

# Molecular Mechanisms of Phase Change in Desert Locusts

*Rudra Gouda, M. N., Sachin, S. Suroshe, and Subramanian, S.*

Locusts, a type of short-horned grasshopper in the Acrididae family, usually exhibit solitary behavior but can transform into gregarious swarms under specific conditions. In English, the term “locust” refers to grasshopper species that, when crowded, undergo density-dependent phenotypic plasticity, forming swarms from groups of immature hoppers (Shrestha et al., 2021). Boris Uvarov, a pivotal figure in the foundation of the Anti-Locust Research Centre, introduced the concept of phase polymorphism in 1921 to elucidate the changes observed in locusts. Uvarov focused on the migratory locust, demonstrating that the previously considered separate species, *Locusta migratoria* and *L. danica* L., actually represented two phases termed solitaria and gregaria. Charles Valentine Riley and Norman Criddle played significant roles in understanding and controlling locusts, as documented by Egerton in 2013.

Solitary locusts prefer isolation, while gregarious locusts thrive in swarms, exhibiting social behaviour. Swarms in locusts are a response to overcrowding, with heightened stimulation of the hind legs leading to increased serotonin levels. This hormonal shift results in notable changes such as alterations in coloration, intensified feeding, and enhanced breeding. The transition to the swarming form occurs after multiple contacts per minute sustained over four hours. Massive locust swarms can reach staggering numbers, comprising billions of individuals and covering extensive areas, with population densities reaching up to 80 million per square kilometre (200 million per square mile). The release of serotonin

during contacts among desert locusts induces mutual attraction, a crucial factor in the formation of swarms. The initial bands of gregarious hoppers are termed “outbreaks.” When these bands merge into larger groups, it’s referred to as an “upsurge.” Continued aggregation of upsurges from separate breeding locations on a regional level is known as a “plague.” During outbreaks and early stages of upsurges, only a portion of the locust population becomes gregarious, with scattered bands of hoppers spread across a wide area. Over time, the insects become more cohesive, and the bands concentrate in a smaller area.

During the desert locust plague spanning Africa, the Middle East, and Asia from 1966 to 1969, locust numbers surged from two to 30 billion over two generations. However, the affected area decreased significantly from over 100,000 square kilometers (39,000 sq mi) to 5,000 square kilometers (1,900 sq mi). In 1980, a substantial African locust outbreak impacted over 360,000 hectares in northern Senegal (Walsh 1986). The historically significant desert locust has invaded 31 million square kilometers across 52 countries in Africa, the Near East, and Southwest Asia (Anonymous, 1968). Australia faced a major outbreak in 1998 (Hinton and library, 2007). In 2001, locusts affected southern Russia and concurrently plagued China’s Yellow River basin, Bohai coast, and northern Xinjiang. From 2003 to 2004, China experienced a vast locust impact, resulting in substantial crop losses. In 2010, New South Wales saw an extensive locust-infested area of about 390,000 square kilometers, causing significant economic losses (Miao et al., 2015). In 2013, locusts from Egypt reached Israel,

covering 800 hectares of desert, affecting half of Madagascar, and causing food shortages (Marei et al., 2015). The 2020 locust outbreak, identified by the Food and Agriculture Organization (FAO) as the most severe in 70 years, devastated 70,000 hectares of land in Somalia and Ethiopia, highlighting the global and varied impacts of locust outbreaks on agriculture and food security (FAO, 2020)

### **What triggers them to form a swarm**

Guaiacol, a compound found in the gut of desert locusts, is produced through the breakdown of plant material by the gut bacterium *Pantoea agglomerans*. This process contributes to the production of pheromones that are involved in causing locust swarming (Dillon et al., 2002). Research conducted by Guo et al. (2013) has shown that serotonin plays a role in promoting the transition to the solitariness phase in migratory locusts. During swarming, gregarious adult locusts exhibit migratory behaviour where they move in the direction of the wind. They can cover distances of approximately 150 km per day. The wind direction determines the displacement of the adult locusts and swarms.

### **Phase polyphenism and its evolution in locusts**

Changes in locusts' adaptive traits are closely linked to shifts in their environment. For instance, gregarious locusts typically demonstrate reduced fecundity and engage in more extensive migratory flights compared to their solitary counterparts. Gregarization also impacts other traits, including development, longevity, lipid accumulation, and the size of eggs or offspring. This shift towards allocating energy to flight rather than reproduction is a consequence of the gregarious phase. A recently reported example of an adaptive phase trait is the cold hardiness of locust eggs. Solitary locust eggs with enhanced cold hardiness have a better chance of surviving winter, contributing to the maintenance of their population size in the subsequent year. Changes in body colour and behaviour are common

responses to fluctuations in population density. Recent research, utilising phylogenetic analyses, theoretical models, and population genetics, has provided insights into the evolutionary history of locusts and the mechanisms driving their adaptations. Phase-related characteristics exhibit significant similarities among different locust species within each monophyletic group. The evolution of swarming behaviour in locusts has independently occurred multiple times in various lineages globally, indicating that phase change is a convergent phenomenon. Theoretical studies suggest the roles of interspecific interactions, such as predation, and intraspecific interactions, like cannibalism, in the evolution of density-dependent phase polyphenism. Genetic variation between non-outbreking and outbreking populations of *Locusta migratoria* indicates that historically outbreking populations display a higher degree of parentally inherited density-dependent phase changes and greater gene flow. Mitochondrial genomic evidence indicates that *L. migratoria* exhibits lower genetic differentiation, with two lineages displaying similar degrees of phase polyphenism, likely contributing to the maintenance of the south-north cleavage pattern. However, the specific genetic factors responsible for the evolution of locust-phase polyphenism remain unknown. The availability of genomic resources has opened up new avenues for future investigations into the genetic basis of locust phase change.

### **Omics of Locust Phase Change**

#### **Genetic Analysis of Locust Phase Change**

The conditions that trigger a phase transition in locusts may vary from those that sustain it, and the apparent disparities between the extreme phases may be a consequence of the phase shift rather than being the cause of it. Consequently, the task of identifying biochemical and molecular markers of locust phase transition becomes increasingly intricate. Recent studies have utilised advanced

methods in functional genomics, including transcriptomics, microarrays, proteomics, differential displays, and metabolomics, to investigate the biochemical and molecular alterations linked to locust phase transition. Nevertheless, these investigations have offered only restricted understanding of their molecular roles, although providing vital information regarding the genetic pathways that regulate alternate phenotypes.

### **Genes and Transcriptomic Profiles**

The study of phase-related gene expression in *Schistocerca gregaria* involved analysing brain tissue using differential display reverse transcriptase polymerase chain reaction. This technique detected eight distinct bands, one of which displayed an 80% similarity in sequence with the SPARC protein found in *Drosophila melanogaster*. The precise contribution of SPARC to locust phase transition is still unknown, despite its established significance in nematode worm motility and shape, as noted by Rahman et al. in 2003. At the same time, a separate Expressed Sequence Tag (EST) database was created for *S. gregaria*. A study identified and categorised 214 Differentially Expressed Genes (DEGs) into five Gene Ontology (GO) terms: multicellular organismal development, neurological system processes, stress response, precursor metabolite and energy generation, and cellular macromolecule biosynthesis. Individual locusts that were alone showed improved resistance to the ageing process, as indicated by the increased activation of genes related to antioxidant mechanisms, detoxification, and the renewal of anabolic processes. Conversely, sociable desert locusts exhibited a greater number of transcripts associated with sensory processing, nervous system development, and plasticity. An analysis of data from *S. gregaria* and *L. migratoria* showed that solitary and gregarious locusts had comparable patterns of differential gene

expression. These findings indicate that there are shared molecular pathways that drive locust phase shift, even among distinct evolutionary lineages, as explained by Badisco et al. (2011).

### **Proteins and Peptidomes**

Several studies have examined the protein and peptidome profiles linked to the transformation of locusts between different phases. Researchers employed 2D gel electrophoresis to produce polypeptide maps of hemolymph extracted from fully developed adult male locusts (*S. gregaria*) in a specific investigation. A total of 238 polypeptide sites were discovered, out of which 20 locations showed differential expression between solitary and gregarious locusts. Significantly, three sites were exclusive to solitary locusts, whereas 17 were exclusive to gregarious locusts. Field observations of solitary and social locusts confirmed the phase-specific manifestation of these 20 polypeptide spots. After 15 days of treatment with a juvenile hormone (JH) analogue, nine out of the 17 polypeptide spots related to gregarious behaviour were suppressed. Nevertheless, there was a scarcity of data on the molecular weight and isoelectric point of these proteins, and their actual identities remained unknown, as described by Wedekind-Hirschberger et al. in 1999.

Researchers combined high-performance liquid chromatography (HPLC) with matrix-assisted laser desorption/ionization time-of-flight mass spectrometry (MALDI-TOF MS) to analyse the peptidomes of the solitary and gregarious phases of *S. gregaria* in a separate study. From this study, two primary proteins were identified: a 6-kDa peptide and a serine protease inhibitor called SGPI-2. These proteins showed varying levels of expression in the two stages. The 6-kDa peptide, provisionally designated as PRP (phase-related peptide), was found in large quantities in the hemolymph of adults raised in a group, with a concentration of 0.1 mM. As the

locusts shifted from being social to solitary over multiple generations, the level of PRP gradually declined. Despite thorough study, the exact role of PRP remained uncertain. It had no protease inhibitory, antibacterial, or antifungal properties, and had no effect on yellow protein expression, cuticle pigmentation, or the synthesis of the pheromonal chemical phenylacetone nitrile. The eggs absorbed PRP, and gregarious females had higher PRP concentrations than eggs from solitary *S. gregaria*. Immunocytochemistry and mass spectrometry analysis demonstrated robust positive immunostaining in the follicle cells of the ovary and the seminal vesicle tubes of the male accessory gland complex in *S. gregaria*. The findings indicate that PRP may act as a maternal factor in defining the phase state of the offspring. However, additional trials are needed to determine its exact role, as reported by Rahman et al. in (2008).

### Metabolites and Metabolomics

Metabolomics, when used alongside transcriptomics and proteomics, is a valuable method for studying metabolic patterns in living organisms. This approach offers important insights into biological processes and the function of genes. Metabolomic analysis encompasses the utilisation of several analytical instruments, including gas chromatography/mass spectrometry (GC/MS), high-performance liquid chromatography (HPLC), nuclear magnetic resonance (NMR) spectroscopy, mass spectrometry (MS), and optical spectroscopic techniques.

A particular investigation employed high-resolution NMR spectroscopy to reveal the metabolic patterns in the hemolymph of gregarious and solitary *S. gregaria* locusts. This approach enabled the detection of more than 20 naturally occurring substances, such as trehalose, ethanol, lipids, amino acids, organic

acids, and the polyamine putrescine. Lenz et al. (2001) reported that solitary nymphs had higher concentrations of putrescine, trehalose, and lipids, whereas gregarious nymphs showed increased amounts of acetate and ethanol.

### Molecular Regulation of Body Coloration

During the phase transition of locusts, noticeable fluctuations in body colour are noticed. Gregarious locusts exhibit a conspicuous coloration pattern of black and orange, which remains uniform within the same group. On the other hand, solitary locusts have camouflaged hues that span from green to brown, which are controlled by external conditions including humidity and temperature. Extensive research has been conducted on the endocrine regulation of phase colour polyphenism in locust species, such as *L. migratoria* and *S. gregaria*. Juvenile hormone (JH) is essential for the initiation of green body pigmentation. The introduction of extra corpora allata, which are responsible for the generation of juvenile hormone (JH), or the injection of synthetic JH or JH analogues might induce the development of green pigmentation in gregarious nymphs of *L. migratoria*. Nevertheless, the green coloration in solitary nymphs is eliminated following allatectomy with precocene III, and the body pigmentation found in gregarious nymphs fails to develop (Tawfik et al., (1999).

Researchers produced an albino version of *L. migratoria* in *S. gregaria* and discovered a neuropeptide called [His7]-corazonin, which is composed of 11 amino acids, in the corpus cardiaca of both *S. gregaria* and *L. migratoria*. This neuropeptide causes dark pigmentation, but it does not produce the bright yellow body colour that is typical of last-instar gregarious nymphs in *S. gregaria*. Although the connection between JH and [His7]-corazonin has been investigated, the precise variables that regulate yellow coloration remain incompletely comprehended (Tawfik et al., (1999).

During the phase transition of adult male *S. gregaria*, the outer layer of the body undergoes a transformation and becomes a vibrant yellow hue within a span of 10 days, which occurs simultaneously with reaching complete sexual maturity. The yellow colour is caused by the presence of the yellow protein, which attaches to beta-carotene and is synthesised by epidermal cells that are part of the cuticle. The yellow protein is composed of 250 amino acids and has a molecular mass of 25,682 Da, without any chromophore present. Notably, the protein does not have cysteine residues and has low concentrations of methionine and tryptophan. The transcription of the yellow protein gene in adult males raised in crowded environments commences on day 5 and reaches its highest level on day 12 (Tawfik et al., 1999).

#### Molecular Regulation of Disease Resistance

Higher population density frequently corresponds to elevated rates of parasitism and disease, causing organisms to allocate greater resources towards disease resistance mechanisms that span immunological, behavioural, chemical, and physical defences. The statement is consistent with the density-dependent prophylaxis (DDP) hypothesis, which is based on three fundamental assumptions: (a) parasite transmission typically thrives in denser populations; (b) potential hosts can modify their physical characteristics in response to signals associated with population density; and (c) defences against parasites incur a cost. Species that display density-dependent phase polyphenism, such as the gregarious adult *S. gregaria* or *L. migratoria*, are likely to demonstrate density-dependent plasticity. Studies have shown that sociable locusts display higher levels of resistance to the fungal disease *Metarhizium anisopliae* var. *acridum* when compared to solitary locusts. The gregarious locusts have increased antibacterial activity and somewhat greater hemocyte numbers. Nevertheless, no noticeable disparities have

been detected between the different stages in terms of phenoloxidase activity, encapsulation, or behavioural fever responses. Pacifastins, a group of serine protease inhibitors present in the hemolymph and CNS of arthropods, are thought to play a role in the preventive immunity of gregarious locusts. Pacifastins have a function in the innate immune system where they hinder the activation of the prophenoloxidase (PO)-activating mechanism or hinder the entry of fungi. Researchers have discovered eight pacifastin-like precursors in locusts, which contain 22 distinct peptides. Research has shown that the levels of the pacifastin SGPI-2 in the hemolymph are elevated in adult *S. gregaria* that were raised in solitary conditions, as opposed to those raised in crowded conditions. The levels of SGPI-2 rise in subsequent generations of locusts that have been raised in isolation. Furthermore, the influence of SGPIs on the activation of prophenoloxidase in the hemolymph of adult *S. gregaria* that were grown in a group has been investigated. SGPI-1 and SGPI-2 failed to suppress the initiation of PO activity in reaction to the immunological elicitor laminarin. Nevertheless, the fat bodies of locusts that were injected with laminarin 20 hours prior exhibited elevated transcript levels of two pacifastin-like peptide precursors (SGPP-1 and SGPP-2), which encode SGPI-1, SGPI-2, and SGPI-3 (Ramhan et al., 2003).

#### Regulation of Behavioral Phase Change

Solitary and gregarious locusts exhibit contrasting behaviours while adjusting to alterations in their social surroundings. A behavioural test has been created by researchers to measure the behavioural phase state. This allows for the investigation of stimuli and the underlying neurophysiological, ecological, and molecular mechanisms involved in locust phase transition (Roessigh et al., 1993).

A comprehensive model for behavioural phase shift at ecological and physiological levels has been

suggested, mostly based on research conducted on *S. gregaria*. When solitary locusts are exposed to crowded environments, their behaviours rapidly shift towards those exhibited by gregarious locusts, a phenomenon known as gregarization. The shift is triggered by two sensory pathways: (a) a combination of visual and olfactory detection of other locusts; and (b) repetitive activation of hindleg mechanoreceptors by physical contact with other locusts. The temporal patterns of behavioural phase shift differ among locust species. *S. gregaria* exhibits swift gregarization and gradual solitarization, while *Chortoicetes terminifera* undergoes comparable temporal patterns for both phenomena. Conversely, the process of gregarization in *L. migratoria* is far less rapid when compared to solitarization. Moreover, the particular process of phase transition reported in *S. gregaria* may not necessarily have general applicability to other species of locusts. In the case of *C. terminifera*, the process of behavioural gregarization is triggered by touching the antennae rather than stimulating the hindlegs (Roessigh et al., 1993).

Extensive modifications in the architecture, circuits, and physiology of both the central and peripheral neural systems can impact the path of behavioural phase shift. Ultrastructural examinations have demonstrated that solitary locusts generally have a greater abundance of sensilla on their antennae, frons, and outer hind femur in comparison to gregarious locusts. Solitary locusts exhibit heightened sensitivity to olfactory responses and touch stimuli associated with aggregation pheromones compared to gregarious locusts. The cerebral mass of sociable *S. gregaria* locusts is almost 30% more and has a larger central complex compared to solitary individuals, despite having smaller primary visual and olfactory neuropils. The neurons that are responsible for phase-related behavioural responses exhibit significant differences between the two phases. For example, there are several phase-dependent changes

observed in descending contralateral movement detectors (DCMDs), tritocerebral commissure giants (TCGs), and slow extensor tibiae (SETi). Alterations in the concentrations of different possible neurotransmitters and/or neuromodulators in the central nervous system (CNS), including octopamine, serotonin, dopamine, GABA, glutamate, acetylcholine, tyramine, and citrulline, could have a crucial impact on the restructuring of the CNS during phase transition. Hormones such as juvenile hormone (JH) also play a role in regulating phase-related behaviour and the activities of key neurons (Roessigh et al., 1993).

### Serotonin's Role in Gregarious Behavior

Research has investigated the function of serotonin in triggering and maintaining social behaviour in the locust species *S. gregaria*. The study revealed a positive correlation between the amount of serotonin in the thoracic ganglia and the level of gregarious behaviour caused by different durations of crowding. This establishes serotonin as a crucial trigger for behavioural gregarization. Nevertheless, its contribution to the preservation of social behaviour in the long run was restricted, since the levels of serotonin in long-term social locusts were less than 50% of those in long-term solitary locusts.

Serotonin injections in *L. migratoria* were found to elicit gregarious behaviour to some extent. However, when paired with crowding treatment, they resulted in a greater tendency towards solitary-like behaviour compared to serotonin injection alone. There were no notable disparities in serotonin levels detected in the brain tissues during both phases of *L. migratoria*. A recent study investigated the impact of single and multiple serotonin injections, administered at different doses, on the attraction and avoidance behaviour of *S. gregaria*. The results indicated that serotonin had transient effects on particular locomotor activities and did not have a role in regulating gregarious behaviour. The specific processes via which serotonin affects this behaviour are not yet well understood, as previous

studies have typically concentrated on individual behavioural factors to describe the overall phase state, using binary logistic regression models. The investigations emphasise the fact that the regulatory mechanisms in the central nervous system (CNS) that control the start and continuation of phase change are particular to each species. They also emphasise the complex interaction between neurotransmitters (Tanaka & Nishide, 2013).

### **Macromolecule Kinases in Phase Transition**

The investigation focused on the role of two macromolecule kinases, cyclic adenosine monophosphate-dependent protein kinase A (PKA) and, cyclic guanosine monophosphate-dependent protein kinase (PKG) in the phase transition of *S. gregaria*. The use of drugs and RNA interference techniques showed that PKA, not PKG, is essential in influencing the tendency of locusts to display gregarious behaviour. Administration of the PKA inhibitor KT5720 or double-stranded RNAs specifically targeting the PKA regulatory subunit C1 gene led to a decrease in sociability in solitary locusts following a one-hour period of forced exposure (Ott et al., 2010). On the other hand, using RNAi to target the inhibitory R1 subunit resulted in a greater degree of gregarization. The involvement of adenylyl cyclase/PKA signalling has been shown to be crucial in multiple types of plasticity, such as sensitization, fear extinction, learning and conditioning, and addiction. While there has been a hypothesis suggesting a correlation between serotonin and PKA, the study failed to show any data supporting this association. Furthermore, although the contribution of PKG to the short-term transformation of locusts into swarming phase has not been verified, there was an observed increase in PKG activity in the brains of gregarious desert locusts. This implies that PKG may play a role in other behavioural characteristics such as regulating foraging and feeding (Ott et al., 2010).

### **Epigenetics of phase change**

A recent study has revealed a correlation

between DNA methylation and phenotypic plasticity in eusocial insects. DNA methylation is involved in the regulation of alternative splicing and gene expression. DNA methylation is the process of adding a methyl group to the C5 position of cytosine residues, specifically at CpG sites where cytosine is followed by a guanine nucleotide. Unlike plants and vertebrates, insect genomes typically have minimal levels of DNA methylation. CpG methylation is mostly observed within gene bodies or transcriptional units, rather than non-genic regions. For instance, when the DNA methyltransferase 3 (Dnmt3) gene is suppressed in honey bees, worker larvae who are not fed royal jelly can nevertheless mature into adult bees resembling queens, with fully formed ovaries. This suggests that DNA methylation plays a role in determining the caste of bees. Regarding *S. gregaria*, the application of liquid chromatography-mass spectrometry study has unveiled that around 1.3–1.9% of cytidines undergo methylation. Upon searching the locust EST databases of *S. gregaria* and *L. migratoria*, two DNA methyltransferase genes, namely Dnmt1 and Dnmt2, were identified, however Dnmt3 was not detected. In addition, the levels of Dnmt1 and Dnmt2 varied in a tissue-specific manner during different phases of *S. gregaria*. In a study conducted by Falckenhayn et al. (2013) using genome-scale bisulfite sequencing, it was found that locusts have higher overall methylation levels compared to other invertebrates. A significant fraction of locust transposons, which are movable genetic elements, were found to be methylated, as reported by Falckenhayn et al. in 2013. This research highlights the importance of DNA methylation in influencing the ability of certain insects, such as *S. gregaria*, to adapt to different environments and regulate their biological processes. It offers valuable insights into the intricate relationship between epigenetic changes and environmental signals in controlling

the development and characteristics of these insects.

## Conclusion

In conclusion, the phase change in desert locusts is governed by intricate interactions among genetic, biochemical, and physiological factors. Extensive studies have elucidated the involvement of genes, proteins, metabolites, and neurotransmitters in orchestrating the shift from solitary to gregarious behavior. Notable findings include the role of specific genes like SPARC, the differential regulation of metabolic pathways, and the influence of serotonin as a key neurotransmitter in initiating gregarious behavior. However, uncertainties persist, including the exact functions of phase-related proteins and the genetic factors propelling the evolution of density-dependent phenotypic plasticity.

Prospects involve delving deeper into these intricacies using advanced genomic and proteomic techniques. Unravelling the precise functions of phase-related proteins and understanding the genetic drivers of density-dependent phenotypic plasticity will contribute to a comprehensive grasp of locust phase polymorphism. This continued research promises to unveil additional layers of complexity in the molecular basis of phase change, offering valuable insights into the evolutionary adaptations of locusts and the potential development of targeted strategies for pest control.

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## **AUTHORS**

**Rudra Gouda, M. N\* , Subramanian, S.**

Division of Entomology, Indian Agricultural Research Institute, New Delhi.

**Sachin, S. Suroshe**

All India Coordinated Research Project on Honey Bees and Pollinators, New Delhi.

\*Email: [rudragoudamn@gmail.com](mailto:rudragoudamn@gmail.com)

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