Locust swarms: the evolution of a powerful force of nature

Locust swarms are a severe agricultural threat. The destruction of crops and pasture jeopardises many livelihoods and adversely impacts global food security. To address this issue, **Dr Hojun Song**, a distinguished Entomologist at Texas A&M University, is conducting ground-breaking research, focused on locust swarm evolution. Understanding how and why locust swarms occur is crucial if we are to develop effective control mechanisms.

Locust swarm invasions are swift and incredibly destructive. Black swarm clouds race across the sky, creating an ominous solar eclipse-like effect. Moments later, the plague of locusts descends, attacking every crop, tree and blade of grass in their path.

Suffice to say, locusts are a major global pest, threatening the agricultural industry and affecting the livelihood of at least one tenth of the world's population. Desert locusts (*Schistocerca gregaria*), typically found in Africa and the Middle East, are one of the most harmful species because of the great distances they can cover, wreaking widespread havoc. It is estimated that 20% of the world is affected by desert locusts. A large desert locust plague can contain up to 150 million individuals per km^2. Half a million locusts weigh approximately 1 tonne, and 1 tonne of locusts eat as much food in one day as about 10 elephants, 25 camels, or 2,500 people.

In addition to the desert locust, there are more than a dozen species of locusts, affecting every continent. In 2016–2017, the South American locust (*Schistocerca cancellata*) had a massive population upsurge in Argentina and Bolivia for the first time in 60 years. The Central American locust (*Schistocerca piceifrons*), which normally swarms in Mexico, is now devastating other countries in Central America.

Losses caused by locust swarms greatly impact food security – an already vulnerable area due to the increasing global population. Dr Song and his team are dedicated to improving our understanding of the evolution of locust behaviour and the genetic mechanisms behind swarming with the aim of developing an effective method of controlling these pests, to protect defenceless crops.

ALL LOCUSTS ARE GRASSHOPPERS...

...But not all grasshoppers are locusts. Locusts are a type of grasshopper, capable of undergoing reversible changes to their physical appearance and behaviour based on population density – a phenomenon known as 'locust phase polyphenism'. This is an example of phenotypic plasticity, whereby an organism can alter its appearance/behaviour in response to environmental changes.

Locust phase polyphenism was first observed by the Russian entomologist Sir Boris Uvarov in 1921. He primarily studied the migratory locust (*Locusta migratoria*) and desert locust and discovered that during the 'solitarious phase' (low population density), individuals, vibrant green in colour, are repelled from each other. However, during the 'gregarious phase' (high population density), individuals are attracted to each other, forming large cohesive units. They then grow larger, have an increased metabolic rate and become darker in colour, with striking yellow and black markings.

Dr Song's research has enhanced our understanding of the evolution of swarming locusts

Central American locust swarm

Interestingly, the desert locust belongs to the genus *Schistocerca*, which includes both swarming locust and non-swarming, sedentary grasshopper species. This raises a number of questions: why do certain species exhibit this swarming behaviour whilst others do not? What are the fundamental molecular mechanisms underpinning the behavioural and physical changes? And how does the environment influence this polyphenism? Using a series of innovative experiments in a comparative framework, Dr Song and his research team investigated each of these questions.

REARING EXPERIMENTS

While we know a lot about the desert locust, it is not clear whether other species in *Schistocerca* can respond to changes in density. The only way to address this question is by conducting a standardised rearing experiment, in which these grasshoppers are reared both in isolated and crowded conditions from hatchlings, and the resulting phenotypes (colour, behaviour, and gene expression patterns) are quantified at the last nymphal instar stage. Using this framework, Dr Song and his students have been able to quantify density-dependent phenotypic plasticity across several species of *Schistocerca*. The results are very interesting because there seems to be a lot of variation in terms of the species' ability to respond to density. For example, two non-swarming *Schistocerca* species, native to Florida (*Schistocerca americana* and *S. serialis cubense*) exhibit morphological and behavioural changes, similar to those of the desert locust. Two other sedentary species (*S. rubiginosa* and *S. lineata*) develop black patterns when crowded, but behaviour does not change. Another sedentary species (*S. nitens*) from Texas does not change either colour or behaviour when crowded.

Ryan Selking feeding hoppers

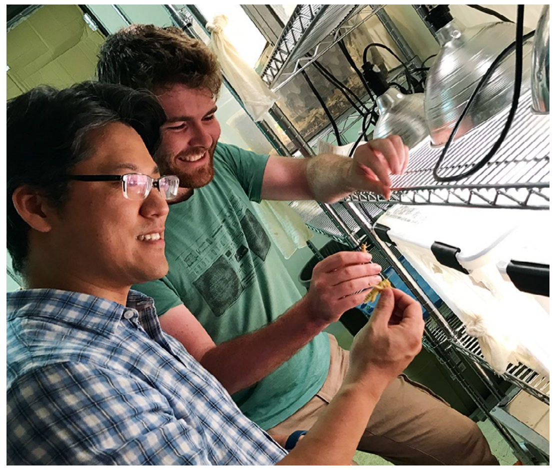
Dr Song has studied the evolutionary relationship among *Schistocerca* species and found that the desert locust is the earliest diverging species in the genus. What is more interesting is that the desert locust is the only species found in Africa, and the rest of the genus (about 50 species in total) are found throughout North, Central, and South America. Dr Song suggests that the ancestral *Schistocerca*, which was probably similar to the current-day desert locust, originated in Africa and colonised the New World by transatlantic flight about 6 million years ago. The rearing experiments reveal that most *Schistocerca* species have the genetic capacity to change colour when crowded, because it is an ancestral physiological trait for the genus, but the ability to change behaviour has been lost and regained multiple times throughout the diversification of *Schistocerca*. Most sedentary species do not show behavioural plasticity in their natural environment, because it is not adaptive for them to do so. Furthermore, three swarming species within *Schistocerca* are not evolutionarily close to each other, which suggests that swarming behaviour evolved repeatedly within the genus.

MOLECULAR MECHANISMS UNDERPIN PHENOTYPIC PLASTICITY

Swarming occurs due to positive feedback processes. A combination of sight and smell or touch alone can trigger behavioural gregarisation. When locusts come into contact with each other, tactile stimulation of mechanosensory receptors located on the hind leg activates sensory pathways. These transmit signals to the central nervous system, resulting in the release of the neurotransmitter serotonin, which is responsible for initial aggregation behaviour. In fact, following initial physical stimulation, serotonin levels rapidly increase three-fold, over a period of just a few hours. However, this increase is transient: serotonin levels only remain elevated for around 24 hours and then decrease. Maintenance of swarming behaviour and the physiological changes associated with gregarisation is controlled by a variety of molecular and biochemical pathways. From an ecological point of view, locusts generally live in a harsh environment, where availability of resources is often unreliable and food shortages can occur. Interestingly, food deficiency can cause cannibalism in desert locusts and research suggests that collective movement may have evolved because of this behaviour. Much of what we know about locust phase polyphenism is based on decades of research on the desert locust, but it is not clear that this can be directly applicable to other locust species. Dr Song has developed another model system to understand the molecular basis of locust phase polyphenism.

The Central American locust (*S. piceifrons*) is one of the most important insect pests in Mexico and Central America as it swarms nearly annually in Yucatán Peninsula, Mexico. Nevertheless, not much is known about how this species swarms. Dr Song and his team visited Yucatán in 2015 to collect these locusts, and brought them back to his lab in Texas to establish a colony. By rearing these locusts in both isolated and crowded conditions, Dr Song is able to induce solitarious and gregarious phases, and he has generated density-specific transcriptomes from this species as well as from other closely related sedentary species. Now, his team is in the process of identifying which genes are differentially expressed between two phases, and which genes are specific to the locust, but not in sedentary grasshoppers. So far, many

Central American locusts marching



Hojun Song and Bert Foquet looking at locust colony

At locust workshop

genes that are important for metabolism, immune system, and cellular processes associated with phase change, appear to be highly differentially expressed in the Central American locust, but much less so in other closely-related, non-swarming species. Based on these candidate genes that appear to be important to swarming behaviour, Dr Song is planning to understand their molecular functions by using RNA interference (RNAi) knock out. Hopefully, in the next few years, we will have a better understanding of key genes and regulatory networks that are important for density-dependent phenotypic plasticity. In other words, we will be able to understand what makes locusts different from grasshoppers from a molecular perspective.

CONTROL OF LOCUST SWARMS

Overall, Dr Song's research has enhanced our understanding of the evolution of swarming locusts. This knowledge will be of great value when developing ways to control destructive swarms.

Currently, pesticides are used as a swarm-control mechanism. However, chemical controls can cause great harm to the environment and are highly toxic to non-dangerous invertebrates such as honeybees. Perhaps a more effective, safer way would be to inhibit swarm formation by manipulating specific molecular pathways in locusts – for example, by inhibiting serotonin receptors or knocking out important genes for phenotypic plasticity to prevent gregarisation. Nevertheless, further research will need to be conducted before this technique can be commercialised.

Studying both locusts and non-swarming sedentary grasshoppers that are evolutionarily related provides a unique perspective for understanding the evolution of swarming behaviour

Q&A

What are the adaptive advantages of swarming in locusts?

Locusts show an extreme form of phenotypic plasticity, which typically evolves as an adaptation to heterogeneous environmental conditions, and swarming is one extreme of this plasticity. Gregarious nymphs are brightly coloured, and there is evidence that at least in the early stage of gregarisation they feed on toxic plants, which makes their colour warning colouration. Being in a group that all show warning colouration can be adaptive because it can provide protection from visual predators. Locusts are typically in a nutritionally poor state, and being in a crowd provides an opportunity to cannibalise each other to obtain necessary nutrients, which has been shown to be a major driver of locust collective movement.

What causes these large locust swarms to disband?

Disbanding is the result of the opposite extreme of density-dependent phenotypic plasticity, which we refer to as the solitarious phase. Solitarisation can happen if the environmental conditions that promote the maintenance of the gregarious phase no longer persist. Usually, we consider the habitat structure to be the main factor for promoting solitarisation. Studies have shown that it takes longer for gregarious locusts to become solitarious than the solitarious locusts to become gregarious. This is the reason why we often see large migrating swarms in nature, but we rarely see swarms dissipate. Whether there is a molecular mechanism which promotes solitarisation is a completely open question.

Could environmental factors such as climate change result in more frequent swarms?

I believe so. There have been some studies suggesting that there is a positive correlation between the frequency of El Niño phenomenon and the frequency of locust outbreaks, at least in the migratory locust in China and the Central American locust in Mexico. If the habitat that is normally not conducive to locust gregarisation changes due to climate change, then it is possible to predict that locusts will expand their range accordingly. In fact, recent upsurges of locusts in Central and South America are probably somewhat related to changes in environmental conditions.

How can we effectively control locust swarms?

This is a million dollar question. Locusts are very difficult to control because they are extremely mobile and honour no political boundaries. If you spot adult swarms today, it is already too late to control because the swarm will migrate to somewhere else tomorrow. Locusts also happen to affect many developing countries without proper infrastructure to survey and manage them. Therefore, early warning systems and preventative management are critical for effectively controlling locusts. Because of the vast areas that locusts affect, there needs to be effective survey methods to determine where they are and whether they are likely to develop into plagues. If we can keep them under the threshold of gregarisation and swarm formation, these locusts will be like regular grasshoppers, relatively harmless to agriculture. Right now, there are efforts to develop effective remote sensing technologies to survey and monitor locusts.

What's your research focus over the next five years?

I plan to focus on understanding the biology, ecology, and evolution of the Central American locust using an integrative approach. We have a lab colony of this species that we can experimentally manipulate to understand the mechanisms of phase change. We also have colonies of other closely related species that do not swarm, so we can compare and contrast molecular bases of phenotypic plasticity in a comparative framework. I go to Yucatán every year to study the locusts in the field, and we can verify our lab-based findings in the field. Finally, in the next five years, I hope to sequence the genomes of the Central American locust and other related species to understand what makes locusts different from grasshoppers at a genomic scale.

Detail

RESEARCH OBJECTIVES

Dr Song's research focuses on locust swarms. The molecular mechanism behind locust's ability to form swarms in response to change in population density is poorly understood, and is an area that Dr Song and his research team particularly consider.

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BIO

Dr Song completed his BS at Cornell University, and received his MS and PhD at the Ohio State University. He was a postdoctoral research fellow at Brigham Young University before starting at the University of Central Florida. He moved to Texas A&M University in 2015 where he is currently an Associate Professor.

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