</i> 8% predation by birds and spiders 40% unexplained loss in instars 1 & 2 which they interpreted as removing unsuitable genotypes</p> <p>Roffey and Stower (1983) also found the highest mortality (76%) in the first instar.</p> <p>Assume the following hopper mortalities:</p> <p>during instar 1 80% during instars 2-5/6 20% at each moult 5%</p>	<p>Little quantitative work exists on mortality in gregarious populations.</p> <p>Ashall & Ellis (1962) found high losses during instar 1. Cannibalism reached 30-50% when poor rains led to inadequate vegetation and caused greater losses than predation.</p> <p>Greathead (1966) found that predation and parasitism varied greatly with habitat, season and locality.</p> <p>Assume the following hopper mortalities under very favourable conditions:</p> <p>during instar 1 70% during instar 2 20% during instars 3-5 10% at each moult 5%</p>																																										
MULTIPLICATION RATES																																											
<p>Observed rates 16 Tamesna, Niger 1967 (Roffey and Popov, 1968) 0.03 Wachiro, Eritrea 1960 (Stower and Greathead, 1969) 0.14 (mean)0-0.5 (range) Arkiko, Eritrea 1953/4 (Roffey and Stower, 1983)</p> <p>Suggest using the following Relationship with rainfall and habitat Total rain (mm) in months M₋₁ and M₀</p> <table border="1"> <thead> <tr> <th>25</th> <th>30</th> <th>40</th> <th>60</th> <th>80</th> <th>100</th> <th>120</th> </tr> </thead> <tbody> <tr> <td>0.01</td> <td>0.10</td> <td>0.30</td> <td>1</td> <td>3</td> <td>10</td> <td>16¹</td> </tr> <tr> <td></td> <td>0.01</td> <td>0.10</td> <td>0.30</td> <td>1</td> <td>3</td> <td>10²</td> </tr> <tr> <td></td> <td></td> <td>0.01</td> <td>0.10</td> <td>0.30</td> <td>1</td> <td>3³</td> </tr> <tr> <td></td> <td></td> <td></td> <td>0.01</td> <td>0.10</td> <td>0.30</td> <td>1⁴</td> </tr> <tr> <td></td> <td></td> <td></td> <td></td> <td>0.01</td> <td>0.1</td> <td>0.3⁴</td> </tr> </tbody> </table> <p>¹⁻⁴ see text</p>	25	30	40	60	80	100	120	0.01	0.10	0.30	1	3	10	16 ¹		0.01	0.10	0.30	1	3	10 ²			0.01	0.10	0.30	1	3 ³				0.01	0.10	0.30	1 ⁴					0.01	0.1	0.3 ⁴	<p>Observed rates varied from 0.005-1.6 with control and natural enemy losses included 0.005 Short Rains failed 1955 (Joyce, 1962) 0.5 Long Rains 1961 status not given (Joyce, 1962) 1.6 Short Rains good 1957 (MacCuaig, 1958)</p> <p>Maximum 11 for a single laying and 22 for two layings without natural enemies or control and where females lay 70 eggs per pod. 16.5 for insects that lay 100 eggs. (Greathead, 1966 who makes no adjustment for fewer eggs being laid in second and subsequent pods)</p> <p>Maximum of 14 in a generation without natural enemies or control and where females lay 70 eggs per pod and deposit 50% eggs at first laying (Joyce, 1962, used Greathead's data but allowed for fewer eggs in subsequent layings).</p>
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Egg development

Eggs need to absorb approximately their own weight of water to complete their development (Shulov, 1952; Roonwal, 1954; Hunter-Jones, 1964). This is normally accomplished in the field within the first few days after laying. Should they absorb insufficient water at this time, eggs in the laboratory may remain dormant for up to 80 days (Shulov and Pener, 1963). Popov (1965) reports a case of eggs hatching in Saudi Arabia 60 days after laying and a week after heavy rain broke the dormancy.

The incubation period depends upon soil temperature, providing that the eggs have absorbed enough water to complete development. Wardhaugh, Ashour *et al.* (1969) demonstrated relationships between mean screen temperatures (12-34°C) and incubation periods (10-65 days) during a series of field-cage experiments in Saudi Arabia. Draper (in Pedgley, 1981) suggested that the relationship based on Pradhan's (1945) work gave better results at lower temperatures and this relationship was used by Reus and Symmons (1992) to predict incubation periods (Table 3c).

Pedgley (1981) summarized field reports of incubation periods from each seasonal breeding area for the period up to 1966 and suggested that they should be used in conjunction with the development period maps (Symmons, Green *et al.* 1973) and the subsequent model (Reus and Symmons, 1992) to give guidance on potential variation. The duration of incubation was 10-14 days in summer breeding areas of Africa, Arabia, India and Pakistan where mean air temperatures exceed 25°C. At higher altitudes with lower temperatures in Ethiopia, durations were longer, but rarely exceeded 20 days. Durations rose to over 30 days in October during second generation summer breeding in India, a month when temperatures decrease rapidly. Mean air temperatures exceed 25°C throughout the year in most Long and Short Rains breeding areas in eastern Africa and reported incubation periods were again 10-14 days rising to 20 days at altitude. Incubation periods of 11-15 days were usual in coastal areas around the Red Sea and Gulf of Aden but they were higher though rarely exceeded 20 days during the winter in cooler areas north of 20°N. In the winter-spring breeding areas of Arabia and the Middle East temperatures decrease to a minimum in January. Between November and February, reported incubation periods increased from 15 to over 60 days and then decreased markedly to 11-15 days between March and June. Variation was apparent between warmer coastal and cooler interior sites and between southern and northern areas. In the Eastern Region, breeding on winter rains is confined to the coastal areas of southern Iran and western Pakistan and incubation reports varied from 15 to 22 days. Laying occurred further north and at higher altitudes between February and March and incubation periods shortened as temperatures rose. They were highly variable ranging from 10 to 40 days. By May, laying had ceased in coastal areas, temperatures had risen and incubation periods were mainly between 14 and 21 days. In the winter-spring breeding area of Northwest Africa, the pattern of incubation periods is similar to that in the Eastern Region but much longer periods were reported. Laying in the coldest month, January was restricted to the western coast of Morocco and the northwestern coast of Libya. From February as temperatures rise, laying was more widespread and occurred at greater altitudes. During these cooler months reported incubation periods were highly variable, ranging from 17 to 62 days. The Table does not show if there was a difference between coastal and interior sites and between southern to northern areas.

Hopper development

Hatching usually occurs within two to three hours of dawn. Although all eggs from a pod usually hatch on the same day, different pods within a group may hatch over two to three days. Hatching may be more protracted after a long incubation, a period of six days being noted in Hasa, Saudi Arabia (Pedgley, 1981).

Most studies on the duration of hopper development concerned the effects of temperature and humidity. Laboratory and field cage studies showed a linear relationship between temperature and development that can be used to estimate hopper durations (Table 3c). Less variation exists in the duration of hopper than of egg development because hoppers are able to regulate their body temperature by moving in and out of the sun.

Determining hopper development periods from field reports gave fewer complete records than for incubation periods and data from an area were often grouped (Pedgley, 1981). This is because where hatching was observed hoppers are usually controlled before fledging whilst most reports of fledging come from areas where hatching was unobserved. There is also less certainty about relating records of hatching and fledging because hopper bands march. A general pattern for each breeding area follows. In the summer breeding areas, most hopper development periods lay within the range 30-39 days, with 40 percent in the range 30-34 days. Longer periods occurred in the mountains of Ethiopia and during

second generation breeding. Hopper development periods during the Short Rains in eastern Africa were more uniform with 63 percent lying between 35 and 39 days (range 32-45 days). A greater range (27-47 days) was reported during Long Rains breeding. In neither season was there a marked effect of altitude on the duration of development. On the coastal plains around the Red Sea and Gulf of Aden, development periods were generally short during the warmer months (April- September) when 71 percent lay between 30 and 39 days (range 24-39 days). The range during the cooler months was 28-48 days. Development periods are longer at the beginning than the end of winter-spring breeding in Northwest Africa, Arabia, the Middle East and the Eastern Region. Field records varied from 25-57 days but longer periods probably occur.

Egg and hopper mortality

Egg mortality

Greathead (1966) summarized the few studies on egg mortality in gregarious populations (Table 3d). All the studies took place in the Central Region and showed four regular and important causes of death. Three caused constant losses: unsuitable sites leading to desiccation, mould and bacterial damage (under ten percent); inviability (ten percent), failure to hatch (three to four percent). He found that losses due to predation and parasitism were more variable. Generally, the losses were between 10 and 40 percent but occasionally an individual eggfield was destroyed. Popov (1965) found similar losses and noted some regional differences as he moved north, from the Savanna to the Saharan zones, in West Africa and between different agricultural habitats in Pakistan (Table 4).

Even fewer data exist on egg mortality among solitarious populations. Roffey and Popov (1968) recorded no parasitism or predation of eggs in Tamesna and very few inviable eggs. Greathead (1966) suggested that the parasite, *Scelio* would prove to be an important cause of mortality, but to date records do not support this suggestion.

TABLE 4. Regional variation in egg mortality rates (after Popov, 1965)

Cause of losses (%)	WEST AFRICA			ARABIA Arabian interior	PAKISTAN		
	Saharan (Tamesna)	Sahelian (Adrar des Iforas)	Savanna (Gourma)		Dry farming	Irrigated crops	Rain-fed crops
Natural enemies	2	5-20	>80	33	22	9	1.5
Poor sites	2-7	2-7	2-7	10	8	5	1
Inviability	5	5	5	5	2-3	2-3	2-3
Hatching failure	2	2	2	2	2.5	2.5	2.5
Maximum total	14	34	94	50	35.5	19.5	8
Number eggs/pod	65-75			not given	65.5		
Multiplication rate from laying to hatching	25-32		4-5	17	22.5	28	30

Hopper mortality

Greathead (1966) summarized data on parasitism and predation among hoppers. He noted that rates varied greatly. Whilst agreeing with Dempster (1963) that rainfall was a major factor affecting survival, he disagreed with the assumption that natural enemies would be unable to breed throughout the year and thus could never be effective in controlling hopper populations. In support of this view, he cites the importance of natural enemies in Red Sea habitats close to wadi cultivations where they caused high mortality in studies by Waloff (1963) and by Stower and himself (1969). In addition, he notes that rates of predation can be high in seasons and places where locust and bird migrations coincide. He concluded, after estimating the rates of mortality from other factors, that natural enemies would have little effect on reducing large gregarious populations but could hasten the decline of diminishing populations.

Only two complete studies on hopper mortality exist for solitarious populations. Both took place on the coast of Eritrea near or in seasonally cultivated areas on parts of *dissocians* populations. In addition, these habitats are not typical of many solitarious breeding areas because they contain considerable areas of perennial vegetation (Stower and Greathead, 1969; Roffey and Stower, 1983). In both studies, unexplained mortalities were high in early instars. Roffey and Stower (1983) recording the highest

mortality of first instars (76 percent) in open parts of the habitat. Stower and Greathead (1969) found an unexplained loss of 50 percent in the first two instars and attributed it to the elimination of unsuitable genotypes. They also noted that these early losses were so widely observed, that they may be universal. Greathead (1966) reviewed mortality of eggs and hoppers in solitary and gregarious populations and suggested the mortality rates given in Table 3d.

Multiplication rates

Multiplication rates in swarming populations

Quantitative estimates of numbers of the parental and filial generation of gregarious populations exist but include mortality from chemical control. For example, Desert Locust Survey measured the sizes of the parent and filial swarms with aircraft at the beginning and end of Short Rains breeding on the Somali Peninsula in 1955 and 1957 and of Long Rains breeding in 1961. The numbers of locusts present were then calculated using density estimates that were based on photographs and on mortality counts of swarms made in the same area (Joyce, 1962). The results indicate the variability of multiplication rates but are confined to a single geographical area that is somewhat atypical of Desert Locust habitats.

The multiplication rate was very low (0.005) in 1955 when the Short Rains failed. The parent population was large, between 3 100 and 3 900 km² of swarms that probably contained 10¹¹ locusts. After poor breeding and a hopper control campaign, only a few small swarms formed containing no more than a few hundred million locusts. As a result, the Somali Peninsula remained free from swarms until the 1956-1957 upsurge. The multiplication rate was higher in 1957. MacCuaig (1958) estimated multiplication as exceeding 1.6. The parent swarms measured 2 600 km² and contained about 1.6 x 10¹⁰ locusts. The progeny formed after a generally good Short Rains breeding and a large-scale ground campaign against the hoppers was 1 300 km² of medium to dense swarms containing 2.5 x 10¹⁰ locusts. MacCuaig estimated that chemical control killed 3 x 10¹¹ locusts and speculated that the multiplication rate could have been as high as 20 without control and natural mortality. He surmised that the effect of natural enemies would have reduced the multiplication rate to 10. Joyce (1962) calculated a multiplication rate of 0.5 for Long Rains breeding in 1961 but did not comment on the quality of the rains. In that year, the parental population was about 4 x 10¹⁰ in 500-600 km² of medium dense swarms and the filial population was about 2 x 10¹⁰ locusts in 500 km² of swarms. He attributed 24 percent of the 99.5 percent population reduction to control operations and natural enemies.

Multiplication rates in non-swarming populations

Multiplication rates from the two quantitative studies on *dissocians* populations on the Eritrean Coast were low. Stower and Greathead (1969) recorded a rate of 0.03 between laying and fledging and Roffey and Stower (1983) recorded an overall rate of 0.14. In the latter study, the rates for the six sub-populations involved, ranged from 0 to 0.48. Two less complete studies provide evidence of multiplication rates that led to gregarization. The authors of both studies commented on the small impression made on the populations by natural enemies. Roffey (in Joyce, 1962) estimated that an initially solitary population on the northern coastal plain of Somalia increased up to 1 000 times over three consecutive generations despite intensive control measures against the third generation. Multiplication rates for a single generation varied between 4 and 10 times. Observers concluded that the few predators present would have been unable to affect population levels markedly because the groups of hoppers were so widely distributed. Roffey and Popov (1968) calculated that an initial population of 5 x 10⁶ adults in Tamesna, Niger laid approximately 10⁹ eggs and became about 80 x 10⁶ late instar hoppers. This represents a multiplication rate of about 16. In contrast to the Eritrean studies, mortality due to natural enemies was low.

Biotic factors may have considerable effect on eggs and hoppers in certain locations and under certain circumstances, but there is little doubt that the main factor governing breeding success is rainfall. Experience further suggests that some habitats are more likely to result in high multiplication rates than others should they receive similar amounts of rain. A first attempt is made in Table 3d to indicate regional variations in multiplication rates following different totals of rain in the month (M₀) in which breeding began, and the preceding month (M₋₁). Other factors considered were the size of the habitat, its ability to produce a substantial cover of broad-leaved food plants and the potential size of its predator and parasite populations. The values proposed are tentative and need validating in the field. The values observed among dissociating populations at Arkiko, Eritrea (class 4 line 2) indicate the tentative nature of our initial suggestion of four classes.

- **Class 1 areas** support the highest multiplication rates. They have a significant proportion of sandy or silty soils that produce a substantial cover of broad leaved food plants such as *Tribulus* and *Heliotropium* after rain. The 'green' areas produced exceed 100 ha. Class 1 areas have low parasite and predator populations both because locust breeding frequency is low and because they are remote from areas of higher rainfall that support permanent vegetation or cultivation.
Examples: Tamesna in Mali and Niger; Mourdi in Chad and Soutouf in southern Morocco.
- **Class 2 areas** support substantial but lower multiplication rates either because breeding frequency and hence predator, parasite load is higher or because they contain a lower proportion of broad leaved plants.
Examples: Indo-Pakistan border; the edges of the Central Saharan Massifs, the Red Sea coastal plains away from cultivations; Oman, inland from the Jebel Akhdar.
- **Class 3 areas** have a high predator and parasite population either because they are higher frequency breeding areas or because they are close to cultivated areas. Multiplication rates are also depressed because broad leaved herbs are not dominant.
Examples: Rajasthan in India; Baluchistan in Pakistan and Iran; the interior of the Sudan, of Saudi Arabia and of Yemen.
- **Class 4 areas** have similar characteristics to those in class 3 but they are small and isolated. The second line of values was those observed among a dissociating population at Wachiro and at Arkiko (Stower and Greathead, 1969; Roffey and Stower, 1983).
Examples: Red Sea coastal plains adjacent to cultivations.

Fledgling behaviour

For the first few days after fledging, the individuals, whether solitary adults or gregarious march, bask and feed like hoppers. Then, increasing numbers take short and then longer and higher flights, as their integument becomes hard enough to allow sustained flight. Whole groups start to leave band areas about three to six days after fledging. During the next few days, the groups coalesce, and start to form swarms. About two weeks after fledging, swarms and solitary locusts do one of three things:

1. emigrate;
2. mature rapidly and breed again in the same general area;
3. migrate short distances and breed several months later.

Emigration is most likely to occur if the vegetation is beginning to dry out. This happens when seasonal rains are moderate and no rains fall late in the season. Locusts will then emigrate as long as temperatures below the threshold for flight (<20°C) do not occur in the evening for solitary adults or in the morning for swarms.

Rapid maturation and further breeding occur if annual and perennial vegetation remains green and the soil is moist 5-15 cm below the surface. This is likely if early rains were heavy or more usually if further falls of 25 mm occur in the month when late instars are present.

Locusts migrate when it is warm enough for flight. They do not migrate for long distances in cool weather as temperatures quickly fall below the threshold for flight. They breed when temperatures rise and sufficient rain (25 mm) falls in a month to induce maturation. For example, some second generation monsoon swarms forming in November and December may overwinter in Punjab, northern India and breed the following spring.

TABLE 5. Fledgling behaviour

SOLITARIOUS POPULATIONS	GREGARIOUS POPULATIONS
SWARM FORMATION in days from fledging	
Not applicable	Days 1-3 integument hardens, fledglings begin to fly. Days 3-6 groups start to leave band area and to form swarmlets. Days 7-10 swarms form. Days 14-21 swarm formation completed but they may be <100 km downwind of the breeding area.
DURATION FLEDGING TO MIGRATION if mean daily temperature 25° C	
Use swarm values	10% ready to migrate in 10 days 20% ready to migrate in 11 days 40% ready to migrate in 12 days 20% ready to migrate in 13 days 10% ready to migrate in 14 days

Phase change:

An important task of any population model is the ability to predict phase change between solitary and gregarious forms which alters behaviour, colour, morphometry, endocrine physiology, reproductive development and fecundity. Simpson, McCaffery and Hägele (1999) with their colleagues have recently clarified the effect of vegetation dispersal and concentration at low percentage cover on phase change in a series of laboratory and field experiments. They selected behaviour to analyse phase change because it represents the first visible sign of change, occurs rapidly in response to variation in population density, and can be monitored continuously. In contrast, colour and morphometry, other easily and frequently monitored changes, alter solely when an insect moults. In addition, they argued that behaviour provides positive feedbacks that drive phase change towards one or other extreme, and allows underlying physiological mechanisms to be correlated with a high degree of temporal resolution.

Behavioural gregarization was acquired rapidly and 4-8 hours after crowding the behaviour of individuals was indistinguishable from those of crowd-reared, gregarious locusts. Only tactile stimulation applied alone was able to cause gregarization. The sight and smell of other locusts applied singly was ineffective but elicited gregarious behaviour in combination. They also demonstrated that females use the extent and recency of their crowding and the phase of their mate to affect the phase-state (behaviour and colour) of their offspring by adding a gregarizing factor to the foam surrounding the eggs. Behavioural solitarization differed according to the duration of crowding that preceded isolation. Isolated locusts, crowded for 24h or 48h and then re-isolated, lost their gregarious behaviour as rapidly as it had been gained. In contrast, re-isolated crowd-reared nymphs partly solitarized in the first hour but required isolation over several stadia before further solitarization occurred. This ability to gregarize or solitarize offspring as late as egg-laying and differences in dissociation with crowding history have important implications for the initiation and disappearance of swarms in field populations.

In nature, increases in vegetation abundance precede gregarization and subsequent studies explored the effect that varying the micro-structure of the experimental environment had on the distribution of locusts and hence their phase status. Isolated-reared locusts presented with a single food source, perch or warm spot increased their grouping over time and behaved gregariously after 4 hours. Whereas, multiple sites, especially food sources inhibited interaction and gregarization (Bouächi, Simpson and Roessingh, 1996).

A further refinement was to examine the effects on gregarization of varying locust density and the distribution of a fixed number of resource sites (Collett, Despland *et al.*, 1998). They used fractal geometry to describe vegetation distribution because it often exhibits self-similar structure at different scales which would be of practical importance in predicting phase-change if found to be true for desert locust habitats over a wide range of scales. They studied vegetation distribution at scales similar to the size of the test locusts both in the laboratory and in simulations from an individual-based model, in which behavioural decision rules for the 'virtual' locusts, were based on parameters derived from previous experiments. In their studies, fractal dimensions represented low, medium and high indices of

clumping and the highest possible fractal dimension when all 20 sources were in a single clump was 1.28. The resource would fill progressively more of the space being studied as the fractal dimension rises towards 2. An initial laboratory experiment showed that population gregarization increased with locust density and fractal dimension (clumpiness) of the food sources. Simulations produced similar results. Average simulated population gregarization was unaffected by initial phase-state suggesting that a single equilibrium level of gregarization exists for a specific habitat and population density. Gregarization due to locust interactions on or moving between food patches occurred whether or not phase-behaviour was included in simulations but gregarization was critically related to resource distribution only when phase-behaviour was included and the 'virtual' solitary locusts could avoid contact in scattered vegetation and received frequent contacts leading to mutual attraction in clumped vegetation (high fractal dimension). Gregarization increased gradually with population size when food sources were at low fractal dimensions. In contrast, when the resource was concentrated, gregarization increased rapidly and synchronously in relation to population density as the contact rate between individuals exceeded the gregarization threshold. The model predictions were then tested in laboratory experiments where different patterns of food resource representing a range of fractal dimensions was presented to solitary-reared locusts at different densities for 8 h after which their behavioural phase was assayed (Despland, Collett and Simpson, 2000). The amount of time spent feeding was similar for all fractal dimensions but insects in a high fractal dimension habitat were more active; moved farther, spent more time walking and climbing and less time quiescent than when habitats were less clumped. Insects under high fractal dimensions also formed more aggregations and higher levels of crowding and synchronous activity occurred. The more active individuals were found to be more gregarized when assayed

Despland and Simpson (2000) devised a field experiment to test the effect of vegetation micro-structure on small semi-field populations and showed that phase differences related to vegetation structure were maintained over short periods and were transmitted to progeny. Field arenas, containing an oviposition site, enclosed food plants that gave approximately 13% ground cover but were distributed at low (0.96), medium (1.54) and high fractal dimensions (1.78). Adult behavioural phase state assayed at the end ten days in an arena was found to be progressively more gregarious with increasingly clumped vegetation. Insects kept with clumped vegetation showed other features of gregarious populations, they formed basking groups and mature males became yellow. Behaviour of hoppers with parents from clumped vegetation, tested within 4 hours of hatching, were more gregarious than progeny of adults kept in more scattered vegetation. Such clear-cut differences were not found with offspring colour.

These experiments demonstrate the important role that vegetation micro-structure plays in desert locust gregarization over spatial scales of centimetres to a few metres. They do not cover the role vegetation plays in the high levels of population growth that precede the appearance of swarms in the field as outbreaks and more importantly upsurges leading to plagues develop. Some indications of factors noted in field observations associated with gregarization are presented below. Areas to be studied are on quite a different scale to those outlined above since rains giving rise to vegetation within which populations increase over a number of generations affect tens of thousands of square kilometres. A feature common to many accounts is the emphasis on high densities of non-gregarious locusts within large areas of well-developed vegetation. Roffey and Popov (1968) found populations had not fully gregarized at densities of 30-40/m² where the vegetation cover was 60% but that bands and, or swarms appeared among less dense parts of this populations (>20/m²) as vegetation dried where vegetation cover was low (<20%) suggesting that clumping at an appropriate scale may have occurred in the latter areas but not in the former. Despland (2003) hopes to relate the fractal characterization of landscapes at such larger areas to their outbreak history. If successful such studies may begin to bring greater clarity to the ecological role that these larger area patterns play in upsurge development.

Gregarization

Airborne concentration

Gregarization, in the field, is preceded by concentration and multiplication. Waloff (1966) discusses the importance of airborne concentration of solitary adults in gregarization. She notes the appearance of gregarious populations following breeding on the exceptionally abundant rains associated with low-level convergence systems and also records swarms formed by the direct effects of convergent airflow. A well-documented example of the first category, was the tropical cyclone in Oman in October 1948 that formed the initial event of a major plague upsurge. The cyclone is thought to have concentrated locusts from surrounding countries into a relatively restricted area made suitable for breeding by the

associated heavy rains. Rainey (1965) describes these and similar earlier events and Bennett (1976) describes the role played by a later cyclone in Oman on the development of the 1968 plague. Waloff (1966) suggested, however, that the direct increase in density was less important than the concentration of adults into the areas of associated rainfall where multiplication by breeding could occur. Several authors, Rao (1942), Rainey (1951), Cochemé (1966) and Skaf (1978) not only described the effects of large-scale synoptic convergence, but have deduced or demonstrated swarm formation due to the effects of meso-scale convergence. Bhatia (1961) deduced that the passage of a trough of low pressure over Rajasthan did not produce swarms but concentrated mature adults sufficiently for their progeny to form bands.

Concentration into green habitats

Waloff (1966) tentatively suggested that swarm formation by convergence may occur more readily among maturing adults or among those that are also being grouped by environmental factors. Roffey and Popov (1968) showed that solitary adults selectively landed in the greenest habitats. They found that adult densities were 50-100 times greater than if the insects had been randomly distributed throughout the area.

TABLE 6. Gregarization processes

CONCENTRATION OF SOLITARIOUS ADULTS BY SELECTIVE SETTLING IN GREEN VEGETATION						
	Concentration factor					
	Very green	Fairly green	Slightly green			
A.	1 000	200	50	A. High contrast habitats with relatively small areas of green annuals and few or no perennials e.g. Tamesna		
B1.	200	50	20	B. Low contrast habitats with considerable perennial vegetation form two groups:		
B2.	50	25	10	B1. With wadis, e.g. Red Sea and Gulf of Aden coastal plains; Adrar des Iforas; Air; Mouydir; Tademait; Baluchistan (interior)		
				B2. Without wadis e.g. Indo-Pakistan summer breeding area, Baluchistan coastal plains		

CONCENTRATION WITHIN HABITAT DURING MATING AND LAYING	
Assume laying groups may form if average adult density is 2/ha	

EFFECTS OF VEGETATION ON GROUP FORMATION				
Type of plant growth		Hoppers per plant inducing grouping		
		instars	1-2	3-5
small, open growth	e.g. <i>Malcomia</i>		10	5
medium, open growth	e.g. <i>Aerva</i>		40	20
large, open growth	e.g. <i>Panicum</i>		100	50
	dense growth e.g. <i>Tribulus</i> and <i>Heliotropium</i>		200	100

EFFECTS OF VEGETATION COVER ON MARCHING						
Density inducing marching	Vegetation cover					
	1%	2%	5%	10%	20%	50%
Hoppers '000/ha:						
Instars 1-2	40	80	200	300	400	500
Instars 3-5	20	40	100	150	200	150

POPULATION EXTENT AND NUMBERS REQUIRED TO PRODUCE DAY-FLYING SWARMS	
Numbers	Areas of hoppers producing 10⁷ adults
Field records are rare but suggest	40 ha of high density hoppers in dense
10 ⁶ locusts required for daytime flights	vegetation, or
10 ⁷ locusts required for swarm emigration	500 ha hoppers in sparse vegetation

Concentration within habitats during breeding

Further concentration occurs in habitats that promote maturation. This results from a range of activities including males searching for females and females searching for suitable laying sites. Roffey and Popov (1968) found groups of laying females at densities comparable to those in swarms. Often the first reports of groups or swarms in a breeding area are of copulating or breeding adults.

Grouping and band formation among hoppers are influenced by their density and the time over which they have interacted. The latter is affected by the weather, by the vegetation cover and its composition, size and mode of growth. Group formation in initially solitary hoppers is rare in early instars. Early instars do form groups, however, if the adults were densely grouped for laying. More normally, small numbers of early instars disperse into the vegetation. Grouping starts if numbers increase because more hoppers hatch in the area than die. Basking groups forming an hour or so after sunrise are often an early sign of incipient gregarization. Later, hoppers will start to display other gregarious behaviour such as marching, providing that recruitment continues to greatly exceed losses. While group formation is a necessary precursor to the development of full gregarious behaviour, it is usually present for at least a week before behaviour such as marching begins.

Guichard (1955) stressed the complex and unstable role of plant communities as promoters and inhibitors of gregarization. Normally, the dense growth habit of the food plants *Tribulus* and *Heliotropium* inhibits gregarization but heavy feeding may reduce the leaves sufficiently to promote it. Consequently, the hopper densities assumed to induce marching (Table 6) do not increase linearly with vegetation cover. Roffey and Popov (1968) found that hoppers did not march at average densities of 30-40/m² in dense green *Tribulus* habitats that had up to 60 percent ground cover whereas, others in 'open' habitats with scattered *Aerva* bushes and *Lasiurus* tussocks, formed marching bands at average densities of 10-20/m². A further complication is that marching hoppers may not behave as gregarious populations in other respects. After fledging, they may fly by day but observations show that this does not always happen.

Gregarizing populations

A common factor preceding gregarization is heavy rain that allows sufficient vegetation to develop and within which population numbers increase. The small swarming populations that appear are particularly prone to disperse or to be destroyed by predators (Ellis and Ashall, 1957; Ashall and Ellis, 1962; Greathead, 1966). Records of day-flying swarms produced unambiguously from initially solitary populations are rare. One of three 2-3 ha swarmlets seen in Malian Tamesna flew away by day (Roffey and Popov, 1968). In contrast, Roffey and Popov (1968) saw no daytime flight among adults in Tamesna of Niger, which fledged from 80 x 10⁶ late instar hoppers.

Waloff (1966) found that conditions favouring local outbreaks (convergent airflow and associated heavy rainfall) were similar but shorter than those associated with plague upsurges. The initial requirement for an outbreak was rains to support marked population increase and at least partial gregarization for one or two generations in a seasonal breeding area. An upsurge occurred if the resultant populations migrated to an area where rains allowed further successful multiplication and gregarization. A plague could develop after a sequence of successful breeding over at least three to four generations. How much rain constitutes 'heavy' and precedes outbreaks and upsurges is unknown, in part due to the paucity of rain gauges near many outbreaks. Some indication may be gained from upsurge studies such as those by Bennett (1975, 1976), Chandra, Sinha and Singh, (1988), Pedgley and Symmons (1968), Skaf (1978) and by Roffey (1982).

Bennett (1975, 1976) demonstrated the changing proportions of swarming locusts and the decreasing area infested as an upsurge develops into a plague. She traced the main upsurge sequence leading to the 1968 plague from three periods of heavy rain in the south-eastern interior of the Arabian Peninsula. The first, in November 1966 affected 20 000 km² and the second and third, in March and April 1967, affected 200 000 km². Three generations probably bred within these areas and many gregarizing locusts were present by the autumn of 1967. Some emigrated and augmented a contemporaneous outbreak developing in the southwest of the peninsula. Bennett estimated the gross infested area and the numbers of locusts for the next five generations. The gross infested area expanded very rapidly for two generations from 20 000 km² to over 100 000 km² as the numbers of not fully gregarious locusts increased from <1 x 10⁶ to 6 x 10⁹. At this stage about half of the population (3 x 10⁹) moved eastwards out of this sequence. The remaining locusts, now fully gregarious, moved from Arabia to the summer breeding area of the Sudan. About half of the Sudanese progeny migrated to Morocco and the remainder moved to the Red Sea coastal plains. Once gregarization had occurred, the gross infested

area fell dramatically and for these generations was 10 000 km² and 5 000 km² although numbers continued to rise sharply through 1.8 x 10¹⁰ to 3 x 10¹⁰. Control measures and natural mortality then ended this plague.

Phase change: dissociation

Dissociation must arise when the stimuli promoting gregarization disappear and the distance between individuals and the duration of separation increase. The demonstration that recently acquired gregarization is more rapidly lost than that kept over many generations (Simpson, McCaffery and Hägele, 1999) may partly explain the poor cohesiveness of the small, initial swarms during an outbreak. Although *dissocians* populations are quite common (Stower, Davies and Jones, 1969), it is not always clear how they arise. Population reduction from chemical control is sometimes the cause. More often, the cause is poor breeding success due to marginal rainfall, whether or not natural enemies also cause heavy losses. The values for these thresholds are unknown.

The field evidence on densities at which swarms dissociate and behave as solitary adults is not clear enough to suggest values. Some tentative values relating to hopper dissociation are in Table 7. Hoppers dissociate after hatching if the density of egg-pods was low. The studies of Simpson, McCaffery and Hägele (1999) suggests that this females did not add the gregarizing factor to the egg-foam when laying at low density. The density at which hoppers dissociate varies with vegetation type and the cover that it provides. For example Roffey and Stower (1983) observed complete dissociation in a uniform sward of *Cenchrus* even though the density of first instar hoppers was up to 20/m²; suggesting that the uniform vegetation micro-structure was insufficiently clumped to promote gregarious behaviour.

TABLE 7. Hopper dissociation thresholds

EGG-POD DENSITY INDUCING DISSOCIATION							
< 0.1/m ²							
NUMBER OF HOPPERS PER PLANT INDUCING DISSOCIATION							
related to plant growth type							
Type of plant growth		instars	1	2	3	4	5
Small, open growth	<i>e.g. Malcomia</i>		1	1	1	1	1
Small, dense growth	<i>e.g. Cenchrus</i>		20	5	3	2	1
Medium, open growth	<i>e.g. Aerva</i>		3	2	1	1	1
Large, open growth	<i>e.g. Panicum</i>		5	3	2	1	1
dense growth	<i>e.g. Tribulus & Heliotropium</i>		20	10	5	3	2
Large leafed	<i>e.g. Pennisetum</i>		10	5	3	2	1

Population sizes

Eggfields and hopper bands

As mentioned in the earlier section on laying, groups of swarms tend to split up as they mature and lay. Each time a swarm lays, it gives rise to several eggfields. All are laid within a day or two and usually within a few kilometres of one another. Other swarms within the invading group lay a series of eggfields nearby. In addition, locusts lay egg-pods in groups at the most favourable sites within an eggfield. Consequently, a fourfold classification for eggs and subsequently hopper distribution is given below in increasing order of size:

1. *bands* form from groups of egg-pods within an eggfield;
2. *band zone* encloses all the bands hatching in one eggfield;
3. *infested zone* includes the band zones of all neighbouring eggfields;
4. *gross infested area* includes all infested zones in a seasonal breeding area.

A further complication is that gross infested area can be for an individual season or for a period of years; the former being considerably smaller than the latter. Roffey (1965) describes the area covered by bands within a band zone as the infestation rate. This terminology is not universally applied which makes it difficult to extract population sizes from reports of hopper infestations.

Roffey (1965) notes that eggfields frequently cover 10-20 km². Consequently, the 50-100 hoppers from individual pods usually emerge into an area containing large numbers of hoppers hatching from the hundreds or thousands of pods from the same egg-pod group. They stay in dense groups for a day or so after hatching. These groups range in size from a few hundred square centimetres to hundreds of square metres and roughly match the size of the original egg-pod groups. Within a day or two, the hoppers start to move and the groups begin to coalesce into bands. As the hoppers grow, they spread out, as much as 5-10 or even 20 times to occupy band zones often exceeding 100 km². They march farther and continue to coalesce but less rapidly than in the first week. Populations examined in detail in Kenya and India, contained many small and few large (> 1 km²) bands. Similarly, hopper bands reported in northern Somalia in 1957 confirmed that band size increases with age. Only 0.02 percent of first instar bands were recorded as very large (>360x720 m), whereas the percentage for fourth and fifth instars was 5.5 percent.

TABLE 8. Maximum extent of seasonal breeding areas showing annual ranges for India, 1959-1962 and West Africa, 1957-1960

RAINS	PERIOD	LOCALITY	GROSS INFESTED AREA (km ²) All seasons (single seasons)	BAND ZONES (km ²)	REFERENCE
Winter, spring	December-May 1955-1961	Red Sea Coasts Gulf of Aden Coasts	200 000		Joyce, 1979
Short	November-December 1955-1961	Ethiopia, Ogaden Somalia NE Kenya, Tanzania	600 000		Joyce, 1979
Long	April-June 1955-1961	Ethiopia, Ogaden Somalia Northern Kenya	500 000		Joyce, 1979
Summer	July-October 1955-1961	Eritrea Central Ethiopia Sudan, NW Kenya	700 000		Joyce, 1979
Summer	August-September 1950-1958	Sudan	300 000		Joyce, 1965
All	July-March 1959/60-1962/63	India	(15 200-157 000)		Kohli, 1963
Summer	July-October 1950-1961	Mauritania Senegal Mali, Niger	560 000 (2500 - 220 000)		Besnault <i>et.al.</i> 1962
Summer	July-October 1957-1961	Mauritania Senegal Mali, Niger	560 000 (4000 - 220 000)	500 - 9000	Besnault <i>et al.</i> 1962

Areas within which seasonal breeding has occurred at least once are large although the gross infested area for individual seasons during plagues is much smaller (Table 8). The values in this table may not be strictly comparable as their methods of estimation differ. In addition, they are based on reported infestation and only Besnault, Roy and Rosetti (1962) record areas from which no reports were received. The West African gross infested areas were estimated from the number of infested 1300 km² units (20 minutes longitude x 20 minutes latitude) shown in the annual maps. They would have been about 3 times larger had solely infested degree squares been known. Joyce (1979) may also have used 20 minute squares as he was using these units to study the distribution of breeding (Joyce, 1962). Kohli (1963) cites both the number of villages and the number of square kilometers infested each year where infested area/village ranges from 8-47km². Joyce (1962) presented data on the sizes of hopper bands destroyed in control campaigns in Eastern Africa and Arabia from 1955-1960. These indicate that gross hopper infestation sizes must have been very variable. He was able to demonstrate for the first time that population estimates of the right order of magnitude could be obtained from field data. He found that bands occupied up to 3 percent of the band zones (which he called gross infested areas) and that the few large bands in the population accounted for most of the area infested. He also showed, for practical purposes, that band sizes follow a log-normal distribution, with many small and a few very large ones. He also demonstrated, from examining 1300 km² units (20 minutes longitude x 20 minutes latitude),

that locusts laid more frequently in some areas during a season. When he considered the whole study period (1950-1958), he found that some units were high frequency breeding areas.

Joyce (1979) pointed out that hopper bands occupied only a small part of a band area (gross infested area in his terminology). The area actually infested by hopper bands varied from 0.25 percent in the 1961 Short Rains breeding in Somalia to 3.5 percent in a heavy 5th instar infestations in Kenya in 1954/55. At hatching, this latter infestation had occupied only 0.4 percent of the infested area. The small proportion of land occupied by hoppers posed a problem for ground survey teams who were shown to locate only a fraction (<0.001-0.1 percent) of the bands that crossed their survey tracks. For the large plague populations present at the time, systematic aerial survey using two traverses in all 400 km² units in a breeding area provided adequate data for control teams. Subsequently, Roffey (1965) cautioned that airborne observers frequently failed to find bands where trees and shrubs provided substantial ground cover and when bands were in extensive areas of tussock grasses.

Swarms

The introduction of aerial survey in eastern Africa from 1952 enabled acceptable estimates of population numbers to be made for the first time. Swarm sizes were measured accurately from the air and were multiplied by densities of swarms that had already been estimated in two ways. The first was by sampling dead locusts killed approximately *in situ* by overdosing swarms (Rainey, 1958; MacCuaig, 1958; Joyce, 1962; Gunn, 1979). The second was done by taking vertically oriented photographs of passing swarms at regular intervals and calculating the volume density from the sizes of the images (Gunn, 1979).

Swarm densities

Volume densities in some stratiform swarms varied from 1-10/m³, whereas in cumuliform swarms it generally ranged from 0.001-0.1/m³. The very low volume densities (0.001/m³) were observed in northern Somalia during mornings as swarms were dispersed in the strong southwesterly winds blowing towards the convergence zone. Densities increased to 0.1-2/m³ as swarms were concentrated by the convergence zone in the afternoons (Joyce, 1962).

TABLE 9. Sizes of Short Rains swarm infestations on the Somali Peninsula

YEAR	EXTENT OF INFESTATIONS km ² (LOCUST NUMBERS)		NOTES
	Parent	Progeny	
1955	3 500 (10 ¹⁰)	negligible (few hundred million)	Multiplication rate 0.005. Short rains failed. Area swarm-free until the 1956/57 upsurge
1956	0	0	Recession
1957	2 500 (1.6 x 10 ¹⁰)	1 300 (2.5 x 10 ¹⁰)	Multiplication rate 1.6. Good Short Rains and campaigns
1958	1 300	negligible	Poor Short Rains
1959	1 300	negligible	Good control and heavy parasitism in some areas
1960	2 000 (7.5 x 10 ¹⁰)	500 (2 x 10 ¹⁰)	Multiplication rate 0.26. Eighty percent of parent population killed but hoppers in one road-free area of dense bush were undetected until they fledged. They escaped control when unusual winds moved them out of range of air bases.

Joyce (1962, 1965) estimated that densities of four medium dense swarms killed in northern Somalia in 1960 varied between 20-150/m². This accords well with MacCuaig's earlier estimate (1958) of 7-100 locusts/m² for swarms sprayed in the same area. An average figure of 40-50/m² taken from these estimates was often used or cited in subsequent estimates of locust numbers (Roffey, 1965; Waloff, 1966; Joyce, 1979; Rainey, Betts and Lumley, 1979 p320; Symmons, 1992). Courshee (1990) used a lower value of 10/m².

Swarm infestations

Joyce (1962) reported the total area of swarm infestations and the numbers of locusts present at the beginning and end of the Short Rains campaigns between 1955 and 1960 (Table 9). These illustrate both the effects of rain on population developments and the growing effectiveness of control in the Somali Peninsula. The latter was based on first attacking parent swarms when they were held along the convergence zone between June and October and then switching to large scale hopper campaigns. Roffey (1965) suggested a threefold classification (Table 10) to describe regional swarm infestations that contain between 10^9 - 10^{11} locusts. In a major plague, there will be three to four such regional populations present simultaneously.

TABLE 10. Swarm infestation sizes

SCALE	TOTAL NUMBERS IN ALL SWARMS (10^6)	TOTAL AREA OF SWARMS (km^2)
Small	1 000	>10
Medium	10 000	>100
Large	100 000	>1 000

Swarm areas

Individual swarm sizes vary from a few hectares to tens or hundreds of square kilometres. They are formed as groups of fledglings coalesce into swarmlets of a few hectares in the breeding area. The swarmlets continue to merge downwind of the breeding area. The swarms described by Rainey (1963) varied from 0.04-150 km^2 but Joyce (1962) reports several larger ones including large and very large swarms in 1958 and 1959 that measured about 350 and 800 km^2 . Roffey, Popov and Hemming. (1970) reported, however, that swarms seen during recession outbreaks have smaller areas and lower densities and therefore, lower numbers than those found during plagues (Table 11). They noted that these swarms often contained fewer locusts than important contemporary non-swarmling populations. Approximate numbers in small day-flying locusts suggest that populations need to be of the order of 10^7 to emigrate as swarms. Such numbers could arise from 40 ha of high density hoppers or from 500 ha of hoppers in sparse vegetation, but in general, populations occupying less than 100 ha are unlikely to produce a swarm. Gregariously behaving populations of 10^7 - 10^9 , frequently fail to maintain their coherence as swarms (Roffey, Popov and Hemming, 1970).

TABLE 11. Sizes of infestations during recessions

SWARM AREA km^2	LOCUST NUMBERS 10^6	LOCATION, YEAR
3.7	2.5-3	Ethiopia, 1964
0.6	0.1	Ethiopia, 1966
0.005	not given	Iran, 1964
0.1	not given	Iran, 1964
0.42	0.035	Niger, 1967
4.4	not given	Sudan, 1978
POPULATION AREA km^2		
110 (@ 1 200-4 000/ha)	Tens of millions	Chad, 1966
100 @ 10/100 paces)	1.5	Chad, 1964
30 000 (Red Sea Coast)	56	Eritrea, 1950
13	2	Eritrea, 1964

The total numbers of swarms in an infestation were first enumerated early in 1954, when 50 swarms, together measuring 1 000 km^2 , entered Kenya (Rainey, 1963a). The population was estimated to contain 5×10^{10} locusts. The largest swarm measured 200 km^2 and the five largest together measured 700 km^2 . Joyce (1962) used data solely from Eastern Africa, that fell into Roffey's medium and large category. He found that the log-normal distribution of band sizes continued after fledging and offered a method of predicting swarm size (Table 12). Data added for infestations in the tens of square kilometres to reflect many upsurge populations remain invalidated.

TABLE 12. Distribution of swarm areas within populations of different sizes

PERCENT OF SWARMS	TOTAL AREA OF SWARM POPULATION (km ²)					
	2 500	1 300	650	260	130	10
	constituent swarms smaller than:					
5	195	95	49	18	8	0.6
10	205	100	52	20	10	0.8
25	285	140	70	30	15	1.2
50	415	200	100	40	20	1.6
75	580	310	155	55	30	2.3
90	750	375	185	75	35	2.7
95	905	450	225	90	45	3.5

Qualitative swarm and band sizes

Two systems have been used to link qualitative terms to hopper band and swarm sizes. FAO changed the number of qualitative categories from three (Pedgley 1981) to five (FAO 1994) to describe more adequately the smaller infestation sizes characteristic of recession populations (Table 13). Note that swarm sizes are generally unreliable unless estimated by aircraft or radar (Uvarov, 1977).

TABLE 13. Qualitative swarm and hopper band size categories

CATEGORIES	HOPPER BAND AREA		SWARM AREA	
	Pedgley 1981	FAO 1994	Pedgley 1981	FAO 1994
Very small		1-25 m ²		< 1 km ²
Small	25-2500 m ²	25-2500 m ²	<1 km ²	1- 10 km ²
Medium	0.25-8 ha	0.25-1 0 ha	1-100 km ²	10-100 km ²
Large	8-30 ha	10-50 ha	>100 km ²	100-500 km ²
Very large	>30 ha	>50 ha		>500 km ²

Control and population parameters

A brief survey of past and present control measures and their effectiveness follows because most Desert Locust population parameters were estimated during control campaigns. Rainey, Betts and Lumley,(1979), argued plausibly that control was not applied at an appropriate scale to destroy whole populations until the decline of the 1949-1963 plague. Plagues have become less frequent since the 1960s, but the relative causative roles of improved control and of the arrival of drier weather and modified global wind-circulation are still unclear.

Before the 1960s, control had become increasingly successful at reducing populations. Until the 1900s, farmers protected their own crops. Subsequently, governments increasingly coordinated crop protection in their own countries. Crops were saved but the methods available, burning, beating with sticks, building barriers and digging trenches, made little impact on population numbers. Two things made population reduction more effective: the introduction of arsenical baits against hoppers in the 1930s and internationally coordinated campaigns that from the 1940s that attacked major populations no matter how far from cultivations. Control with persistent pesticides from the late 1940s and the gradual introduction of aerial spraying and then barrier spraying against hoppers in the 1950s and 1960s made large-scale population reduction more achievable. Control became especially effective in areas such as northern Somalia and immediately south of the Anti-Atlas in Morocco where swarms are semi-static for many weeks. Subsequently, dieldrin, which was both persistent on vegetation and cumulative in the locust, was replaced by organophosphates and synthetic pyrethroids that have short persistence and are not cumulative. This made control more difficult because targets have to be identified and sprayed accurately and the insects must be hit by a lethal dose of pesticide.

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