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What Are Locusts and What Are Not?

Locusts (from the Latin 'locus ustus' = 'burnt place') are short-horned grasshoppers (Orthoptera: Acrididae), distinguished by their density-dependent behavioral, physiological, and phenotypic polymorphism. Under low population densities, locusts exist in the so-called 'solitarious phase.' Solitarious nymphs are characterized by camouflage coloration, infrequent social interactions, and sedentary behavior. When crowded, locusts develop into the 'gregarious phase' with nymphs often strikingly colored in dark brown or black with contrasting yellow, orange, or red. The gregarious nymphs form cohesive groups or ‘hopper bands,’ capable of long-distance, concerted marching. Adults of the gregarious phase differ from solitarious individuals by having longer wings and shorter hind femora, as well as by some less conspicuous morphological traits.

The most spectacular differences between the phases are in behavior: the solitarious adults avoid each other except for mating, while the gregarious adults pack together in swarms; they migrate, feed, mate, and lay eggs in crowds. The swarms contain from several thousand to 40 billion individuals. Swarms are capable of sustained day-time flights covering distances from several dozen to several thousand kilometers. In 1988, swarms of the Desert locust took off from the coast of West Africa, crossed the Atlantic Ocean and landed in the Caribbean Islands and northern shores of South America, covering over 5000 km in 6–10 days. Solitarious adults also can make long-distance flights although they fly individually and at night. The differences in pigmentation between the adults of the gregarious and solitarious phases are not as striking as in the nymphal stage (Figures 1 and 2).

Out of more than 12 000 described grasshopper species in the world, only about a dozen exhibit pronounced behavioral and/or morphological differences between phases of both nymphs and adults, and should be considered locusts. In other words, all locusts are grasshoppers, but not all grasshoppers are locusts. The capacity to produce a swarming phase appeared independently a number of times within the family Acrididae and is considered as a relatively recent trait in grasshopper evolution. The most economically important locust species and their geographic distribution are presented in Table 1. The term 'locust' is sometimes erroneously applied to periodic cicadas (e.g., '17-year cicada'), which belong to a different insect order, Homoptera. Another misnomer comes from the plant kingdom (e.g., 'black (or yellow) locust tree' Robinia pseudoacacia or 'honey locust tree' Gleditsia triacanthos, both from the legume family) (Figures 3–6).

Economic Importance

Locusts have been the enemies of humans since the dawn of agriculture. They are mentioned in ancient writings such as the Torah and the Koran. In the Old Testament of the Bible, locusts constitute the infamous Eighth Plague of Egypt. Locust swarms often brought devastation and hunger to entire nations. According to the Roman historian Pliny the Elder, in 125 BC, 800 000 people died in the Roman colonies of Cyrenaica and Numidia (territories of contemporary Libya, Algeria, and Tunisia) from famine caused by a locust plague. In 1958 in Ethiopia, locusts destroyed 167 000 tons of grain, which is enough to feed 1 million people for a year. Locust outbreaks have occurred on all continents except Antarctica and can affect the livelihood of one in ten people on Earth.

Besides the direct economic losses to crops, locust outbreaks may be devastating to ecological processes by destroying vegetative food sources for many animal species. The passages of locust swarms may cause human demographic changes. In contemporary society, subsistence farmers abandon fields that are wrecked by locusts and move into cities, adding to the demand on urban infrastructures in already overpopulated and impoverished settings. Locust-control efforts, which are essentially chemical, can produce negative environmental impacts and continue to be very costly. In 2003–2005, to curtail a Desert locust outbreak that affected 8 million people in Africa, 13 million ha (approximately the area of the state of New York) was treated with broad-spectrum neurotoxic insecticides in 26 countries. The cost of the campaign including food aid to the affected population amounted to half a billion US dollars.

While insect pests destroy annually 14% of crops worldwide, the annual crop losses from locusts are estimated at only 0.2%. The seemingly low figure is misleading because the perception of locust damage is scale-dependent. Locust swarms can be compared to other natural disasters like hurricanes or tornadoes. For an entire national economy, the total crop losses from locusts may seem negligible, but for a given farmer or cooperative, even a brief passage of a locust swarm may result in a complete destruction of the whole season’s work. This is particularly relevant to subsistence farmers in developing
countries. As such, the socio-political consequences of a locust plague are difficult to translate into simple monetary terms.

**Life Cycle**

The life cycle of any locust species includes a sequence of embryonic (egg), nymphal, and adult stages. Females lay eggs, using short hook-like valves of the ovipositor at the tip of their abdomen to bore into the top layer of the soil. During oviposition, a female extends her abdomen three to four times its normal length by means of elastic intersegmentary membranes. The duration of oviposition depends on soil properties, particularly compactness, and lasts from 30 min to 2 h. Eggs are laid in packets called egg-pods. The number of eggs in an egg-pod depends on the species and is often correlated with the body size of the females. The smaller, Moroccan and Italian locusts have respectively 18–42 and 20–60 eggs in their egg-pods, while the larger Migratory and Desert locusts have 40–120 and 30–146 eggs in their egg-pods, respectively. Egg-pods of the big Red locusts may contain up to 190 eggs. Each female lays one to four egg-pods with about a 10-day interval between successive ovipositions. The initial egg-pod contains more eggs than the subsequent ones of the same female (Figures 7–9).

In the temperate zones, locust embryos develop with an obligatory diapause, meaning that eggs laid in the summer delay hatch the next spring. To enhance survival through long periods of freezing temperatures and to protect from predator attacks, the egg-pods of the temperate locust species, such as Moroccan and Italian locusts, have thick walls made of soil particles cemented by secretions from female’s accessory glands and oviduct. The eggs are cemented together as one by the female’s secretions and form an egg cluster occupying the lower part of the egg-pod. Its upper part consists of a foamy or spongy mass, which hardens after oviposition, and a lid that allows the hatching nymphs to exit. Eggs of most tropical and subtropical locust species incubate without diapause and hatch 2–3 weeks after oviposition. In such cases (e.g., in the Desert or Red locusts), the egg-pods are just clusters of loosely attached eggs with a foam plug on top of them.

During hatching, the newly born nymphs tunnel through the softened foam plug to reach the surface of the soil. Once out of the egg-pod, they immediately undergo an intermediate molt, shedding their embryonic cuticle and becoming first-instar nymphs. With a mortality rate of up to 90%, the first instar constitutes the critical developmental stage for the survival of the locust population. Nymphal development includes 5 (rarely 4, 6, 7, or even up to 9) successive instars separated by molts. In some species, females have an extra instar compared to males. Later instars are distinguished from the earlier ones by their bigger size and more developed wing pads. The rate of development and duration of the nymphal period depend largely on the prevailing weather, primarily air temperature and humidity. Under optimal conditions, each instar lasts 5–7 days with a total of 25–35 days to reach adulthood. Under unfavorable environmental conditions, the nymphs may require 2–3 months to develop fully. After the final molt, or fledging, the nymphs turn into adults.

Adult locusts are characterized by two pairs of fully grown wings. The front pair, or tegmina, are narrow and...
**Table 1**  Main locust species, their body sizes and geographic distribution

<table>
<thead>
<tr>
<th>No</th>
<th>Common name</th>
<th>Latin name</th>
<th>Body length (mm)*</th>
<th>Geographic distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Desert locust</td>
<td><em>Schistocerca gregaria</em> (Forskål, 1775)</td>
<td>♀♂</td>
<td>45–56 50–65 Africa, S. Europe, SW and Central Asia (invasion area)</td>
</tr>
<tr>
<td>2</td>
<td>Migratory locust</td>
<td><em>Locusta migratoria</em> (L., 1758)</td>
<td>♀♂</td>
<td>35–50 45–65 Africa, Eurasia, Australia</td>
</tr>
<tr>
<td>3</td>
<td>Moroccan locust</td>
<td><em>Dociostaurus maroccanus</em> (Thunberg, 1815)</td>
<td>♀♂</td>
<td>15–30 20–40 N. Africa, Europe, Central Asia</td>
</tr>
<tr>
<td>4</td>
<td>Italian locust</td>
<td><em>Calliptamus italicus</em> (L., 1758)</td>
<td>♀♂</td>
<td>15–30 20–42 Europe, Asia</td>
</tr>
<tr>
<td>5</td>
<td>Red locust</td>
<td><em>Nomadacris septemfasciata</em> (Audinet-Serville, 1838)</td>
<td>♀♂</td>
<td>35–50 50–62 Africa</td>
</tr>
<tr>
<td>6</td>
<td>Brown locust</td>
<td><em>Locustana pardalina</em> (Walker, 1870)</td>
<td>♀♂</td>
<td>35–45 40–55 S. Africa</td>
</tr>
<tr>
<td>7</td>
<td>Australian Plague locust</td>
<td><em>Chortoicetes terminifera</em> (Walker, 1870)</td>
<td>♀♂</td>
<td>20–30 30–45 Australia</td>
</tr>
<tr>
<td>8</td>
<td>American Bird locust</td>
<td><em>Schistocerca americana</em> (Drury, 1773)</td>
<td>♀♂</td>
<td>40–50 45–56 S. and Central America</td>
</tr>
<tr>
<td>9</td>
<td>Bombay locust</td>
<td><em>Nomadacris succinta</em> (Johansson, 1763)</td>
<td>♀♂</td>
<td>40–50 55–65 SE Asia</td>
</tr>
<tr>
<td>10</td>
<td>Rocky Mountain locust</td>
<td><em>Melanoplus spreitus</em> (Walsh, 1866)</td>
<td>♀♂</td>
<td>15–25 20–30 N. America</td>
</tr>
</tbody>
</table>

*a* Measured from the tip of the head to the end of the abdomen.

*b* Went extinct in the early twentieth century.

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**Figure 4**  Adult Migratory locust. Photo: A. Latchininsky.

**Figure 5**  Adult Moroccan locust. Photo: A. Latchininsky.

**Figure 6**  Adult Italian locust male. Photo: A. Latchininsky.
leathery, concealing the broad membranous hind wings, which are folded along the main veins fanwise while at rest. Newly fledged locusts have a soft cuticle that hardens in several days. Adult locusts make short wandering flights in the first days after fledging but only after their cuticle hardens can they accomplish long-distance migratory flights. Sexual maturation takes from just a few days to several weeks, after which the locusts start mating. In some cases, such as Desert and Red locusts and tropical tree locusts of the genus *Anacridium*, mating can be delayed by unfavorable weather conditions (e.g., low air temperature or insufficient humidity). The adults can remain sexually immature for up to 9 months. They continue to fly and feed but, if unfavorable conditions persist, they would eventually die without producing offspring. A favorable change of the environmental conditions can trigger sexual maturation and eventual reproduction at any time during this period. In most locust species, maturation is manifest by noticeable changes in pigmentation. Immature Desert locusts are pink and turn bright yellow when sexually mature. Immature Migratory locusts gradually change their coloration from green or brownish to mostly yellowish as they mature. Some other species as the Italian or Australian Plague locust do not exhibit noticeable pigmentation changes associated with sexual maturation. Physiological changes during maturation
include the growth of testes and accessory glands in males and ovarian development and egg growth in females (Figures 10 and 11).

Locust males mature from one to several days earlier than females. The presence of the mature males accelerates the maturation of females. Locusts reproduce sexually; cases of parthenogenetic reproduction are rare. Olfactory and acoustic signals are used to ensure the meeting of prospective mates. Locusts (often both sexes) produce stridulating call signals by rubbing the inner surface of the hind femora over the thickened veins on the tegmina. Copulation lasts from 1 to 20 h. During copulation, the male mounts the female, grasps the tip of her abdomen with his and transfers the sperm packet, called spermatophore, into the female’s genital opening. The female stores the sperm in a special organ called the spermatheca. Locusts can mate multiple times during their adult lives. However, a single copulation is usually sufficient to fertilize all the eggs produced by the female (Figure 12).

In temperate zones, locusts exhibit a univoltine life cycle characterized by only one generation per year and an obligate embryonic diapause. Some subtropical species, such as the Egyptian tree locust *Anacridium aegyptium*, hibernate as sluggish and practically nonfeeding adults during the winter months. Most tropical locusts develop continuously, without embryonic diapause, and under favorable conditions can produce two, three, and rarely even four annual generations.

**Phase Transformation**

The key event in the biology of locusts is the change from a single-living and mostly sedentary solitarious phase to a gregarious phase in which they live in dense bands or swarms, actively migrate and may devastate crops and rangeland. This phenomenon, which is nonexistent among nonswarming grasshoppers, is called locust phase transformation. Besides the conspicuous behavioral, morphological, and color changes, the extreme solitarious and gregarious locust phases differ in food selection, nutritional physiology, metabolism, reproductive physiology, neurophysiology, endocrinology, pheromone production, longevity, and molecular biology. Locusts are polymorphic, and the extreme phases are connected by a continuum of intermediate, transitional forms (phase transiens). It takes at least four consecutive generations to complete the phase transformation from a typical solitarious phase to a fully gregarious phase. Phase transformation is a cumulative, but also a reversible, process that requires suitable environmental conditions. The process is density dependent and starts when locust density exceeds a certain threshold. In the Desert locust, behavioral changes first become manifest when the density of the young nymphs exceeds approximately 50,000 individuals per ha or 5 per m². For older nymphal instars, the threshold is 5000 per ha, and for adults it is 250–500 per ha. At these density levels, the locusts start switching from their solitarious tendency of avoiding each other to a proclivity for forming sustained cohesive groups...
and moving in a concerted way. Most other locust species have higher phase transformation thresholds than the Desert locust.

Recent studies have shown that different locust phases are produced by different expressions of genes in response to crowding. Locust species vary in the number of phase traits they exhibit. Some, like the Australian Plague locust, produce only behaviorally different phases. In others, like Desert, Migratory, and Moroccan locusts, in addition to behavior, the solitarious and gregarious phases are distinguished by morphology and pigmentation.

The sight and smell of conspecifics trigger behavioral changes in solitarious locusts after only 4 h of crowding above the phase transformation threshold. When the locusts meet up, their nervous systems release serotonin, an evolutionarily conserved mediator of neuronal plasticity. Serotonin causes the locusts to become mutually attracted, which is a prerequisite for swarming. Once the locusts start to aggregate together, their interactions increase and a positive feedback loop accelerates the changes toward the gregarious phase. At this point, the direct mutual contacts between the individuals become the most powerful gregarizing stimuli. Tactile receptors on external side of the hind femora of nymphs are particularly sensitive to such contacts. Their repeated stimulation by crowded locusts enhances the expression of gregarious phenotypic traits, particularly the contrasting black and orange, yellow, or red pigmentation. However, the locusts may revert to solitarious behavior after 4 h of resolation.

Phase characteristics not only develop during the lifespan of a locust, but are also being transferred from mothers to offspring. This maternal effect is mediated through certain chemicals secreted by females into the foam substance surrounding the eggs. Such a mechanism allows for maintaining and developing phase status across generations. Behavioral, chromatic, and physiological changes are followed by emerging traits of gregarious morphology, but these changes become noticeable only several (at least four) generations after gregarization starts. Tropical locusts which have multiple generations per year can build up a dense gregarious population and mass migrate in hopper bands and swarms in just 2–3 years. In temperate zones, where locusts have a single annual generation, it usually takes them longer to accomplish the transformation from the solitarious to gregarious phase and to build up a swarming population.

The concept of the locust phases was first put forward in 1921 by the Russian entomologist Boris Petrovich Uvarov (1888–1970), who was the founder and first director of the Anti-Locust Research Centre in London. Uvarov postulated that the two phenotypically very different forms of Locusta, which were then considered as separate species L. danica and L. migratoria, were in fact the two extreme phases of a single species. Similar phase differences were later found in other locust species. Uvarov’s ‘phase theory of locusts’ emphasized the crucial role of phase transformation in developing locust outbreaks and had important practical applications for locust population management.

Environmental Conditions Leading to Phase Transformation

Most of the time, locusts lead a solitarious life, and this may be considered as the normal state of their populations. At some points in time, however, changes in their environment may initiate the gregarization. In the case of the Desert locust, such changes are triggered by abundant rains that promote lush vegetation growth in an otherwise arid milieu. The locusts start to congregate on the patches of green vegetation, forming loose groups at first, and dense hopper bands later. They feed and march together, and increasingly become phenotypically gregarious. Similarly, rains in the arid zones trigger gregarization of the Australian Plague locust. In the case of the Migratory locust, which inhabits reed stands in wetlands along rivers and lakes, it is the excessive drought that usually initiates the aggregation of locusts and their consequent gregarization. The locusts concentrate on few remaining patches of reeds and start producing hopper bands with gregarious behavior and appearance. Drought is also responsible for initial concentrations of the Moroccan locust in the Mediterranean semi-deserts and Central Asian arid steppes. The hoppers crowd together on few patches of green grasses and forbs which emerge in early spring. Such concentrations may eventually lead to the appearance of the gregarious phase. These examples show that habitat discontinuity or patchiness, which can result from a variety of meteorological events, is the most important condition for initial locust gregarization and phase transformation. If the resources, particularly vegetation, are distributed in a uniform fashion, the chances that the locusts will start to produce gregarious populations are low. For example, locust outbreaks originating from dense forests are unknown. Mosaic habitats which represent a combination of green vegetation clumps and areas of bare ground are most favorable for producing and maintaining the gregarious phase.

Although the ecological conditions leading to the initiation of phase transformation are well understood for most locust species, outbreaks (the spectacular hopper band movements and swarm flights) still often remain ‘unexpected.’ The main reason for this is that the areas of initial locust aggregations are scattered over a vast territory with difficult access and low human populations. For the Desert locust, the area where incipient gregarious populations may form covers 16 million km², which is roughly equal to the areas of the United States and Australia, combined. The total distribution area of the Migratory locust is even larger. Despite efforts to implement efficient locust monitoring using satellite images and automated weather stations, there is always a
threat that in some locations locusts may produce an undetected gregarious population, leading to a large-scale outbreak.

**Gregarious Behavior**

**Hopper Bands**

Gregarious females oviposit in dense groups, which results in simultaneous hatching of large number of hoppers in close proximity to each other. In the mornings, the hoppers form very dense groups staying on the ground and basking in the sun. Once their body temperature rises, they start marching. The concerted, directional movement of dense hopper bands may represent an antipredator strategy: the grouped nymphs saturate the predators with sheer numbers and are much less likely to become their victims than individual hoppers living on their own. At the same time, the members of the band suffer from intraspecific competition for nutritional resources and from cannibalistic pressure. The hopper band migration is a ‘forced march’ driven by cannibalism. Until a band encounters new nutritional resources, the hoppers need to move to escape attacks from behind by the hungry members of the same band (Figures 13 and 14).

The sizes of hopper bands vary from several square yards to many acres. The record figure, 110 km², comes from a Moroccan locust band observed in Iraq. Accordingly, the number of hoppers in the band can be astronomically high. The density in the band is highest during early nymphal instars and often reaches thousands per m². The record density of the first-instar hoppers of the Migratory locust is known to reach 80,000 per m²; similar estimates for other species are 37,000 for the desert locust, 28,000 for the Australian Plague locust, and 21,000 for the Moroccan locust (Figure 15).

The speed of hopper marching and distances traveled by the bands depend on the age of the hoppers, vegetation, relief, and weather. First- and second-instar hoppers rarely travel more than 200 m day⁻¹. Organized marching usually starts in the third instar and continues until adulthood. If the vegetation is sparse, late-instar hopper bands of the Desert and Migratory locusts can travel over a mile per day. The total maximum distances covered by hopper bands during the entire nymphal period are 3 km for the Italian, 10 km for the Red, 17 km for the Moroccan and Brown, and up to 30 km for the Migratory and Desert locusts.

**Swarms**

Adult gregarious locusts spend nights roosting in very dense aggregations on trees, shrubs, or bare ground. In the first days after fledging, when their cuticle is still soft, individual adults can produce only short erratic or escape flights. Group flights start 10–15 days after fledging. At first,
Locusts

Food and Feeding Behavior

Locusts are proverbial for their voracity. However, the view that locusts are ‘chewing automata,’ that is, they devour everything in their way, appears to be far from being accurate. In the solitarious phase, locusts exhibit marked food preferences and feed only on a limited number of preferred plant species. The Desert locust prefers the foliage of trees and shrubs to the herbaceous plants, and among the latter, it clearly prefers forbs to grasses. The Migratory locust, on the contrary, has a preference for grasses and related families of sedges and rushes. The forbivorous Italian locust favors sage shrubs from the genus * Artemisia* and legumes. Food selection includes finding suitable plants, first using visual and then olfactory stimuli. Host-plant choice may be limited by the distribution of deterrent compounds (glucosides, alkaloids, essential oils, organic acids) in nonhost plants. Plants with mechanical defenses (hooks, spines, trichomes) are often avoided. The situation changes when the locusts undergo phase transformation. Crowded locusts are less selective in food searching because they often live under the stress of food and water shortage. Among the factors separating unpalatable from palatable food, the water content of the food plays a significant role. This is one of the reasons why locusts sometimes attack not only habitually rejected plants but also many nonplant substances like textiles, dung, woodwork, wool – even on live sheep! After a long migratory flight, the need to compensate for water losses becomes overwhelming, and upon landing, locust swarms consume literally anything that holds the slightest moisture. The degree of polyphagy in swarming locusts is inversely proportioned to the water requirements of the organism (Figure 17).

Although locusts are essentially herbivorous, they can be cannibalistic or necrophagic, especially if crowded. The impending cannibalism is considered to be one of the driving forces of the concerted hopper marching behavior.

The proverb ‘each locust can eat its weight in plants each day’ holds true only for the nymphal instars, while for adults the ratio of daily consumption to the body weight is lower, about 0.5. The amount of food consumed...
by locusts varies among the species and developmental stages and is proportionate to the insect’s size. Locust hoppers fast before and after each molt, and the duration of this fasting can reach 10–15% of the total nymphal period. At some periods of their life, such as sexual maturation and egg production, locusts become more voracious. Energy expenditures during hopper band marching or swarm flying is often compensated for by increased feeding.

**Egg Laying**

Females of the gregarious phase are well known for laying their eggs in dense groups. Arriving females are visually attracted to those that have already started egg-laying. Furthermore, the soil in which they oviposit attracts other females because of the pheromones that are contained in the secretions surrounding the eggs in an egg-pod. Group egg laying ensures maintaining and enhancing the gregarious status of the population as the resulting hatchlings form dense groups from the first days of their lives. Average egg-pod density is 5–10 per m² and maximum densities range from 500 per m² for the Desert locust to 8000 and 10 000 per m² for the Moroccan and Italian locusts, respectively. In such extreme cases, the soil in which the egg-pods were laid resembles a honeycomb. Multiplying these numbers by the average number of eggs in an egg-pod, it is possible to estimate the number of hoppers which will hatch per unit of area. However, even in the large and fecund locust species which can lay multiple pods containing more than 100 eggs each, the rate of multiplication from one generation to the next does not usually exceed 20-fold. This relatively low multiplication rate is explained by high mortality of eggs and early hopper instars due to predation and unfavorable environmental conditions (Figure 18).

**Conclusion: Locusts as Models**

For decades, locusts have been used as model organisms to study different aspects of individual and group behavior. Their collective migrations are of particular interest because the patterns of hopper band movement and swarm flight are similar to those observed in other animals. Apparently unifying laws and mechanisms exist that govern group movement in animals. This underlying framework may be so general that the individual locusts can be considered as analogs to interacting, inanimate particles. Self-propelled particle models have recently been used to account for the emerging density-dependent transition from wandering solitarious individuals to concerted hopper band marching. On the other hand, the amazing capability of locusts to avoid crashing into each other when flying together in a swarm fascinated car makers in their attempts to create a crash-proof car. This ability appears to be due to the fact that the visual input is transmitted directly to the wings of the locust, seemingly bypassing the brain.

See also: Collective Intelligence; Group Living; Group Movement; Insect Migration; Insect Navigation; Kleptoparasitism and Cannibalism; Orthopteran Behavioral Genetics.

**Further Reading**


Relevant Websites

http://locust.cirad.fr/ – CIRAD (France).