Desert Locust Guidelines

1. Biology and behaviour

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Second edition – 2001

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PREFACE

The Desert Locust plague of 1986-89 and the subsequent upsurges in the 1990s demonstrate the continuing capacity of this historic pest to threaten agriculture and food security over large parts of Africa, the Near East and southwest Asia. They emphasize the need for a permanent system of well-organized surveys of areas that have recently received rains or been flooded, backed up by control capability to treat hoppers and adults efficiently in an environmentally safe and cost-effective manner.

The events of 1986-89 showed that, in many instances, the existing strategy of preventive control did not function well, for reasons including the inexperience of the field survey teams and campaign organizers, lack of understanding of ultra low volume spraying, insufficient or inappropriate resources and the inaccessibility of some important breeding areas. These reasons were compounded by the general tendency to allow survey and control capacity in locust-affected countries to deteriorate during locust recession periods. To address this, FAO has given high priority to a special programme, the Emergency Prevention System for Transboundary Animal and Plant Pests and Diseases (EMPRES), that will strengthen national capacities.

Given the certainty that there will be future Desert Locust upsurges, FAO produced a series of guidelines primarily for use by national and international organisations and institutions involved in Desert Locust survey and control. The guidelines comprise:

1. Biology and behaviour
2. Survey
3. Information and forecasting
4. Control
5. Campaign organization and execution
6. Safety and environmental precautions

Appendixes (including an index) are provided for easy reference by readers.

This second edition has been produced to update sections on technology and techniques that have undergone changes in the seven years since first publication, to modify presentation of the material, to make it easier to understand and to facilitate updates in the future. The revision was carried out by K. Cressman of FAO and H.M. Dobson of the Natural Resources Institute, United Kingdom, with input from many locust and locust-related specialists around the world. This edition will be available in the three key languages of the locust-affected countries, English, French and Arabic.

I would like to extend my gratitude to all those who have been involved in this important contribution to improved Desert Locust management.

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Contents

ACKNOWLEDGEMENTS

FAO is grateful to P.M. Symmons who produced the first edition of the guidelines, to K. Cressman and H.M. Dobson who revised and updated it, and to S. Lauer who produced most of the illustrations. FAO would also like to thank T. Abate, B. Aston, F. Bahakim, L. Barrientos, T. Ben Halima, D. Brown, M. Butrous, M. Cherlet, J. Cooper, C. Dewhurst, J. Duranton, C. Elliott, A. Hafraoui, M. El Hani, T. Galledou, S. Ghaout, G. Hamilton, Z.A. Khan, M. Lecoq, J. Magor, G. Matthews, L. McCulloch, M. A. Ould Baba, J. Pender, (the late) G. Popov, T. Rachadi, J. Roffey, J. Roy, S. Simpson, P.M. Symmons and H. van der Valk for their comments and criticism on this new version. Acknowledgements are also due to R. Mitchell and C. Smith-Redfern for general editorial advice, K. Whitwell for indexing, Medway Design Team, University of Greenwich and Andrew Jones for production of digital artwork and to manufacturers for providing illustrations of their equipment. The Control guideline and parts of the Appendixes are outputs from a project funded by the United Kingdom's Department for International Development (DFID) for the benefit of developing countries and carried out by the Natural Resources Institute. The views expressed in these sections are not necessarily those of DFID.

INTRODUCTION

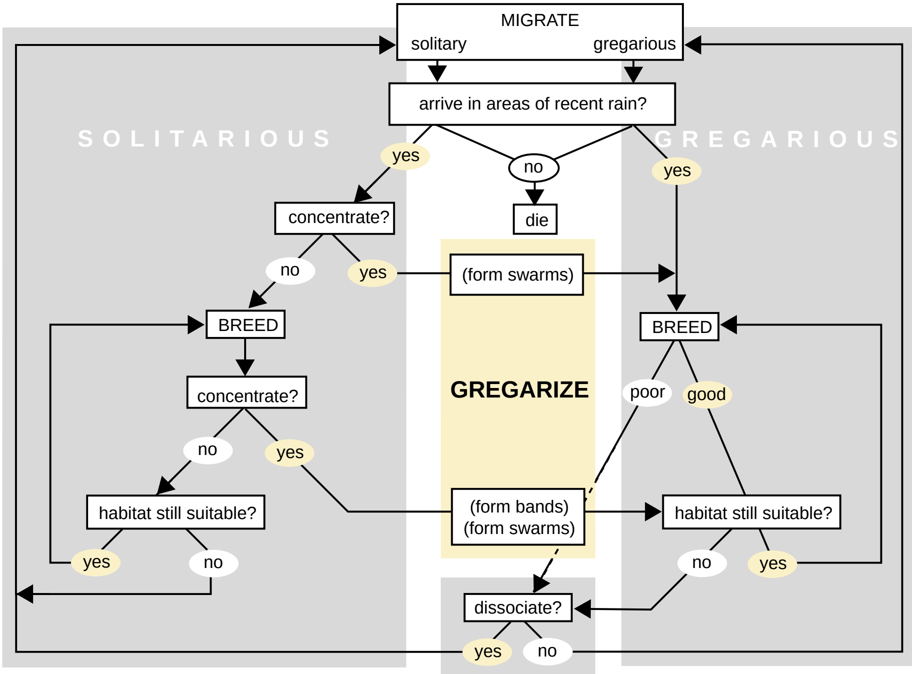
This guideline is intended mainly for use by field staff involved in locust survey and control operations, including pilots of survey and spray aircraft. Some parts will be useful reference material for training new staff and providing refresher training for experienced locust officers. The information and reference data may also be useful for senior managers planning and overseeing campaigns and for donor representatives assessing technical needs.

The guideline contains basic information on the biology and behaviour of the Desert Locust but is not meant to be an exhaustive reference. The reader is encouraged to consult those publications listed in the Literature section of the Appendixes for more information.

Information, advice, procedures and explanations are given on the right-hand pages of the publication; illustrations and summaries are given on the left-hand pages. When appropriate, tips and warnings may appear on either side.

There is also a series of Frequently asked questions (FAQs). These deal with some of the common problems encountered by locust field staff. Answers are given where available, but further research is needed in some areas, and FAO welcomes feedback on new information and solutions.

Figure 1. Summary of Desert Locust population dynamics, showing the influence of the environment on locust behaviour and phase.

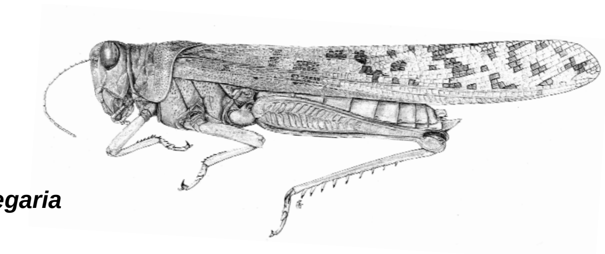


FAQ number 1 (see p. 42 for answers)

Does gregarization occur at a specific threshold, in other words, once there are a certain number of locusts present in a given place?

WHAT ARE LOCUSTS?

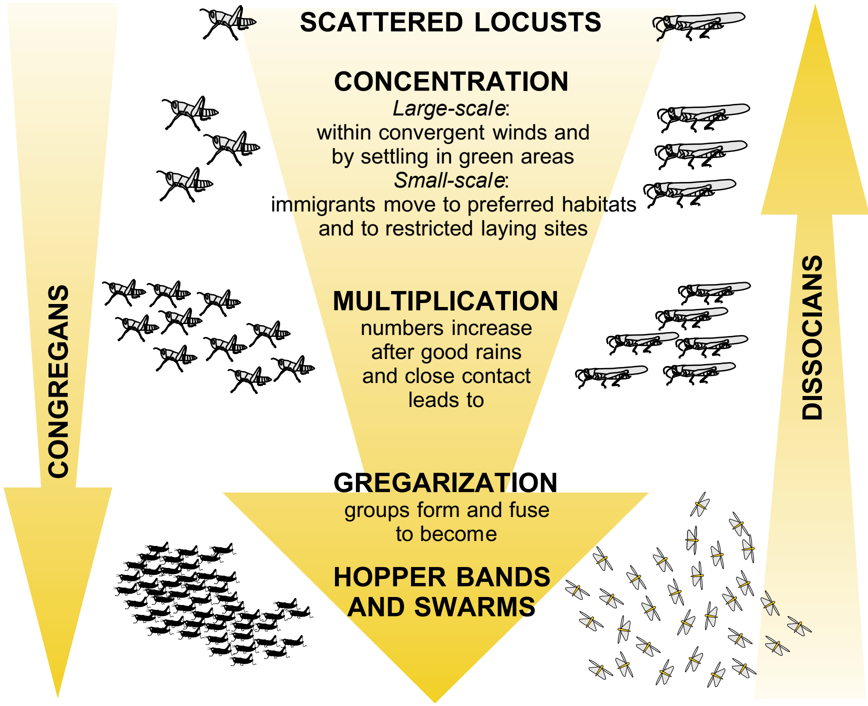
Locusts are members of the grasshopper family *Acrididae*, which includes most of the short-horned grasshoppers. Locusts differ from grasshoppers because they have the ability to change their behaviour and physiology, in particular their colour and shape (morphology) in response to changes in density (see Fig. 1). Adult locusts can form swarms which may contain thousands of millions of individuals and which behave as a unit. The non-flying nymphal or hopper stage can form bands. A band is a cohesive mass of hoppers that persists and moves as a unit. In general, most grasshoppers do not form bands or true swarms. However, the distinction between locusts and grasshoppers is not clear-cut since some of the latter do form bands (e.g. *Melanoplus*, *Acridoderes*, *Hieroglyphus* sp.) or small loose swarms (e.g. *Oedaleus senegalensis*). Locusts such as the Tree Locust have never been known to form bands.



Schistocerca gregaria
(Forskål, 1775)

CLASS	**INSECTA**	
ORDER	**ORTHOPTERA**	Grasshoppers (about 20 000 species worldwide)
SUBORDER	**CAELIFERA**	Short-horned grasshoppers (about 10 000 species worldwide)
SUPERFAMILY	**ACRIDOIDEA**	
FAMILY	**ACRIDIDAE**	Grasshoppers and locusts
SUBFAMILY	**CYRTACANTHACRIDINAE**	
GENUS	***Schistocerca***	
SPECIES	***gregaria***	

Figure 2. Desert Locusts have the ability to change their behaviour, physiology, colour and shape in response to a change in locust numbers. At low numbers, locusts behave as individuals (solitarious phase); at high numbers, they behave as a single mass (gregarious phase). Precise thresholds at which these changes occur are not established. Three processes are involved in phase transformation: concentration, multiplication and gregarization.



Phase terminology

Solitarious	Phase when individuals live mostly separate from each other.
Gregarious	Phase when large numbers of individuals gather together.
Transiens	Intermediate phase when locusts are grouping and starting to act as a single mass and are either changing from solitarious to gregarious (gregarization) or from gregarious to solitarious (dissociation).
Congregans	Part of the transiens phase during which locusts are congregating and are in transition from the solitarious to the gregarious phase. Often used for nymphs.
Dissocians	Part of the transiens phase during which locusts are in transition from the gregarious to the solitarious phase. Often used for nymphs.
Solitaricolour	Showing types of colour associated with solitarious behaviour.
Gregaricolour	Showing types of colour associated with gregarious behaviour.

LOCUST PHASES

Locusts have two different states called phases: solitarious and gregarious. When locusts are present at low densities, the individuals are solitarious. As locust numbers increase, they cluster into dense groups and they become gregarious (see Fig. 2). The transition from the solitarious phase to the gregarious and vice versa is called the transient phase, and the locusts are referred to as transiens. If locusts are on the increase, they are referred to as congregans and, if they are on the decrease, they are called dissocians.

Behavioural changes can take place rapidly. For example, Desert Locusts that have been reared in isolation in the laboratory try to avoid each other when first put into a cage, but in trying to avoid one locust they come into contact with another. Being touched by others, especially on the outer surfaces of the hind femora (thighs), results in locusts being attracted rather than repelled by others, and so they form groups. This switch from repulsion (the solitarious state) to attaction (the gregarious state) only takes an hour or so. If crowded insects become isolated they revert to behaving solitariously. The longer they are kept in a crowd before being isolated, the slower the reversion to the solitarious state. It may take several generations to complete the transition from gregarious to solitarious behaviour. Females can influence the phase of their offspring by adding a gregarizing chemical to the egg pod foam if they have recently experienced crowding, including at the oviposition site. In the field, it can take several generations before crowding occurs and solitary individuals behave fully gregariously. This is often seen during upsurges when bands and swarms become progressively larger and more cohesive.

Morphological changes (changes in colour and shape) take more time. The full gregarious colour takes one crowded generation to develop and shape takes two or more. The differing rates of colour and shape change associated with phase changes often lead to confusion. For example, it is possible to find swarms of solitary (colour) locusts. In these guidelines, the terms gregarious and solitary (or solitarious) refer to behaviour, gregaricolour (and solitaricolour) are used to indicate coloration, and gregariform (and solitariform) indicate shape.

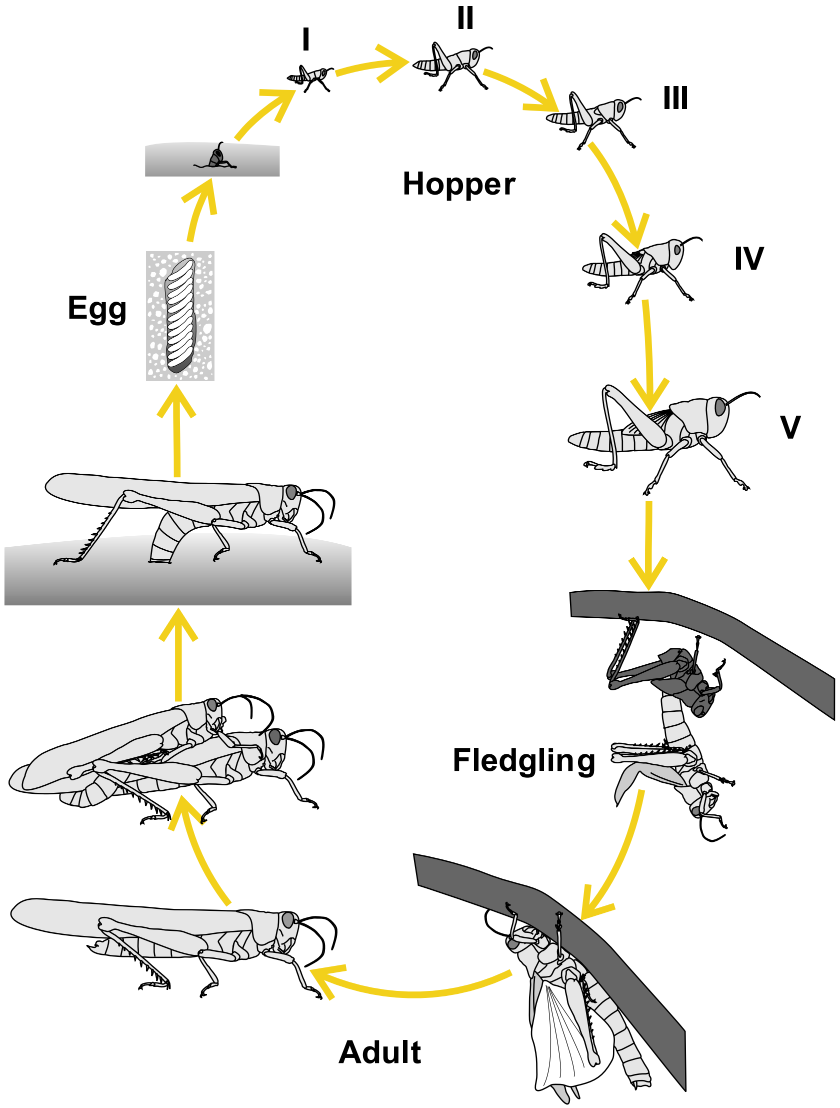
The change in locust colour and shape occurs after the behavioural change. Colour and shape are an indication of how the Desert Locusts have been behaving but may not be a reliable guide as to how the locusts will behave in the future. Therefore, behaviour is the best and most useful phase characteristic to use in locust control work.

Approximate densities at which phase transformation may occur

	Locusts/m²	Locusts/ha
Early instar hoppers	5	50 000
Late instar hoppers	0.5	5 000
Adults	0.025-0.05	250-500

Source: Duranton, J.F. & Lecoq, M. (1990)

Figure 3. The life cycle of the Desert Locust.



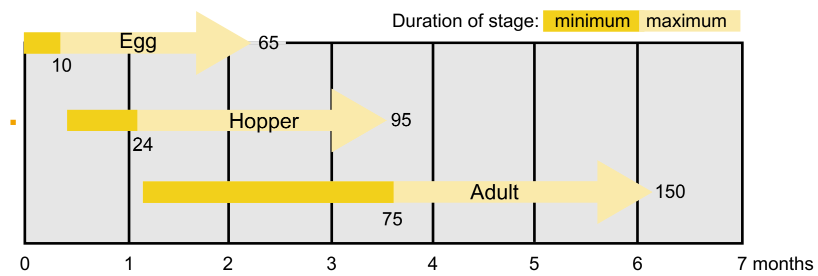
THE LIFE CYCLE

The Desert Locust, like all other locusts and grasshoppers, passes through three stages: egg, nymph (hopper) and adult (see Fig. 3).

Eggs are laid by females. They hatch into wingless larvae or nymphs called hoppers. Hoppers shed their skins five or six times, each time growing in size. This process is called moulting and the stage between moults is referred to as an instar. The final moult from the wingless fifth (or sixth) instar hopper to the winged adult is called fledging. The new adult, known as a fledgling, has soft wings that must dry and harden before it can fly. Adults do not moult and therefore do not grow in size but gradually increase in weight. Adults that can fly are initially sexually immature, but eventually become sexually mature and can copulate and lay eggs.

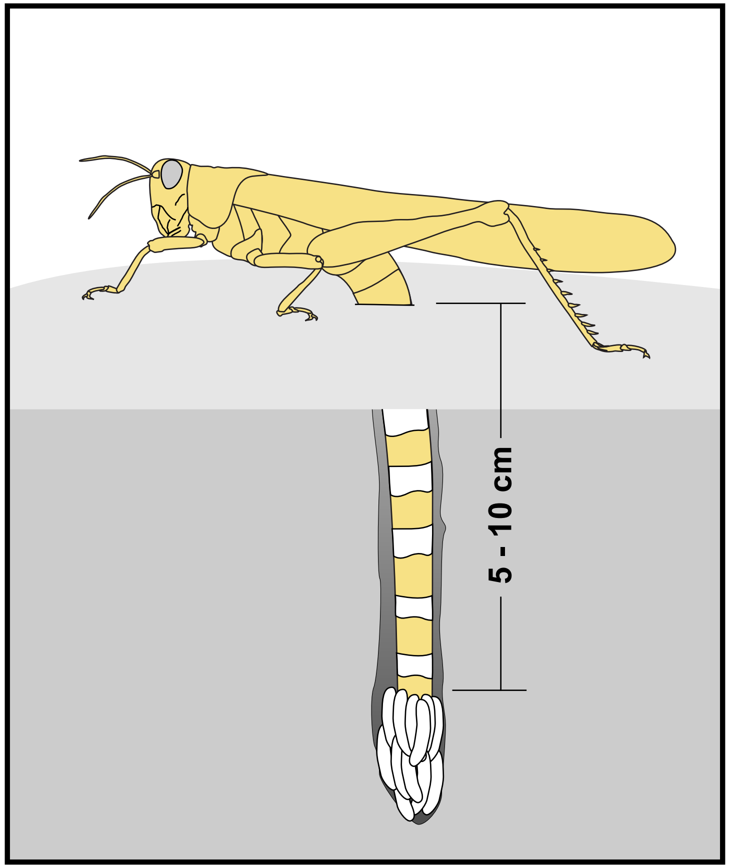
Life cycle parameters

Stages	Egg, hopper, adult	
Duration	Egg	10-65 days
	Hopper	24-95 days (36 days average)
	Adult	2.5-5 months
	Laying-fledging	40-50 days
	Adult maturation	3 weeks-9 months (2-4 months average)
	Total	2-6 months
Larval moults	5-6 (solitarious), 5 (gregarious)	
Phases	Solitarious, transiens, gregarious	
Affected area	16 million km² (recession), 29 million km² (invasion)	



Note: adult maturation may extend up to 270 days in low temperatures or dry habitat

Figure 4. The female bores into the ground with the valves at the rear of her abdomen and lays a pod of eggs. The pod is about 3-4 cm long and is laid about 5-10 cm below the soil surface.



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FAQ number 2 (see p. 42 for answers)

Will locusts lay eggs in areas of dense vegetation?

Eggs

Laying

Eggs are usually laid in areas of bare sandy soil. Generally, the female will not lay unless the soil is moist at about 5-10 cm below the surface. In soft sandy soils, females have been known to lay when moisture is only found at depths below 12 cm. Before laying, the female will often probe the soil, inserting the tip of her abdomen to determine if there is enough moisture. It is important to realize that laying is not always taking place when the females are seen probing. The only sure test is to dig into the ground to check whether eggs have been laid.

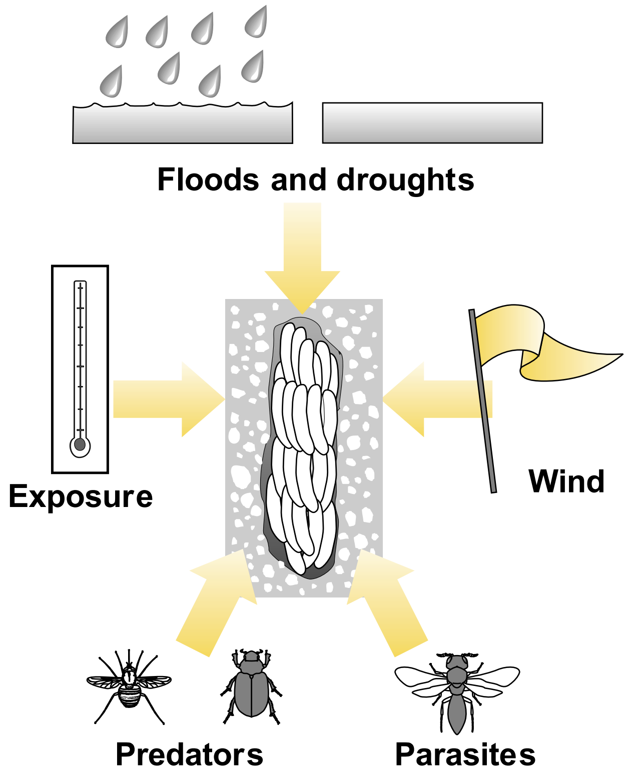
The female lays eggs in batches called egg pods. The eggs look like rice grains and are arranged like a miniature hand of bananas. Once the female determines there is enough soil moisture, she bores into the ground with the valves at the rear of her abdomen and deposits a batch of eggs (see Fig. 4). She then fills up the hole above the eggs with a plug of froth. The pod is 3-4 cm long and is laid so that its top is about 5-10 cm below the surface. This depth requires a great extension of the female's abdomen. The Desert Locust lays pods containing fewer than 80 eggs in the gregarious phase and typically between 90 and 160 in the solitarious phase.

Swarms often lay egg pods in dense groups, with tens and even hundreds of pods per square metre. The males, together with those females that are not ready to lay, may move on. As a result, large swarms split up and males may become separated from females. Laboratory tests show that a laying female leaves a scent that attracts others to lay nearby. In the field, however, it is thought that sight is more important than scent in attracting females to those already laying. This behaviour means that laying occurs in only a small number of the apparently suitable sites. Such behaviour as well as an agent added to the egg pod foam when adult females are crowded will help induce gregarization of the next generation.

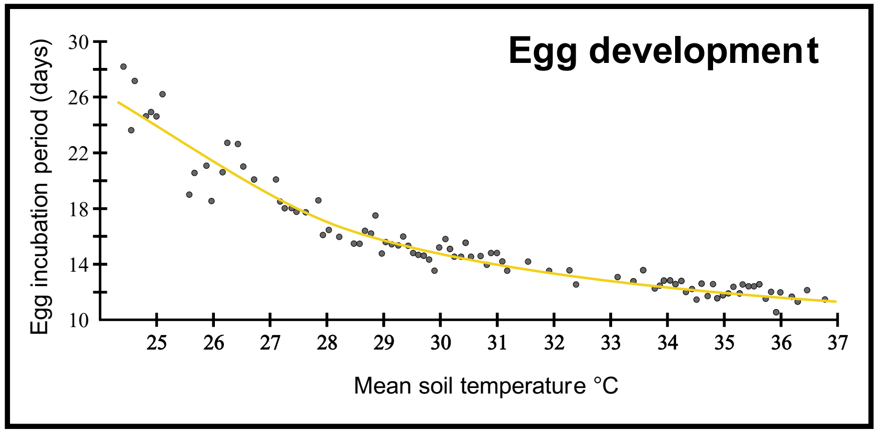
The number of egg pods a female lays depends on how long it takes for her to develop a pod and how long the female lives. The time between layings in the field is about ten days. Adults become rare some six or seven weeks after the first well synchronized laying except perhaps where temperatures are low. This suggests that nearly all females will lay one pod, about 75 percent will survive to lay a second, and perhaps 25 percent to lay a third but very few will manage to lay four pods. An average of two pods per female is the norm.

Because of natural mortality, not all the eggs that a female lays hatch and those that do hatch do not all reach the adult stage. In optimal temperature and habitat conditions, multiplication rates can be as high as 16-20. In other words, a single female can produce up to 16-20 viable locusts in a single generation.

Figure 5. The rate of egg development is a function of soil temperature. Egg mortality can be caused by several factors that vary from habitat to habitat.



Note: Illustrations not to scale



Development and incubation

The Desert Locust nearly always lays its eggs in soil that is wet enough to allow the eggs to absorb sufficient moisture to complete their development. Eggs are rarely laid in dry or nearly dry soil. If eggs were laid in a dry soil, they would desiccate (dry out) unless rain fell soon after laying. The rate of development is therefore exclusively a function of the soil temperature at pod depth (see Fig. 5). There is a reasonably good relationship between soil temperature and screen (air) temperature so rates of egg development can be predicted satisfactorily from air temperatures and even from long-term mean values since temperatures do not vary greatly between years for a given place and time of year in most of the breeding areas. However, there can be exceptions to this, notably during the winter when the weather may be unusually warm, allowing development to continue.

Mortality

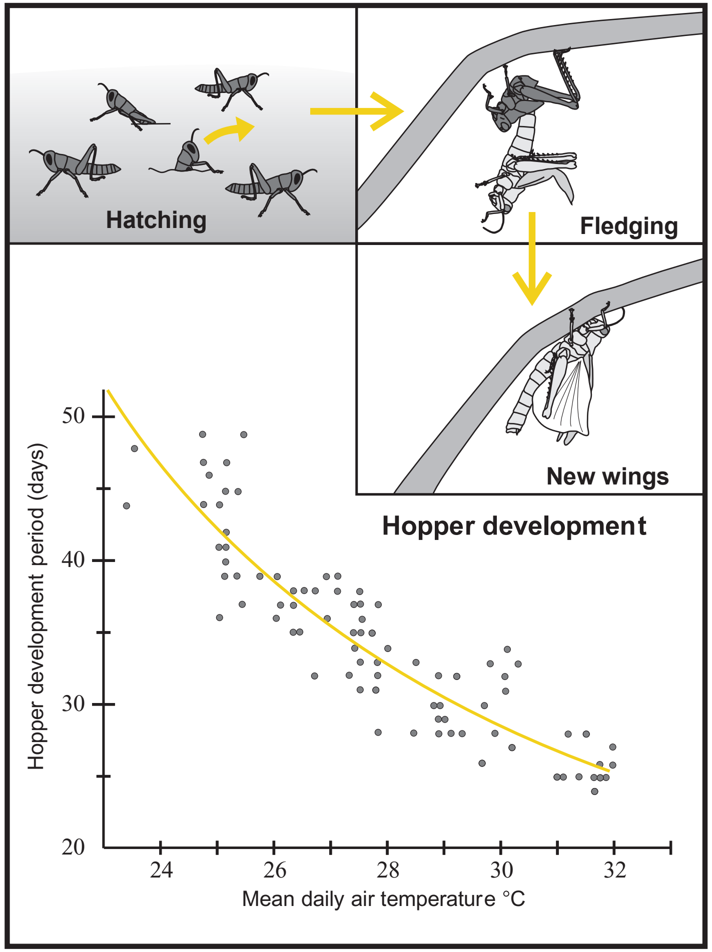
The proportion of eggs that survive to hatching varies widely according to habitat conditions and the presence of egg parasites and predators. Eggs can dry up especially if exposed by wind, and can also be destroyed by persistent flooding; however, such events are not common. High mortality may occur if soil temperatures are above 35°C. Estimates of total losses vary from about 5-65 percent because of inviability (less than 10 percent), failure to hatch (3-4 percent), predation (less than 40 percent) and mould, bacteria and desiccation (less than 10 percent). Average losses are suggested to be about 13 percent in solitarious populations and about 33 percent in gregarious populations.

Egg parameters

Laying depth	5-15 cm
Laying period	7-30 hours
No. times female lays	2-3
Interval between laying	6-11 days
Eggs/pod	150, 120, 60 (solitary); 60-80, 50-70, 35-70 (gregarious)
Eggs/generation	400/female (solitary); 140/female (gregarious)
Egg pod densities	200-500/m² in groups
Average density	5/m²
Pod length	3-4 cm
Incubation period	10-65 days
Mortality	5-65% (range); 13% (average, solitary); 33% (average, gregarious)

Note: some of these figures are typical estimates in the field or laboratory

Figure 6. Hoppers hatch and pass through five or six instars. At the final moult, they develop wings and become young adults (fledglings). Hopper development occurs more quickly at high temperatures than at low temperatures.



Solitary hopper parameters

Instars	5-6
Colour	Green or greenish
Eyestripes	7
Development period	30-39 days (summer breeding areas and Red Sea) 28-48 days (cooler periods, e.g. northwest Africa)
Average duration of L1-L4	6-7 days/instar
Average duration of L5-L6	7-10 days
Mortality	70% (L1), 20% (L2), 10% (L3-L5), 5% (at each moult)

Hoppers

Hatching

During hatching, the emerging hoppers work their way up through the froth plug to the surface. They immediately moult to the first instar. The hoppers then pass through five instars (sometimes six in the solitary phase), shedding a skin (moulting) between each. At the final moult (or fledging), the young adult (called a fledgling) emerges (see Fig. 6). The hopper stages are often denoted as L1, L2, L3 and so on.

Development

The rate of hopper development, as with the rate of egg development, is a function of temperature (see Fig. 6). The correlation with air temperatures is less clear than with eggs because the hoppers can control their body temperature to a considerable extent by basking or seeking shade. There is no evidence that hoppers in relatively dry vegetation develop more slowly.

Survival

The rain associated with egg laying usually produces sufficient vegetation for the hoppers to develop. Hopper populations can die from lack of food but this is unusual. Nevertheless, only a fraction of the hoppers that emerge from the egg survive to fledge. Up to 70-80 percent of the first instar stage can die as a result of inadequate water reserves, cannibalism and predation by ants. As the remaining hoppers grow, another 10-20 percent may die from cannibalism, parasitism and predation.

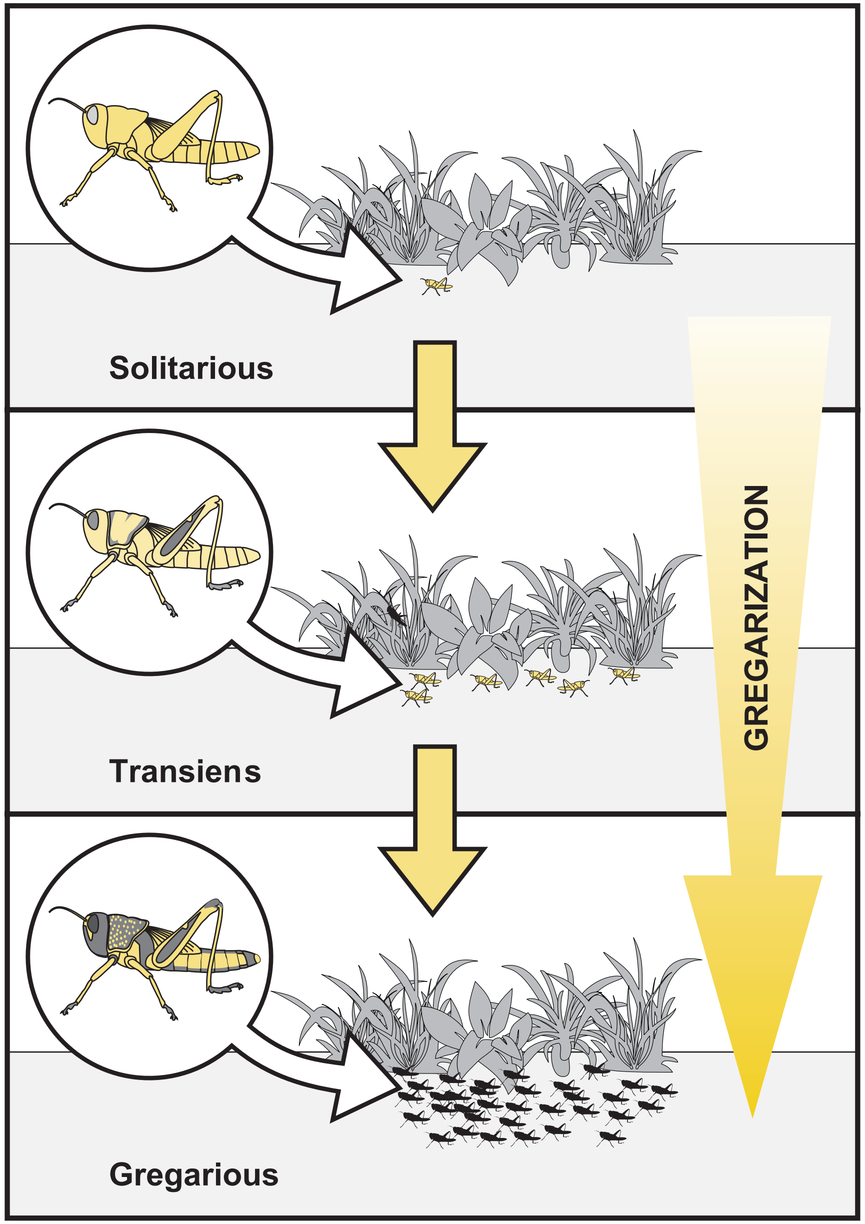
Stages

During recession periods, it is common to find solitarious hoppers of every instar in the same area at the same time. This is partly because laying occurs at intervals, and partly because eggs in the same bed and even in the same pod do not all hatch at exactly the same time. Hopper bands often contain a mixture of instars, although one or two are usually clearly dominant.

Solitary hopper behaviour

Dawn – before sunrise	Hoppers crawl over vegetation or ground and climb to the tops of plants
After sunrise	Descend from the plants to the ground
Early morning	Bask on the ground on the sunny sides of plants, out of the wind
Late morning	Climb back into the vegetation and shelter inside the plants or rest on the highest part of the plants
Afternoon	Descend again from the plants to the ground and bask on the sunny sides of plants
Near dusk	Cease basking and climb back into the vegetation

Figure 7. When solitarious hoppers increase in number, their behaviour changes and they become concentrated and can form groups. This often happens when vegetation starts to dry out. Their colour also changes and dark spots appear.



Groups

As hopper numbers increase in certain habitats, their behaviour changes – they accumulate and become concentrated (see Fig. 7). This can happen when hoppers are sheltering in vegetation, during basking, feeding and roosting, and when they are moving on the ground. During these periods, hoppers start to become attracted by others and form groups. This occurrence may also be indicated by black markings appearing on the green solitary hopper, although behavioural changes occur before colour changes. Grouping can be considered as an intermediate step in the change between solitary phase hoppers and gregarious phase bands.

Because of the variability of locust habitats and behaviour, groups do not start to form when hoppers reach a specific density. Grouping often occurs in open habitats that are less uniform, where there are patches of relatively dense vegetation separated by large areas of bare soil, for example in *Panicum* sp. and *Heliotropium* sp. habitats. On the other hand, when low densities of solitary hoppers are present in uniform habitats consisting of low plants and bare soil or in habitats of uniform dense vegetation, groups are less likely to form.

When groups of hoppers are found in the field, this is an important indication that hopper populations are becoming gregarious and bands are likely to form. This process may be accelerated when large numbers of grasshoppers or other locusts are present.

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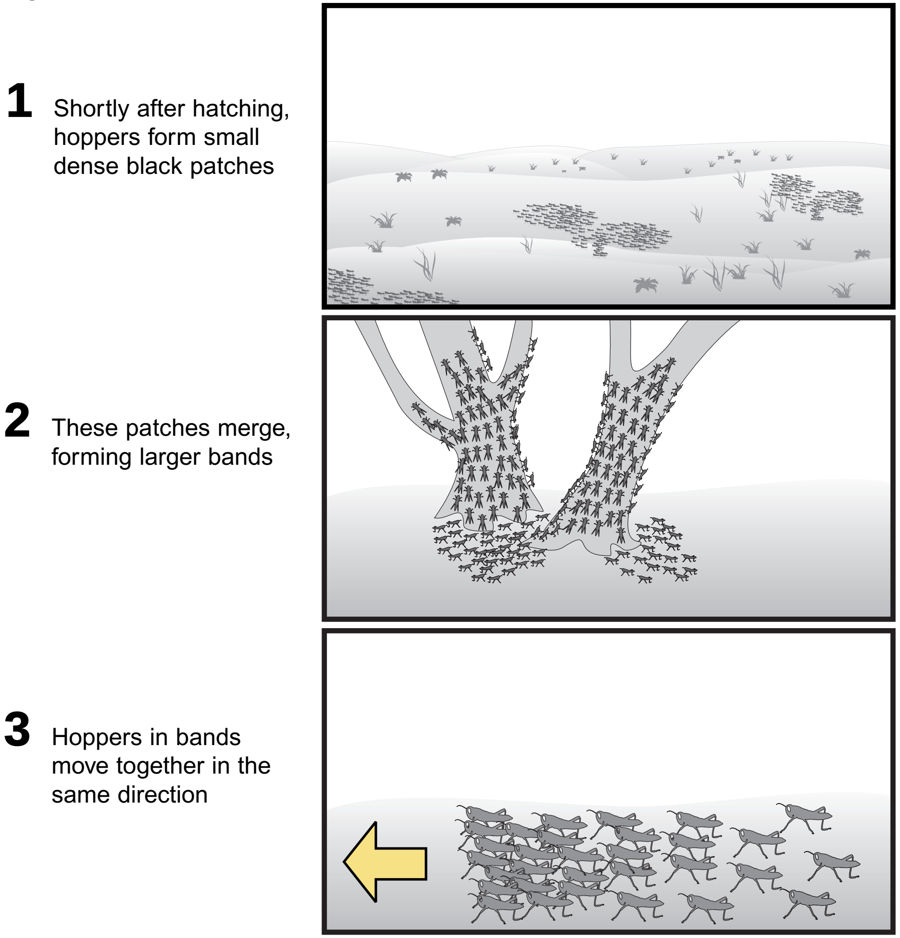
FAQ number 3 (see p. 42 for answers)

How can you tell the difference between hopper groups and bands?

Figure 8. Band behaviour.



Gregarious hopper parameters

Instars	5
Colour	black (L1), yellow with black (L2-5)
Eyestripes	1 (L1), 2 (L2), 3 (L3), 4 (L4), 5 (L5)
Development period	25-57 days
Average duration of L1-L4	6-7 days/instar
Average duration of L5	10 days
Size (mm)	7 (L1), 15 (L2), 20 (L3), 33 (L4), 50 (L5)
Weight (mg)	30-40 (L1), 50-80 (L2), 120-200 (L3), 500-700 (L4), 1000-1200 (L5)
Mortality	70% (L1), 20% (L2), 10% (L3-L5), 5% (at each moult)

Bands

Hatching. Hatching usually occurs at dawn or shortly thereafter and the hatchlings move to the nearest clump of vegetation. Within a few hours of hatching, the hoppers turn black. Usually they do not feed or move much for the first day. As a mass, they may cover no more than a few tens of square centimetres, but contain several thousand insects per square metre, forming small dense black patches (see Fig. 8).

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

Band densities will vary according to band behaviour and instar as well as the habitat and the weather. For example, bands are denser on the ground than those roosting which are denser than those marching. Maximum densities of bands on the ground range from over 30 000 hoppers per m^2 for first instars to just over 1 000 per m^2 for the fifth instar. However, average densities are much lower. For late instar bands, density is probably between 50 and 100 hoppers per m^2. The relative densities of the different instars mean little since the hoppers themselves are increasing in size.

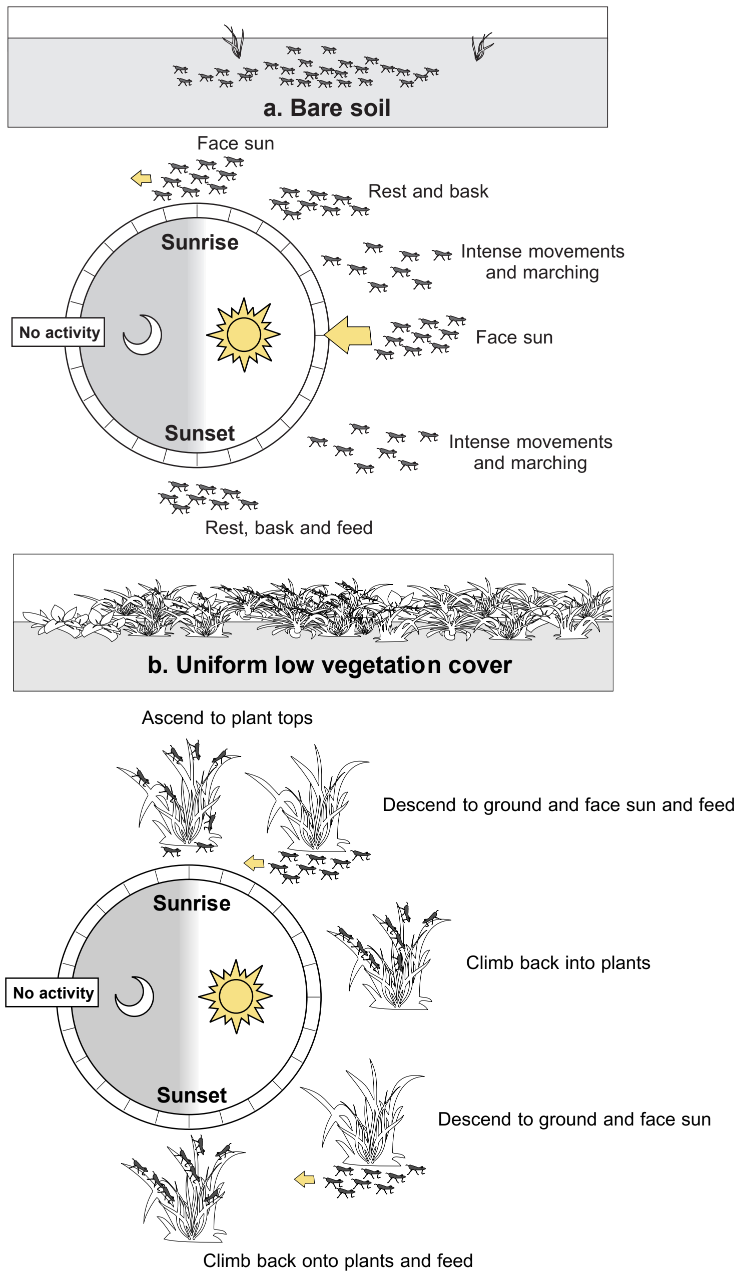
Merging. Individual hopper bands increase in area as the hoppers develop and nearby bands join together, forming much larger bands. This process continues into the fourth instar. First, second and third instar hoppers sometimes get caught up in older instar bands. The increase in the area of hopper bands with age can be even greater than the decrease in density. In the final instar, however, the bands tend to spread out and become less cohesive.

Movement. The rate of band movement varies with temperature, vegetation cover and even with the size and coherence of the band. For example, measurements for predominantly fourth instar bands range from about 200 to 1 700 m in a day.

Generally, bands move only during the day and usually only from two to three hours after dawn until about an hour before sunset. However, there are records of bands moving by night under exceptionally high temperatures or when the moon is full. If the vegetation is very dry, bands may continue moving at night in search of green vegetation. The band usually maintains a constant heading during a day; even a major obstruction is not always sufficient to change its path. The heading is often, but not always, downwind. At midday, bands usually roost in the vegetation.

Time period	Band behaviour
20 min before sunrise – 2.5 h after sunrise	Descend from plants; slow dense marching
45 min – 2 h after sunrise	Ground grouping
1.5 h after sunrise – midday	Marching
Midday – afternoon	Roost in plants
Late afternoon – 1 h before sunset	Marching
80 min before – 5 min after sunset	Ground grouping
Night	Sometimes march a few hours; roost in plants

Figure 9. Effects of (a) bare soil and (b) uniform low vegetation cover on hopper behaviour.



Effects of vegetation on daily hopper behaviour

The behaviour of hoppers during the day is influenced by the habitat. Here, hopper behaviour is described in four main habitat types:

Bare soil (see Fig. 9a). Hoppers usually spend most of their time moving over the bare ground, alternating with resting and basking (facing or parallel to the sun).

Time of day	Hopper behaviour
Dawn – before sunrise	Hoppers crawl over the ground, rest and bask on the ground (facing the sun)
Sunrise – early morning	Rest and bask on the ground
Mid morning – noon	March on the ground
Noon	Hoppers face into the sun
Afternoon	March on the ground
Late afternoon – dusk	Bask
Dusk	Roost and feed (if possible)

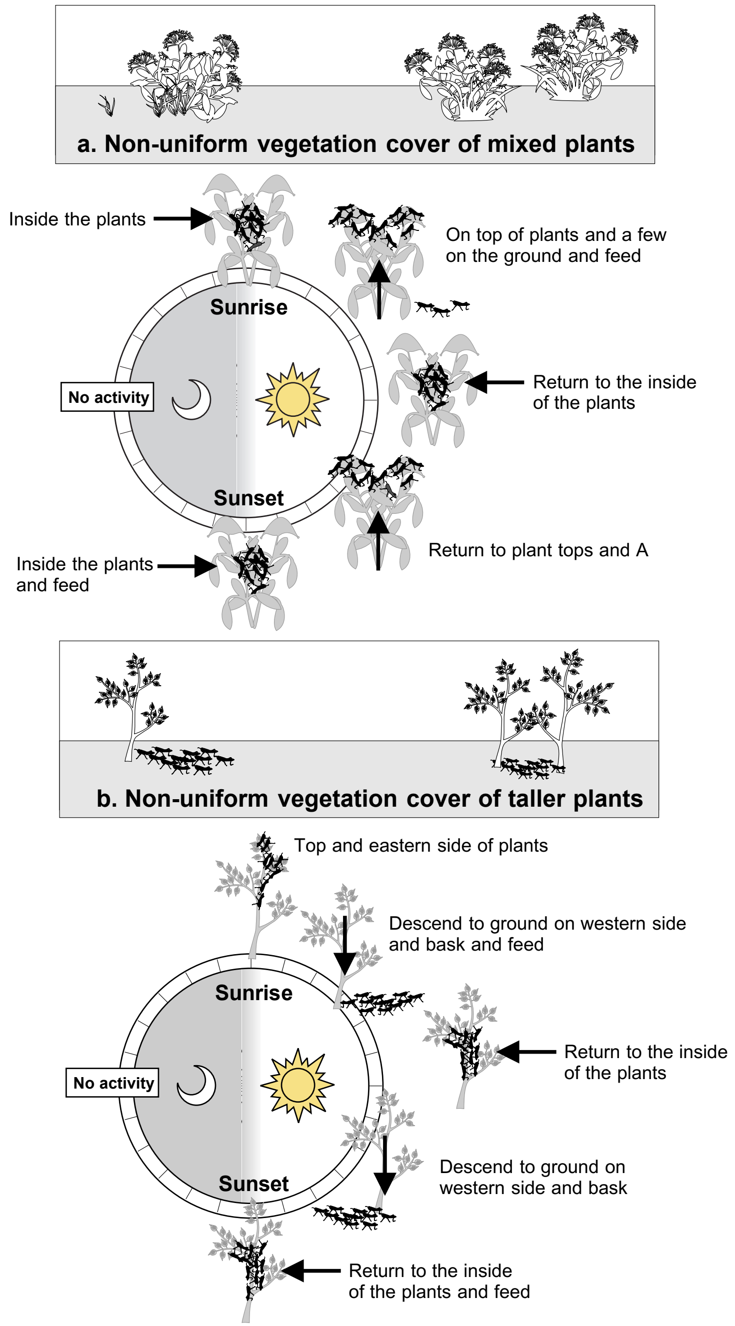
Uniform low vegetation cover (see Fig. 9b). In a habitat where the vegetation is evenly distributed and consists of small, low plants with only small areas of bare ground in between, hopper behaviour is similar to that in bare soil but is modified by movements in and out of the vegetation. Hopper movement is reduced under cloudy skies or in the early hours of clear cold mornings.

Time of day	Hopper behaviour
Dawn – before sunrise	Hoppers crawl over vegetation or ground followed by ascent to the tops of the plants
After sunrise – early morning	Descend from the plants to the ground and bask on the ground on the sunny sides of plants and out of the wind, some feeding
Late morning	Climb back into the vegetation and shelter inside the plants or rest on the highest part of the plants
Afternoon	Descend again from the plants to the ground and bask on the sunny sides of the plants
Near dusk	Cease basking and climb back into the vegetation

Daily displacement distances (m)

	Bare soil		Low vegetation	
	Sunny	*Cloudy*	*Sunny*	*Cloudy*
1st instar	100	50	50	25
5th instar	800	400	400	200

Figure 10. Effects of non-uniform vegetation on hopper behaviour.



Non-uniform vegetation cover of mixed plants (see Fig. 10a). Hoppers spend very little time on the ground and most of the time in the vegetation in habitats consisting of large, dense, low plants (e.g. *Heliotropium* sp.) where the plants are separated by large areas of bare ground. They mainly move up and down within the vegetation during the day. During overcast conditions, hoppers spend nearly all the time in vegetation.

Time of day	Hopper behaviour
Dawn	Hoppers are inside the vegetation
Early morning	Bask on the tops of the plants; a few hoppers may descend to the ground and bask
Midday	Return to the shelter inside the vegetation and feed
Afternoon	Return to the tops of the plants
Late afternoon	Bask on the tops of the plants
Dusk	Move back into the shelter of the vegetation and feed

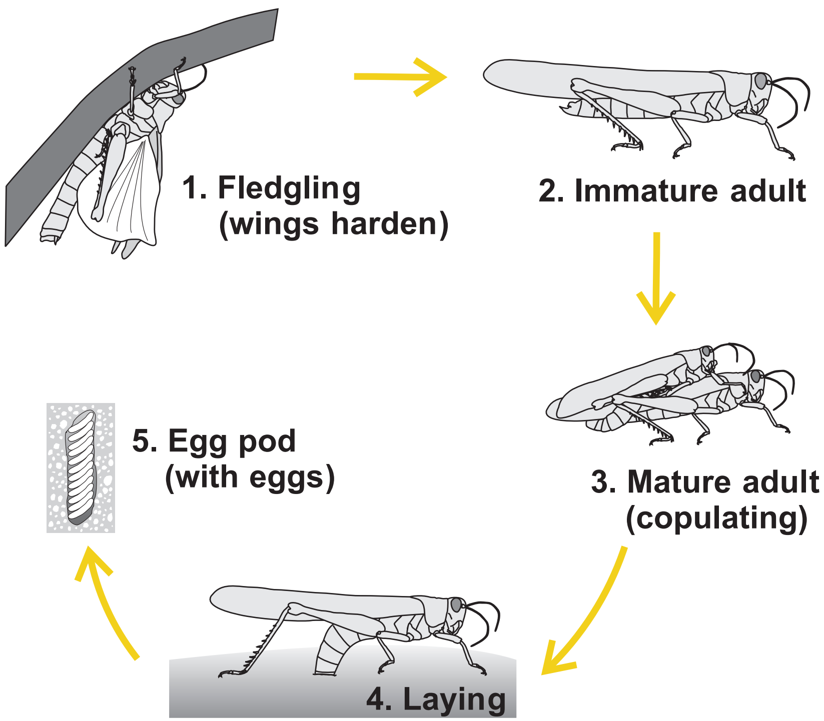
Non-uniform vegetation cover of taller plants (see Fig. 10b). Hoppers move up and down within the vegetation and towards the east and west in habitats where there are relatively tall plants with an open structure (e.g. *Panicum* sp., *Dipterygium* sp. and *Pennisetum* spp.).

Time of day	Hopper behaviour
Dawn	Hoppers move towards the top and eastern side of the plants
Sunrise	Descend to the ground on the eastern side of the plants
Morning	Bask and feed
Midday	Take shelter inside the vegetation
Afternoon	Leave the bases on the southwest side of the plants and move over the ground
Late afternoon	Collect at the bases on the western side of the plants and bask
Dusk	Move into the shelter of the plants and feed

Daily displacement distances (m)

	Mixed vegetation		Tall vegetation	
	Sunny	*Cloudy*	*Sunny*	*Cloudy*
1st instar	2	1	10	5
5th instar	20	10	100	50

Figure 11. On fledging, the adult's wings harden and the adult remains immature until maturation is stimulated by rainfall. In warm temperatures and good vegetation, it takes adults about three weeks to mature and lay eggs. If conditions are dry and cool, adults may remain immature for six months.



Fledgling behaviour

Days after fledging	Part of population ready to migrate
10	10%
11	20%
12	40%
13	20%
14	10%

Note: these figures are estimates at a mean daily temperature of 25°C

Adults

Fledglings and immature adults

It takes about ten days after fledging for the adult's wings to harden sufficiently so that it is capable of sustained flight (see Fig. 11). The adults then remain immature until they encounter conditions that stimulate maturation. This period is highly variable, depending on habitat conditions, and it may involve migration to another area where more favourable conditions exist (see Migration on p. 32-33).

Maturation

Favourable maturation conditions are usually associated with rain. For example, rainfall in an already infested area or locusts invading an area where it has recently rained may trigger maturation. Upon reaching an area where rain has recently fallen, immature adults usually start to mature. A mature locust will cause others to mature which may explain why maturation is well synchronized in swarms.

Adults in an area of lush vegetation with maximum day temperatures of 35°C or more, and with rain to maintain the vegetation growth, can probably lay within three weeks of fledging. At the other extreme, immature adults can survive for six months or more under dry conditions. Adults cannot survive for long under hot dry conditions with little to eat. Although adults can survive during the winter in West Africa south of the Sahara where it is relatively warm, they do not breed.

Males usually become sexually mature before females. The only satisfactory guide to female maturation is egg development within the female which can only be seen by dissection (see p. 38-39 in the Survey guideline). Under most conditions, the female takes about ten days to develop eggs to the stage where they are ready to be laid. At high temperatures with lush vegetation, the time may be less. Egg development within the female is unlikely to occur at temperatures below about 15°C and even with a daily maximum as high as 20°C the adults are likely to remain immature.

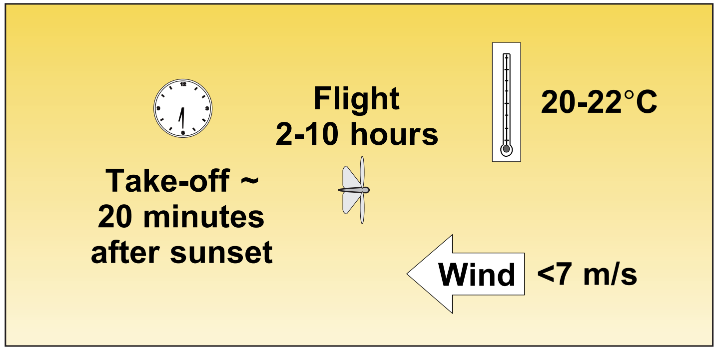
Tip: the Desert Locust is a large, lightly built grasshopper with a strong darting flight that can carry it 30 m or so before it lands. It often lands sideways to the observer on a bare patch of earth. This differs from the heavier Tree Locust which often moves from tree to tree, or the rapid flights of the Migratory Locust that end in a sudden dive to the ground.

?

FAQ number 4 (see p. 42 for answers)

Do Desert Locusts have an overwintering stage?

Figure 12. Solitary adults migrate at night. When the temperature is above 20-22°C and the wind is less than 7 m/s, they usually take off about 20 minutes after sunset and can fly for up to ten hours. However, they usually fly for only a few hours at a time.



Solitary adult behaviour

Colour	Brownish
Maturation period	2 weeks – 6 months
Take-off time	20 minutes after sunset
Take-off temperature	>20-22°C (100% take-off at >27°C)
Take-off wind speed	<4-7 m/s
Flight	Night-time
Flight direction	Downwind
Orientation of adults	Downwind
Ground speed	7-18 m/s (25-65 km/h) or wind speed at flight height + 4 m/s
Air speed (average)	3.8-4.3 m/s (13-15 km/h)
Flight height	< 1 800 m (generally < 400 m)
Flight duration	Up to 10 h (2 h average)
Flight displacement	1-400 km/night

Solitary adults

Solitary adults migrate at night (see Fig. 12). Individuals have been detected by radar up to heights of 1 800 m. It is not known whether all locusts capable of flight migrate, how long they stay airborne during the night and whether they fly on a sequence of nights. It is possible that there are both brief low-level flights, leading to short-range displacements, as well as sustained higher-level flights, resulting in migration. Some solitary locusts may not migrate at all but merely move locally.

The limiting temperature for night flight is about the same as for day flight, namely 20-22°C. This is unexpected since, at the limiting ambient temperature, the body temperature of night fliers must be substantially lower than for day fliers in bright sunshine.

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

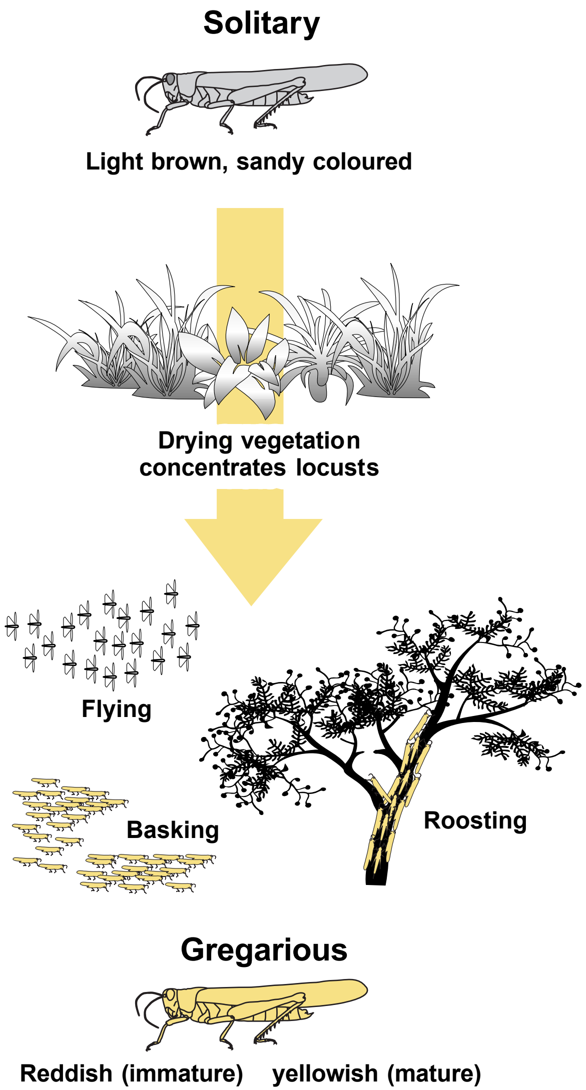
Tip: individual adults are attracted to lights at night. When you see adults arriving at outdoor lights (for example, street lights in urban areas or campfires in the field), this may indicate that they are moving from one location to another.

?

FAQ number 5 (see p. 42 for answers)

Do solitary adults fly during the day?

Figure 13. When vegetation starts to dry up, solitary adults may become concentrated and form groups. This can occur during basking, feeding, roosting and flying. During this process, the adult's behaviour and colour change.



Groups

Like hoppers, solitary adults change their behaviour in response to the environment and numbers (see Fig. 13). For example, at the end of a breeding season during a recession, adult numbers often increase as a result of previous breeding. At the same time, favourable habitats shrink as conditions become dry. This forces the adults to concentrate in those relatively small areas that remain suitable for survival. If adults are mature, this is often associated with laying in the few areas where soil moisture is still available. As a result of concentration, the adults start to react to each other and form groups. This may also be indicated by a change in colour of the adult, although this happens after the change in behaviour. Immature adults may be brown with traces of pinkish colour on their abdomen and wings whereas mature adults will have traces of yellow.

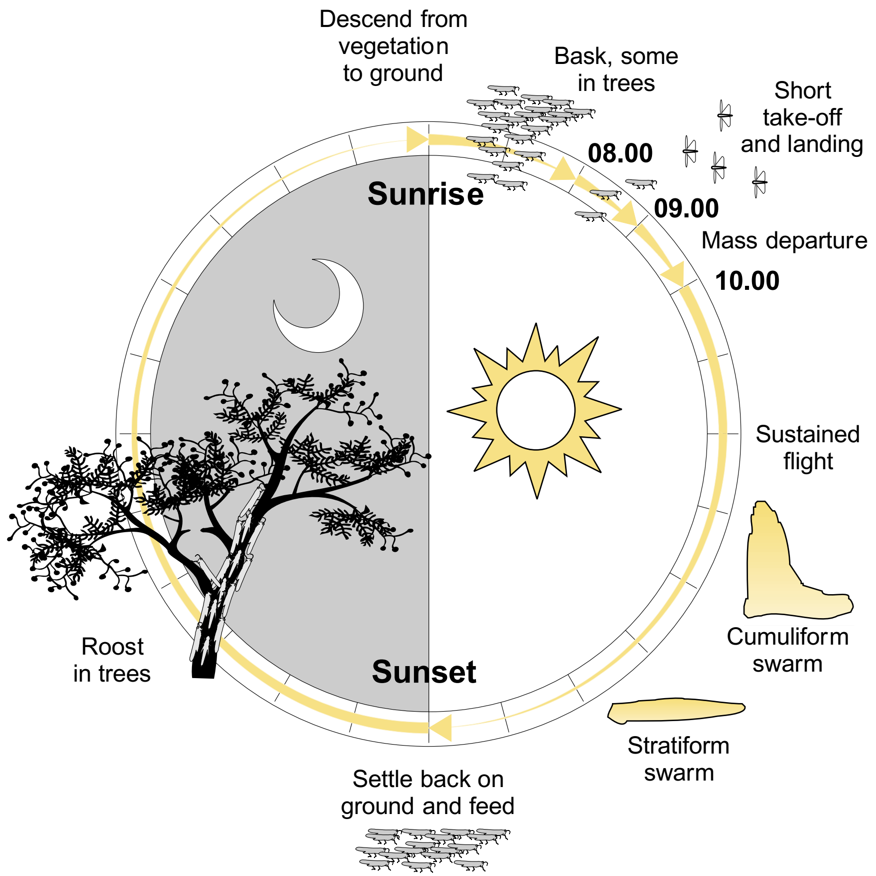
Adult groups may form during basking, feeding, roosting and flying. The latter may occur in areas where winds converge and force the flying locusts to become concentrated. When groups are seen in the field, it is an important indication that the adults are becoming gregarious and may form swarms. This process may be accelerated by other incoming adults or when large numbers of grasshoppers or other locusts are present.

?

FAQ number 6 **(see p. 42 for answers)**

How can you tell the difference between adult groups and swarms?

Figure 14. Swarms spend the night roosting in vegetation. At sunrise, they descend to the ground and warm up by basking in the sun. By mid-morning, swarms take off and will often continue flying until just before sunset when they land and feed. If the weather is unusually hot, swarms may settle at midday before flying off again in the afternoon.



Swarms

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

Structure. Swarms can occur as low-flying sheets (stratiform) or the locusts may pile high in the air (cumuliform), similar to hanging curtains, with the top level as much as 1 500 m above ground (see Fig. 14). Stratiform swarms are flat, usually tens of metres deep, and often occur during cool, overcast weather or in the late afternoon. Cumuliform swarms are associated with convective updrafts on hot afternoons, especially common during the warmer and drier months of the year. Within cumuliform swarms, the locusts in the lowest 400 m or so occur in streams that can take any heading. Streams that emerge from the swarm turn back into the swarm. Locusts at higher levels within a swarm may also form randomly oriented streams or swirling sheets.

Density. Swarm densities vary considerably. The generally accepted figure for an average medium-density settled swarm is about 50 million locusts/km^2 (50 locusts/m^2) whereas the range is 20-150 million/km^2. Swarms generally spread out when flying, typically covering between two and three times the area they occupy when roosting. Volume densities of flying swarms can be as high as ten locusts per m^3.

Swarm behaviour

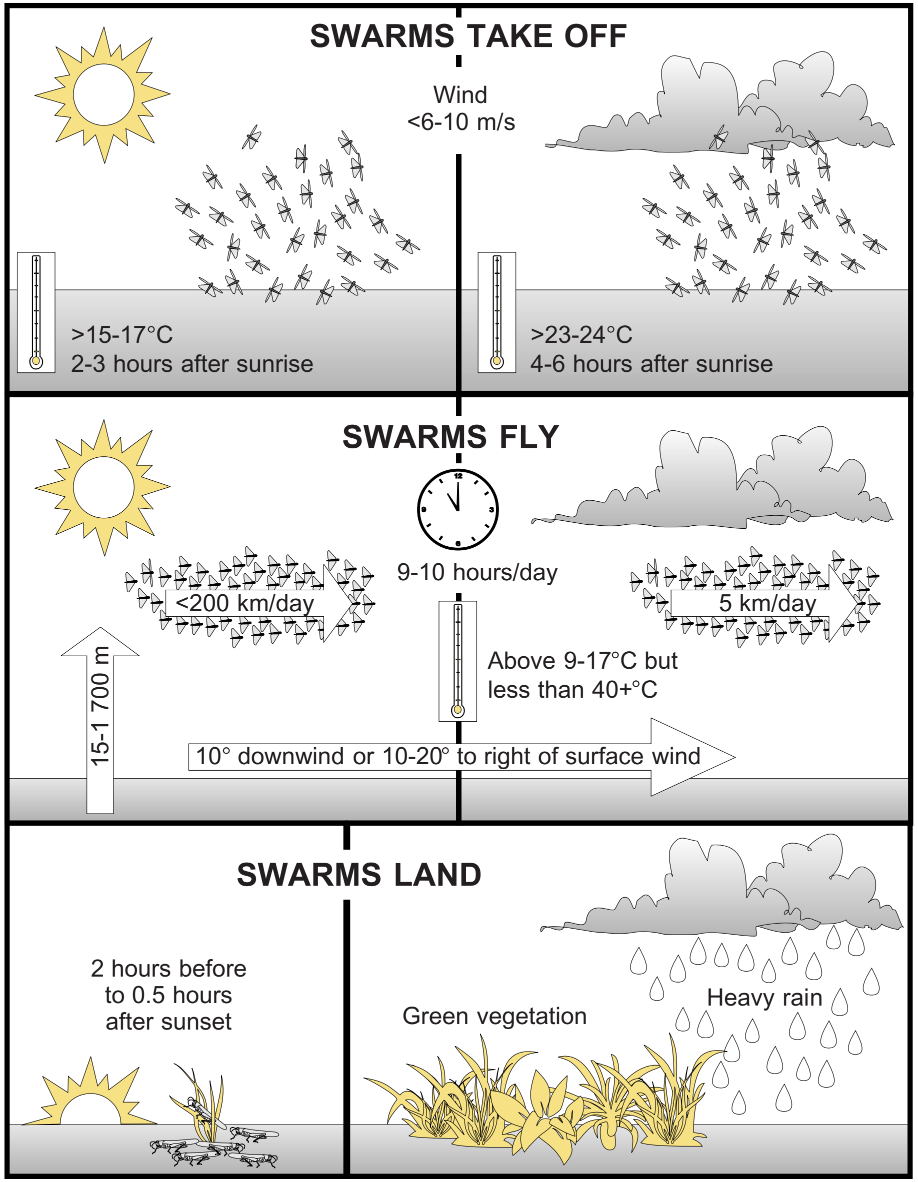
Colour	Pink (immature), yellow (mature)
Maturation period	2 weeks – 6 months
Density (ground, average)	50/m^2 (500 000/ha)
Density (ground, range)	20-120+ /m^2 (200 000 - 1 200 000+ /ha)
Density (flying)	1/1 000 m^3 – 10/m^3

?

FAQ number 7 (see p. 42 for answers)

Do swarms fly at night?

Figure 15. Take-off, flight and landing parameters of swarms.



Take-off. Generally, morning swarm activity starts with descent from the vegetation on which the swarms roosted overnight (see Fig. 14). The locusts often bask on bare ground with their bodies sideways to the sun in order to get the greatest warming effect. As the temperature increases, groups of locusts take off and then land several times (see Fig. 15). Like aircraft, the locust lands and takes off into wind. Intermittent flight occurs in a rolling manner. At the leading edge of a swarm, adults descend in mass, turning into the wind to land. At the trailing edge, they take off into the wind. As the swarm clears overhead, the adults then turn to catch up with it.

Flight. By mid-morning, or earlier if the temperature is warm enough for sustained flight, the whole swarm takes to the air. Sustained flight is rare if temperatures are below about 20°C. This limiting temperature is higher under overcast conditions (about 23°C).

Displacement. Swarms may fly up to nine or ten hours in a day, moving downwind, although mature swarms may sometimes move a short distance upwind if the wind is light. A swarm is usually displaced at slightly less than the wind speed and may easily move 100 km or more in a day. It is not clear with cumuliform swarms which wind level determines displacement. Swarms may be towed along by winds aloft or they may be held back by winds near the surface which are usually slower and often blow from a different direction. Although locusts within a swarm may be oriented in different directions, the overall result is a downwind displacement. With many swarms, a considerable proportion of the locusts spend some of the time on the ground, so the swarm nearly always moves at less than the wind speed. In the absence of wind, locusts fly at about 3-4 m/s.

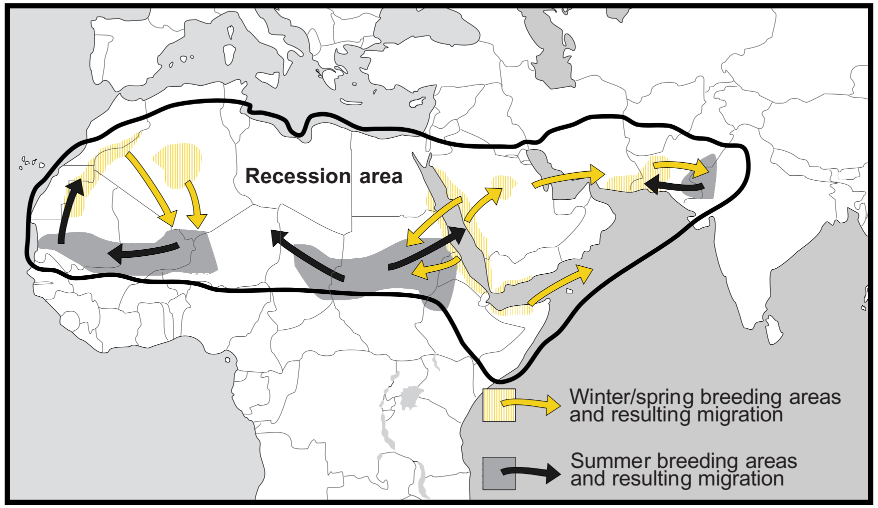
Landing. Young immature swarms occasionally continue flying after dark on warm evenings but, as a rule, swarms start to settle about an hour before sunset as convection dies away. Very high airborne densities can occur during this period.

Swarm migration

Take-off time	Warm weather: 2-3 hours after sunrise Cool weather: 4-6 hours after sunrise
Take-off temperature	Sunny: >15-17°C Cloudy: >23-24°C (immature), >26°C (mature)
Take-off wind speed	<6 m/s
Flight	Daytime
Flight direction	Downwind
Ground speed	Draper's formula[1] (vegetated areas), same as wind speed (little or no vegetation), or 0.4-4.4 m/s (1.5-16 km/h)
Air speed (average)	3.8-4.3 m/s (13-15 km/h)
Flight height	15-1 700 m
Flight temperature (day)	>9-17°C <40+°C
Flight duration	9-10 h (min), 13-20 h (max)
Flight displacement	5-200+ km/day
Settling time	2 h before sunset – 0.5 h after sunset

1 $0.9071W - 0.0199W^2 + 0.0049H + 3.7373$ where W = wind speed (km/h) and H = flight height (m)

Figure 16. Within the recession area, locusts move with the winds. These bring them into particular zones during the summer (the Sahel and the Indo-Pakistan desert) and during the winter/spring (northwest Africa, along the Red Sea and Baluchistan).



Spring breeding areas	Summer breeding areas
● Northwest Africa	● Sudan, Eritrea, Ethiopia
● Iran, Pakistan	● East Africa*
● Interior of Saudi Arabia and Yemen	● Sahel, West Africa
● Somalia Peninsula and East Africa*	● Indo-Pakistan border

Winter breeding areas

- ● Red Sea and Gulf of Aden coasts
- ● Somali Peninsula and East Africa*

* during plagues

MIGRATION AND SEASONAL DISTRIBUTIONS

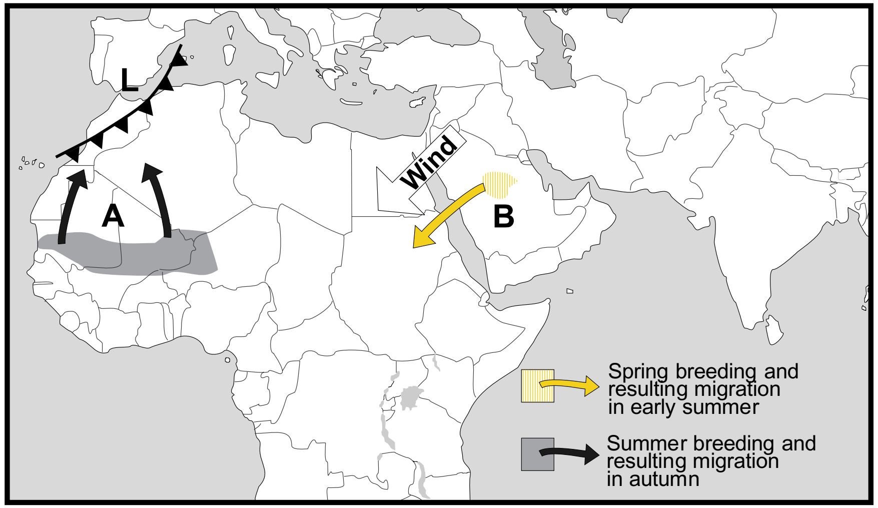
Since both day-flying swarms and night-flying solitary individuals are displaced downwind, the seasonal changes in the mean wind flow bring locusts into particular zones during particular seasons (see Fig. 16). For example, locusts move southwards from northwest Africa into the Sahel of West Africa at the beginning of the summer. During the autumn, they move northwards again but low temperatures at night limit the movement of night-flying solitaries compared with day-flying swarms.

Downwind displacement tends to bring locusts into an area during the season when rain is most likely, for example, the Sahel of West Africa and the Sudan in the summer and the Red Sea coasts in the winter. Once the rain falls, the locusts will mature and breed. By the time the new generation of adults is capable of sustained flight, the seasonal wind pattern may well have changed and breeding conditions become poor. The locusts will then migrate rapidly, often over very great distances, to another area.

All this is true only in a very general way. Often there are movements that take place during periods of particular winds rather than coinciding with the prevailing wind flow. Moreover, rare and even unprecedented movements continue to occur. This is one reason why, in any given year, only part of the seasonal breeding area will be infested. The other major reason for unsuccessful breeding will be failure of the seasonal rains.

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

Figure 17. Locust adults and swarms do not always fly on the prevailing winds but instead may wait for specific types of winds to occur. (A) West Africa. In the autumn, the prevailing winds are from the north. However, swarms will not move south on these winds. Instead, they move northwards across the Sahara on the few days in which there are southerly winds associated with an atmospheric depression (indicated by an L) over the western Mediterranean. This is because the southerly winds are warmer than the northerly ones. (B) Red Sea area. In order for swarms to migrate from the interior of Arabia to central Sudan at the beginning of summer, they can only fly on the rare days when winds are cross-sea upper-level winds.



Factors controlling swarm migration

It is always possible to find a warm enough wind from approximately the right direction to explain why a particular swarm migration has occurred. However, there are often other winds that the swarms could have moved with, but apparently did not. For example, swarms in West Africa frequently move northwards across the Sahara desert in the autumn, transported by warm southerlies associated with depressions in the western Mediterranean (Fig. 17A). The more common northeasterlies are often warm enough to move the swarms back again but that does not appear to happen. On the basis of winds and temperatures alone, swarms should move southwards not northwards from the Sahelian belt of West Africa. Indeed, some Desert Locust swarms do move in that direction. This is commonly referred to as the southern circuit. In the Red Sea area, swarms have crossed from central Saudi Arabia to the central Sudan in the early summer on many occasions, but to do so they must take advantage of the relatively few days when there are cross-sea upper-level winds, and even then the swarms apparently select a particular height (see Fig. 17B). It would seem that there must be either physiological or environmental requirements for migration of which we are at present unaware.

Factors controlling solitary migration

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

Locust migration

If you can answer "yes" to all the following questions, there is a good possibility that the adults or swarms will migrate:

- can the locusts fly?
- is the temperature warm enough?
- is the wind not very strong?
- are ecological conditions dry where the locusts are now?

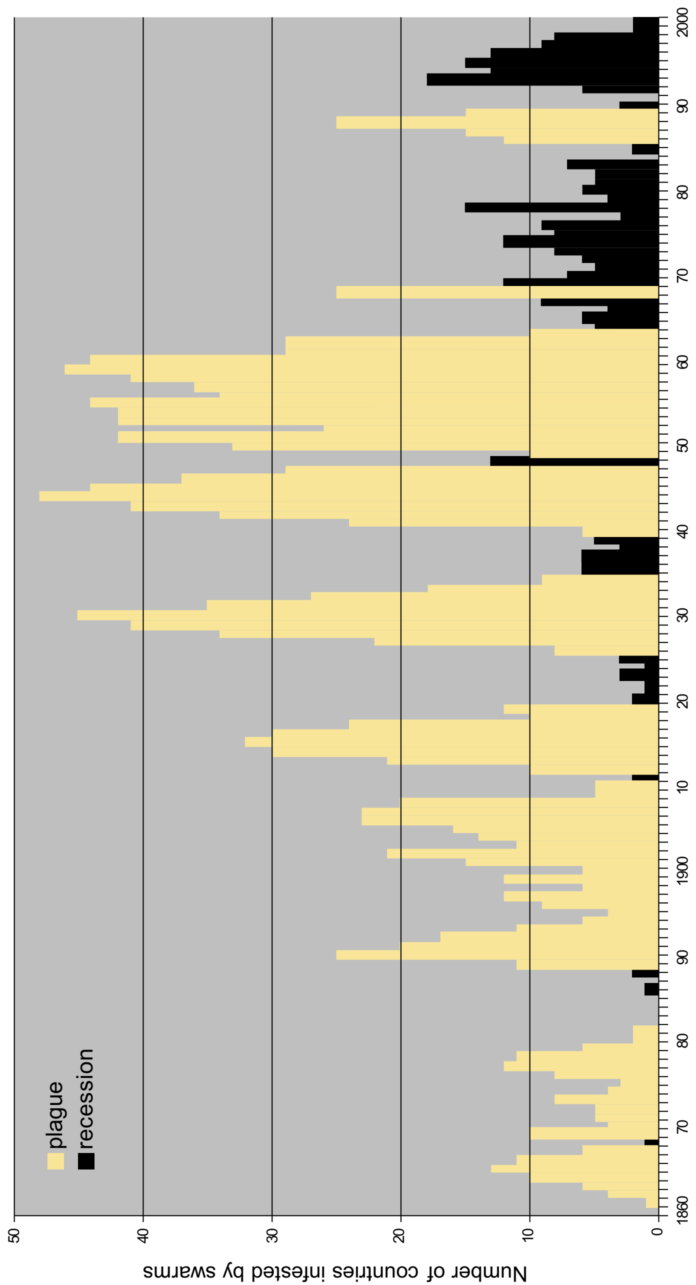


Figure 18. Plague and recession periods of the Desert Locust, January 1860 to December 2000.

RECESSIONS, OUTBREAKS, UPSURGES AND PLAGUES

Desert Locust plagues occur after a series of events in which locust numbers increase. This starts with the normally calm period of recession, followed by localized outbreaks and upsurges from which a plague may develop and eventually decline, returning to a recession period.

Since 1860, there have been nine major plagues and ten major upsurges, interrupted by periods of recessions and localized outbreaks (see Fig. 18). These lasted from several months to several years or more.

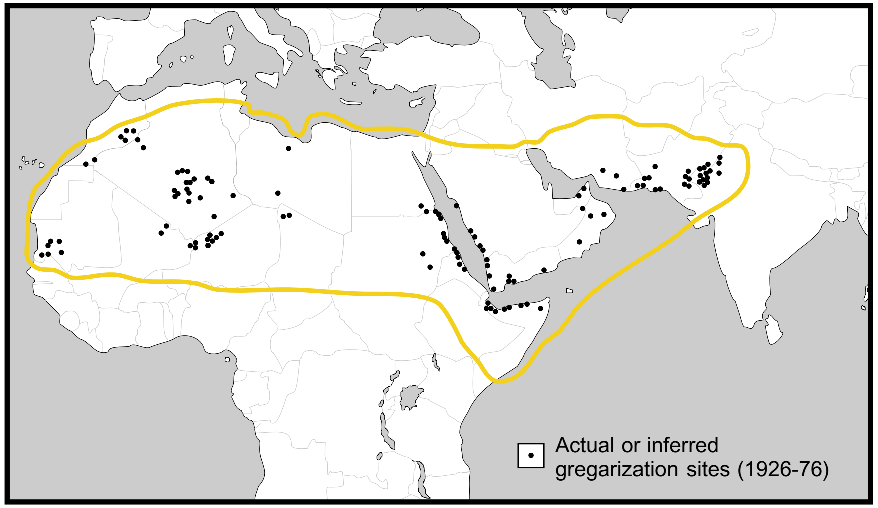
Recessions

The Desert Locust is normally present at low densities in semi-arid or arid areas, away from major agricultural zones. Desert Locusts do not cause significant crop damage, and hopper bands and swarms are rare or completely absent. These periods are called *recessions*.

The area within which these populations are confined and move around within is referred to as the *recession area*. It covers about 16 million km^2 and includes some 30 countries.

Recessions	Upsurges	Plagues	Declines
---	---	1861-67	---
1868	---	1869-81	---
1882-88	---	1889-1910	---
1911	1912	1912-19	1917-19
1920-25	1925-26	1926-34	1932-34
1935-39	1940-41	1940-48	1946-48
1948	1949-50	1949-63	1961-63
1964-67	1967-68	1968	1969
1969-72	1972-74	---	---
1975-76	1977-80	---	---
1981-85	1985	1986-88	1988-89
1990-92	1992-94	---	---
1995	1996-98	---	---
1999-	---	---	---

Figure 19. Widespread gregarization is more likely to occur where average densities are relatively high, by solitary standards, over a substantial area. Gregarization will be accelerated in areas where the favourable habitat is localized thus forcing the locusts to come together. From 1926 to 1976, gregarization has occurred, or can be reliably inferred to have occurred, only in some parts of the Desert Locust recession area as indicated below. These are mostly areas where two generations of breeding can occur in rapid succession.



Source: Waloff, Z. 1981 *In* D. Pedgley, ed. *Desert Locust Forecasting Manual*.

Recent outbreaks

Spring 1996	Yemen: the interior desert of Shabwah
Summer 1999	Sudan: Northern Kordofan and Northern States

Tip: Desert Locust plagues do not suddenly develop overnight. It takes several months of good breeding conditions and increased locust activity before a localized outbreak develops in one or more countries. If not controlled and favourable conditions continue, this can lead to a regional upsurge that may extend to other regions and eventually cause a plague. In many cases, outbreaks or upsurges do not lead to major plagues because of successful control operations, poor rainfall or adult migration to unfavourable areas.

Outbreaks

The transition from a recession situation to one of plague is characterized by outbreaks and upsurges. An outbreak occurs when there is an increase in locust numbers through concentration, multiplication and gregarization, which takes place over several months. While an outbreak is often localized and restricted to certain habitats, it can lead to the formation of bands and swarms unless it is controlled (see Fig. 19).

The early stages of an outbreak are often unobserved. Hoppers may be concealed in the vegetation and easily missed during surveys. Similarly, adults may be present in such small numbers that few, if any, are found. Alternatively, adults may be brought in from a wide area by the low level convergent wind flow, which is likely to be associated with the rain required for the first successful breeding of the sequence.

During the early stages of an outbreak, much of the population is often dispersed widely at well below gregarious densities. Small patches of hoppers are produced and small low-density swarms develop. The swarms often disperse and re-form. At this stage, a large part of the population may still not be in gregariously behaving groups.

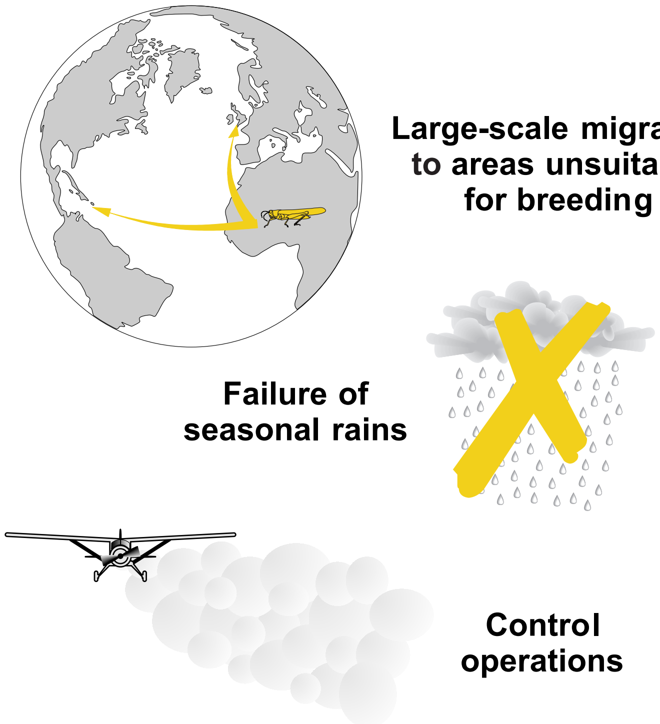
Upsurges

Upsurges are a result of successful breeding over a number of generations by an initially small population. With successive generations, the proportion of the total population in bands and swarms increases until few scattered locusts remain; the total number of locusts increases as does the size and coherence of the bands and swarms. Several outbreaks that occur at the same time followed by two or more generations of transient-to-gregarious breeding can lead to an upsurge.

This situation is dependent upon a series of substantial and widespread rains of which at least the earliest rains occur in the normally arid recession area. As the upsurge develops, there will be migration taking adults from one breeding area to the next one in the chain. More than one upsurge can occur at the same time but in different regions. Many upsurges die out without leading to a major plague. For example, of the five upsurges that have occurred since 1970, only one has led to a plague. This may result from a combination of several factors such as a failure of the rains, causing unfavourable breeding conditions, the migration of adults to an area in which they die shortly upon arrival without laying, or control operations.

The few upsurges that have been analysed carefully have been ones that led to plagues, even if short-lived ones. In these upsurges, the sequence of movements has often been different. Moreover, several seem to have started from areas where recession breeding occurs very rarely. The most commonly infested recession areas may not be the most important ones.

Figure 20. Plagues commonly come to an end through a combination of natural and human factors such as large-scale migration to unfavourable habitats, failure of seasonal rains resulting in lack of food and breeding activity, and control operations.



Plagues

There are periods of one or more years during which there are widespread and heavy locust infestations, the majority of which occur as bands or swarms. These are referred to as *plagues*. A plague can occur when favourable breeding conditions are present and control operations fail to stop a series of local outbreaks from developing into an upsurge that cannot be contained. A major plague exists when two or more regions are affected simultaneously. Plagues are separated by recession periods during which bands and swarms are rare or completely absent, and most of the locusts are present at low densities.

There have been six major plagues of Desert Locusts in the 1900s, one of which lasted almost 13 years. The area in which plagues occur covers about 29 million km^2 which is nearly twice as large as the recession area, and can extend across 57 countries.

Declines

Plagues usually decline as a result of a combination of natural factors and human intervention (see Fig. 20). One natural cause is failure of the rains in an area where successful breeding usually occurs. For example, the short rains in the Horn of Africa failed in 1955, which led to the first break in gregarious populations since 1950. Another cause is migration to areas from where either the adults or their progeny cannot return. A spectacular example is the trans-Atlantic swarm migrations of October and November 1988. Human intervention through control operations also plays a significant role in bringing plagues to an end.

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FAQ number 8 (see p. 42 for answers)

Do Desert Locust recessions, outbreaks, upsurges and plagues occur on a cyclical basis, for example, every seven years?

FREQUENTLY ASKED QUESTIONS (FAQS)

1. Does gregarization occur at a specific threshold, in other words, once there are a certain number of locusts present in a given place?

Answer: No. Desert Locusts exist in many different habitats and under a variety of environmental conditions in the desert. They behave differently in each of these settings. In some cases, gregarization may occur when there are only a relatively few locusts; in other cases, gregarization may not occur when there are large numbers of locusts. This is often related to different types and densities of vegetation.

2. Will locusts lay eggs in areas of dense vegetation?

Answer: No. Locusts require bare ground for laying eggs. In areas of dense vegetation, there is often very little bare ground.

3. How can you tell the difference between hopper groups and bands?

Answer: You should carefully observe their behaviour and their appearance. Groups will contain some hoppers that are starting to behave in the same manner but not all individuals will be doing this. Their colours are a mixture of those commonly associated with solitarious and gregarious individuals, that is, green with some black markings. On the other hand, bands consist of all or close to all of the locusts behaving in the same manner. Their appearance is distinctive: hoppers in bands are either black (when young) or yellow with black markings.

4. Do Desert Locusts have an overwintering stage?

Answer: Strictly speaking, no. But under cool, dry conditions, the development of any stage (egg, hopper, adult) will be longer.

5. Do solitary adults fly during the day?

Answer: Solitary adults may fly during the day when they are disturbed by other animals or by people. However, such flights are usually very short and are not considered as migration from one location to another. Mature males have also been seen flying during the day, looking for females for mating.

6. How can you tell the difference between adult groups and swarms?

Answer: You should carefully observe their behaviour and their appearance. Groups will contain adults that are starting to behave in the same manner but not all individuals will be doing this. Their colours are a mixture of those commonly associated with solitarious and gregarious individuals, that is, a pinkish (immature) or yellowish (mature) appearance. On the other hand, swarms consist of all or close to all of the adults behaving in the same manner. Their appearance is distinctive: pink for immature swarms and yellow for mature.

7. Do swarms fly at night?

Answer: Occasionally during periods of unusually warm temperatures, swarms will fly during the early evening but rarely will they continue to fly during the entire night unless they happen to be over water (sea, ocean).

8. Do Desert Locust recessions, outbreaks, upsurges and plagues occur on a cyclical basis, for example, every seven years?

Answer: There does not appear to be any statistically significant evidence that suggests locust recessions, outbreaks, upsurges or plagues occur with any regularity.