Going Places*
Insect Migration

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We describe various facets of the fascinating world of insect migrations, both those that are often perceived to be newsworthy, as well as the lesser known. In the form of questions and answers, we describe how the phenomenon of migration is specific to certain insects, the factors that influence insect migration, and how insect migration can be studied. We use examples of well-known agricultural pests and endangered butterflies to describe how hormones, biological clocks, genes, and predilection for particular host plants contribute to the process of migration. We exhort the readers to participate in global citizen science initiatives that recognize and document insect migrations in their vicinity.

Introduction

Insect migration has been observed since the days of yore, with allusions in scriptures to a “plague of locusts” devouring crops and causing famine. Migrations of large swarms of desert locusts (*Schistocerca gregaria*, order Orthoptera) in Africa, west Asia and India remain among the earliest records of insect migrations. Readers of this article may be familiar with recent newspaper reports of locust “invasions” in western India and the outskirts of Delhi. Being voracious, polyphagous pests, the arrival of trillions of locusts causes severe economic loss to farmers. The onward journey of these migrants remains to be documented. In contrast, journeys of the monarch butterfly (*Danaus plexippus*, order Lepidoptera) have been studied for at least 150 years in the Americas. Public awareness of the need to preserve these long-distance mi-

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grant butterflies and their habitats has made the monarch butterfly the ‘poster child’ of environmental conservation efforts across the world. Migration is a way of life for an amazing diversity of insects. Exploring answers to questions about insect migration can help us better appreciate the natural marvel and understand the significance of a migratory way of life.

**What Are Some Salient Features of Insect Migration?**

Migration refers to the periodic movement of animals between specific locations over long distances, redistributing populations within a spatially extended range. It results in a temporary change of habitats. Though migration has been reported from all major animal taxa, insects dominate the migratory world. Radar data in 2018 revealed mass migrations of roughly 3.5 trillion insects annually over Europe. In the same year, millions of darner dragonflies were shown to migrate between water bodies in the Southern and Northern United States. The Locust Watch Organization (LWO) estimated the arrival of 70,000–80,000 strong swarms of desert locusts in western India between March and August 2020. Reports on the long-distance movement of migratory insects have been available for several decades from biologists, naturalists, and citizen scientists (*Box 1*).

In addition to covering long distances, insect migrations are typically of long duration, involving seasonal movements from regions with unfavourable conditions towards favourable ones. Migrating insects typically travel between breeding sites and hibernating grounds over one or multiple generations. The longest distances covered annually by any migratory insect is attributed to the painted lady butterfly (*Vanessa cardui*, order Lepidoptera). It takes five generations of this cosmopolitan butterfly to cover a distance of 13000–15000 miles between the African Savannah and Northern Europe. The globe skimmer dragonfly (*Pantala flavescens*, order Orthoptera) undertakes the longest nonstop migration between India and Africa in the autumn and back again in the spring.
Box 1. History of Insect Migrations in India: Naturalists & Citizen Scientists

The 1900s saw some of the earliest publications on migratory insects from the Indian subcontinent. British entomologists and naturalists wrote extensively and engagingly of their encounters with massive movements of insects. Of these, the most famous was Carrington Bonson Williams (1889–1981) from the Rothamsted Experimental Station, United Kingdom. In his article ‘Insect Migration in India’ (1938), he wrote about eastward migrations of butterflies in the Western Ghats before the monsoonal deluge. He mentioned *Tirumala septentrionis*, *Eupoloea* sp., and *Catopsilia pomonis*. In his early writings, CB Williams also cited Major RW Highton, a prolific chronicler of insect life in British India. Highton published a popular book on insect behaviour—*Instinct and Intellect*—with a foreword by Bertrand Russell. In this book, Highton described the migratory flights of the large cabbage white, *Pieris brassicae* in Dharashala, India, along with locusts and dragonflies, as “mob psychosis” making them move in a given direction at all costs! Locusts featured prominently in the works of Uvaravov and Kennedy (1951), who worked on *S. gregaria* and *L. migratoria* at the “Middle East AntiLocust Unit” Locust Study Centers in Egypt during the 1920s and 1930s. The importance of locust attacks for agriculture in northwest India in those times was instrumental in setting up an imperial (British) network of agricultural stations connecting Quetta, Sindh, Baluchistan, Lyallpur, and Pusa. Detailed accounts of locust swarm movements, flights, seasonality, rain and soil conditions, sex ratios, host plant preference and phase change, are available in the compiled works of Rai Bahadur YS Rao and Khan Bahadur Afzal Husain, who established the Indian Society of Entomology and the Pakistan Entomological Society, respectively. The term “locust epidemiology” was first used by YS Rao, who emphasized the need for inter-regional cooperations in minimizing economic damage using insecticide sprays on early larval/nymph stages of the desert locust. Records from major intermittent outbreaks from 1812s and up to the 1960s are available from the region. Locust swarms were recorded east up to Assam in September–October before dissipating. It was also suggested that some locusts attempt a return flight westwards towards Iran. Not much is known about their fate in India, wherein solitary forms co-exist with at least 20 other species of grasshoppers. These fascinating tales of early encounters with insect migrants have been followed up by modern research based on radar monitoring, radio transmitters, isotope analysis and molecular tools. Today, excellent studies documenting types, numbers, altitudes of flight, and seasonal movements of butterflies from the Western Ghats are coming together due to the efforts of biologists and dedicated groups of citizen scientists, hobbyists and journalists. A WhatsApp group is actively engaged in documenting an Indian Butterfly Watch, with results available in the public domain. In the case of odonates, the seasonal abundance of the globe skimmer dragonfly, *Pantala flavescens* has been noted in the Indian subcontinent as early as 1924. In 2021, ITCZ and monsoon wind trajectory analyses over the Indian Ocean were successfully used to describe the flight of this dragonfly between Africa and India, representing the longest non-stop migratory route adopted by any insect. While efforts to follow migratory dragonflies are ongoing, much more needs to be done to document and preserve the habitats of these intriguing insects. It is hoped that the young readers of this article will be encouraged to look to the skies and scan the horizon for the movements of insects.
General migratory trends are to move north from the equator in the summer and south in the autumn. Migrating butterflies in India move from the Western Ghats towards the Eastern Ghats at the onset of monsoons.

Migration is a unique life strategy enabling the species to survive adverse environmental conditions, and insects exhibit remarkable behavioural, morphological and physiological changes at the onset of a migratory phase. Locusts become gregarious (forming swarms) instead of being solitary, the colour of their chitinous exoskeleton changes, and flight muscles bulk up in anticipation of the long flight ahead. Aphids and whiteflies (a group of plant sap/phloem-sucking insects) usually lack wings but produce winged or “alate” generations capable of flight during migration. Monarch butterflies enter a state of reproductive quiescence or “diapause”, have more robust immune systems with lower pathogen load and live longer during their long journey between the United States and Mexico. Hence, insect migration has also been referred to as a “syndrome”, a set of correlated behavioural and other adaptations, in this case to spatial and temporal fluctuations in resources or the environment.

What Are Different Types of Insect Migrations?

Migration has been reported from many taxonomic orders of insects, but it is particularly common in locusts like S. gregaria and Locusta migratoria, dragonflies like Anax junius and Pantala flavescens, and butterflies like D. plexippus and emphV. cardui. The reasons for such a bias in the taxonomic distribution of migratory insects versus related species that do not migrate are unclear. Insect migrants include beneficial pollinators, agricultural insect pests and predators (Figure 1). Monarch butterflies are true migrants in which multiple generations make a forward and return journey across oceans and continental land masses in search of overwintering and breeding sites. Green darner dragonflies are also true migrants that take three generations to reach the great lakes in North America from Mexico, bridging across
aquatic and terrestrial habitats. Apart from true migration, there is **emigration**, in which there is a mass movement of insects in only one direction. This results in habitat changes but is not always followed by a return journey. Such mass emigration is found in many pierid butterflies like large cabbage, white *Pieris brassicae*, and lemon emigrant *Catopsilia pomona*. **Irruptive migration** follows rare events like sudden rains in deserts that result in an overabundance of host plants for caterpillars and nectar for adults. Large swarms of the painted lady butterfly (*V. cardui*) exploit such a plethora of newly available resources. In **nomadic migration**, no regular pattern or route is followed, and breeding sites are ephemeral. Nomadic migrants, like desert locusts, move away from their home range but do not follow predetermined paths. At times, not all individuals of an insect population migrate. This is also known as partial migration. This makes an interesting question for what differentiates those who move away and those who stay.

**Figure 1.** Pictures of some well-known migratory insects. (A) Painted lady butterfly (*Vanessa cardui*, order Lepidoptera) is cosmopolitan in distribution and migratory in the Thar desert during winters. It is spotted frequently in Jodhpur and Jaisalmer. Photo courtesy: Staff of Yamuna & Aravalli Biodiversity Parks, Delhi Development Authority. (B) Large cabbage white butterfly (*Pieris brassicae*, order Lepidoptera) is known to migrate between Shivalik Hills and the north Indian plains during winter. They have been recorded at altitudes up to 4000 m in Kashmir. Photo courtesy: Staff of Yamuna & Aravalli Biodiversity Parks, Delhi Development Authority. (C) Darner dragonfly, (*Anax* sp., order Odonata) is a long-distance migrant that lives in ponds and lakes as nymphs and flies across continents as adults; Source: Pixabay, https://tinyurl.com/dragonfly-22. (D) Desert locust (*Schistocerca gregaria*, order Orthoptera) is a major pest in north Africa and west Asia. Photo courtesy: Atelier Monpli, Wikimedia Commons, https://tinyurl.com/sgre22.
What is the Biology of Large-scale, Long-distance Insect Migration?

There has been a lot of research on the mechanisms used by insects to migrate. Neuroendocrine regulation, especially levels of juvenile hormone (JH), plays a key role in ensuring successful long-distance migration in the monarch butterfly. Processes like reproductive arrest, increased life span and fat storage in migratory insects are typically brought about by the downregulation of insulin signalling pathways and deficiency of JH. Interestingly, these changes in JH occur simultaneously in all individuals in a group, possibly because of a common environmental cue. JH is the endocrine part of the neuroendocrine system responsible for migration. The neuronal part of this system senses the environmental cue, launching the cascade of signals that facilitate migration. In locusts, *S. gregaria* and *L. migratoria*, this synchrony is associated with epigenetic changes wherein levels of DNA methylation, acetylation and phosphorylation are altered [1]. Interestingly, methylated genes are switched on/off when the phase reverses, and gregarious locusts become solitary.

**Biological clocks** also play an important role in the migratory processes of insects. Biological clocks in insects like *D. plexippus*, *S. gregaria*, and *L. migratoria* respond to external cues and changes in the physical environment. Sensors of circadian rhythms are typically located in the antennae of insects. The central clock (CC) in the insect brain perceives sensory inputs and a complex signal cascade ensues. The molecular output of the CC includes a neuropeptide called pigment dispersing factor (PDF) produced in a cyclic manner. Different levels of the PDF peptide are detected in nerve terminals depending upon diurnal/nocturnal signals. PDF also transmits temporal information between various hubs of clock neurons in different brain regions. Communication between these clocks is essential for clock circuitry and maintaining locomotor activity in migratory insects. Several common genes have been identified in fruit flies (*Drosophila melanogaster*) and monarch butterflies that are regulated by circadian rhythms. These include genes like *clock* (*clk*).
cycle (cyc), period (per), timeless (tim) and doubletime (dbt).

In addition to clock genes, at least 40 messenger RNA transcripts of the monarch butterfly have been identified in the brains of individual migrants that are associated with time-compensated, sun compass-oriented flight behaviour (Figure 2). This behaviour orients the flight direction of each insect based upon the sun’s horizontal position in the sky (azimuth), the angle of polarization of ambient light and the dorsal rim of the retina in the compound eye of the insect [2]. Regulatory sequence elements of protein-coding genes have also been found to be responsible for the initiation or maintenance of migratory state. Small RNA molecules that range in size from 20–35 nucleotides, known as micro RNAs, short interfering RNAs and piwi interacting RNAs, participate in the regulation of insect migratory behaviour. These studies emphasize that the complex biology of insect migration mechanisms is only beginning to be decoded.

**Figure 2.** The sun-compass orients monarch butterflies in North America to fly in the south-westerly direction in the autumn (Figure 3A) and in the north-easterly direction in the spring. According to a model (Figure 3B), insect flight orientation is based on celestial cues, sun compass and circadian clocks [15]. Time-compensation clocks are located in the antenna, while the sun’s azimuthal position is detected by the eyes. Neuronal signals arising from (1) photoreceptors in antennae are transmitted to (2) the insect’s compound eye before they are sent to (3) the central complex (CX) in the brain via the anterior optic tubercle (AoTU), which is the presumed site of the sun compass, resulting in directed flight.

**How Do Insects Navigate During Migration?**

Seasonal wind systems that reflect barometric pressure differentials such as monsoons, gulf-stream or the Inter-Tropical Convergence Zone (ITCZ) are utilized by migrating insects to “bor-
row a ride” and save energy during long-distance flights. Migratory insects disperse either in non-cohesive swarms triggered by environmental cues or form cohesive swarms due to complex behavioural interactions. Frequently, smaller cohesive swarms aggregate into very large ones visible on radar screens at airports and weather stations. Flight orientation [3] is not very well understood but is believed to be influenced by several factors like local topography, celestial cues, the Sun’s position, Earth’s magnetic field, gradients of temperature or moisture, wind patterns, and photoperiods. Migratory insects frequently navigate predetermined paths that allow them to escape the onset of unfavourable environmental conditions such as overcrowding and competition for resources, change in phenology of host plants due to climate change, and increase in predator or pathogen populations. It is interesting to note that migratory insect species have evolved to recognize such changes in their abiotic and biotic environments and respond by moving away in search of better conditions [4].

Is There Any Relation Between Choice of Host Plant Types and Insect Migration?

Successful migration depends on the optimum utilization of host plant resources available for larvae or nymphs during the journey. In fact, a raison d’être for migration is the search for sites with host plants suitable for breeding the next generation. As the number, types and quality of preferred host plants shift in time and space, so do insects that feed on them. The long journey of the painted lady butterfly from the Sahel to the Maghreb regions in Africa is influenced by differences in the distribution of larval host plants, especially ephemeral, fast-growing forbs that emerge after sudden precipitation events [5]. Larvae of the monarch butterfly are specialized to feed on Asclepias sp. (milkweed) [6]. This larval food plant is also preferred for oviposition by the female monarch butterfly. Larvae feeding on milkweeds are exposed to ouabain, a deadly cardiac glycoside in their diet, but are resistant to its toxic effects. The ability to seek, find and feed on
unique host plant families (with their unique poisons) is observed in specialist migratory insects like the monarch butterfly and large milkweed bugs (*Oncopeltus fasciatus*, order Hemiptera) that have adapted to ingested ouabain. Not all migrants are specialist feeders. Locusts are polyphagous and can eat almost all aerial plant parts they encounter. Interestingly, their genomes have a large number of genes encoding enzymes that detoxify a broad range of ingested antifeedants and plant poisons. These genes are switched on at the onset of the migratory phase in these insects.

**Does Migration Affect Genetic Variation in a Population?**

Migration tends to genetically link two or more populations together within an expanded distribution range. Genetic markers based on the DNA or proteins of individual insects in a population can be versatile tools for monitoring insect migration. DNA markers typically represent genetic loci from the nuclear genome or non-recombinant, maternally inherited, mitochondrial DNA. Sequencing different genetic loci, repetitive DNA (satellite) regions, and even whole genomes has yielded useful insight into insect migration. When mitochondrial DNA sequences are used, one can estimate the frequencies of different haplotypes in the population(s). A **haplotype** is a unique haploid DNA sequence that differs from others in the population at one or more base pair positions [7]. Haplotype frequencies can be used to estimate haplotype diversity. A study of haplotype diversity in populations of migratory monarch butterflies from Mexico and Costa Rica showed only two predominant haplotypes using the mitochondrial cytochrome oxidase I (mtCOI) locus as a genetic marker. This insect species had very low genetic diversity, but the frequencies of predominant haplotypes were variable at different places. Similar results are also seen with *V. cardui*, red admiral butterfly *Vanessa atalanta* and silver Y moth *Autographa gamma*. Some migratory insect populations can also exhibit high mtCOI haplotype diversity, as in the case of dragonflies like *Pantala flavescens* and the emerald-green dragonfly, *Anax junius* [8].

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Why is It Important to Study Insect Migrations?

A large number of migratory insects, especially butterflies and moths, provide crucial ecosystem services like crop pollination. The adult marmalade hoverfly (*Episyrophus balteatus* order Diptera) pollinates a large diversity of plants during migration across the Mediterranean Sea into Europe, while the larvae feed on aphid pests [9]. It is crucial to conserve the habitats and populations of migratory pollinators over space and time. Migratory insects are integral components of **trophic linkages** and provide food for other fauna. Dragonflies like *Pantala flavescens* are major predators and, in turn, are food for birds along the food chain. Deposition of faeces and carcasses of migratory insects contributes substantial biomass and alters **nutrient fluxes** due to inputs of nitrogen and phosphorus stored in their bodies [10]. In degraded areas devoid of vegetation, such inputs can trigger soil microbial activity and initiate processes of natural restoration [11]. The enormous numbers of migratory insects transport pollen, plant propagules and/or pathogens from geographically disparate locations, often across oceans [12]. Their dispersal or arrival results in a change in the composition and structure of local biotic communities.

Many migratory insects are serious pests of agricultural crops. Harmful pesticides are sprayed worldwide to control these insects, **negatively impacting the environment and biodiversity**. Larvae of the large cabbage white (*Pieris brassicae*), diamond black moth (*Plutella xylostella*) and cabbage looper (*Trichoplusia ni*) are major pests of crucifer crops like cauliflower and cabbage. Polyphagous noctuid moths like the armyworms (*Spodoptera* sp.), bollworms (*Heliothis* sp.), and cutworms (*Agrotis* sp.) are global invasive pests that are migratory by nature. The brown planthopper (*Nilaparvata lugens*) and silverleaf whitefly (*Bemisia tabaci*) are migratory pests from the order Hemiptera that transmit debilitating plant viruses in south Asia. The ability to forecast migrations and track mass movements of the adults is very useful in minimizing damage caused by these insects. Ultimately, knowledge of the migration biology of these insects can help devise
sustainable pest management strategies.

How Are Insect Migrations Tracked?

Since insects are small, numerous, and typically cover long distances during migration, tracking their movement over space and time can be challenging. **Mark-recapture** (Figure 3) has been the classical technique but has several drawbacks. Marking by inks, sprays, or even stickers tends to be unreliable and recapture of a marked individual can be problematic. Radar technologies (Figure 3) have been successfully used to track bird and insect migrations since the 1960s. **Harmonic radar** technology enables tracking flying insects (typically fitted with mini-transponders) over longer distances and at low altitudes. **Vertical looking radar** (VLR) popularised by Jason Chapman at the University of Exeter, samples the air column for insects flying at a variety of altitudes and separates them according to flight speed, direction, body mass and shape. **Doppler radar** data (as used

**Figure 3.** Some techniques used for studying insect migration. **(A)** A freshly-tagged monarch butterfly (*Danaus plexippus*) ready for release during ‘mark-recapture’ experiments. Photo courtesy: Derek Ramsey taken at the Cape May Point State Park, USA; Wikimedia commons; https://tinyurl.com/tagged-mf. **(B)** A worker bumblebee (*Bombus terrestris*) with an installed transponder on its back. These miniature transponders along with harmonic radars help in tracking bees that visit multiple flowers. Photo courtesy: Andrew Martin, Wikimedia commons; https://tinyurl.com/bb-22bb. **(C)** Diagrammatic representation of a vertical looking radar (VLR) set-up used to track an insect in flight. **(D)** Doppler radar image of a swarm of ‘mayflies along the Mississippi River in portions of Wisconsin, Iowa and Minnesota.’ Picture courtesy: Owlana, National Weather Service via Creative Commons; https://www.flickr.com/photos/58415293@N00/188179688.
in weather forecasting) has been used for tracking insect swarms on many continents (Figure 3). However, identifying the insect species that actually swarm remains the bête noire of these tracking methods. Current efforts to integrate morphological databases with radar data may improve the identification of insect species in a swarm. These efforts are bolstered by data from other sources, like large-scale trap surveys (conducted at Rothamsted Insect Survey in the UK), insect density counts, geographical information systems (GIS) and meteorological data. These data can be used successfully to generate mathematical models that forecast invasions by migratory insect pests of agricultural crops [13, 14].

Conclusion

Migratory insects invoke the urgency to save nature and natural processes that fascinate humans. In fact, migration itself has been called an endangered phenomenon. Migratory insects like the monarch butterfly are threatened, and efforts to conserve their numbers are ongoing worldwide. International eco-clubs like the ‘Monarch Watch’ have spread awareness among school students. The development of pollinator-friendly gardens/way-stations and increased planting of food plants for migratory butterflies like the monarch has been an impetus for global citizen science. New fascinating information on insect migrations across countries and continents are coming to light due to the efforts of global citizen scientists. International cooperation is also required in collating meteorological information, weather prediction algorithms, radar and field data to predict pest outbreaks and combat migratory menaces like the desert locust. The coming together of citizen scientists, scientists from different disciplines and government agencies are raising awareness of the life history and uniqueness of insects whose numbers are experiencing huge population crashes. This awareness is important to check the negative impacts of the Anthropocene and global warming on undisturbed habitats that are breeding/hibernating refuges of migratory and other insects.
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Suggested Reading


