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Dragonfly: A Master of Migration

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Insect migration is vital for ecosystems, with trillions of individuals redistributing biomass and nutrients annually. Dragonflies, particularly *Pantala flavescens* are notable migratory insects capable of traveling over 6,000 kilometres across generations. Their migrations are influenced by resource availability, breeding needs, environmental conditions, and competition avoidance. This behaviour includes both seasonal movements and sporadic flights triggered by temperature and wind cues. Despite their well-known life cycle from aquatic nymphs to aerial adults, many aspects of their migration remain under-researched. Dragonflies exhibit diverse flight mechanisms,

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employing four distinct modes: counter-stroking for hovering, phased-stroking for cruising synchronized stroking for acceleration, and gliding for energy conservation. Migratory species show specific wing adaptations for improved endurance, such as elongated forewings and larger hindwings, along with sensory enhancements like enlarged thoracic setae. Specialized flight muscles allow for independent wing control, essential for complex movements. Additionally, physiological adaptations like fat accumulation and rapid development support their migratory behaviour. Recent studies also highlight nocturnal migrations, revealing unique flight patterns and adaptations. Together, these traits underscore the evolutionary success of dragonflies in diverse ecosystems.

Keywords: Dragonfly; migration; Pantala flavescens; hovering.

1. INTRODUCTION

Insect migration refers to the movement of insects from one habitat to another and is a widespread natural phenomenon that contributes significantly to the distribution of biomass, with trillions of individuals migrating annually. This migration is responsible for translocating nutrients and ecological interactions across vast distances, influencing essential ecosystem functions such as pollination, herbivory and predation. Many insects are capable of long-distance migration, often covering thousands of kilometres, sometimes spanning multiple generations (Akhter et al., 2023).

Among various insect species, some of the most well-known migrations include the multigenerational migration of the monarch butterfly (*Danaus plexippus*) in eastern North America, the painted lady butterfly (*Vanessa cardui*) from Europe to Africa and the annual migrations of species such as the fall armyworm (*Spodoptera frugiperda*) and the desert locust (*Schistocerca gregaria*), which travel from North and Central Africa to the Middle East, Arabia, and India. Another noteworthy example is the dragonfly, which undertakes non-stop, long-distance migrations (Flockhart et al., 2013; Stefanescus et al., 2005; Nagoshi et al., 2012; Kennedy, 1951; Anderson, 2009).

Dragonflies (suborder; Anisoptera) are strong-flying insects with robust bodies that hold their wings horizontally during both flight and rest. Out of the approximately 5,200 known dragonfly species, at least 25 to 50 species are migratory (May, 2013). Notably, about 70% of the longest-distance migratory dragonflies belong to the family Libellulidae with *Pantala flavescens* being a prominent species. Despite having a wingspan of just 7.5 centimetres (approximately 3 inches), *P. flavescens* is known to migrate an average of over 600 kilometres (373 miles), with some individuals covering distances exceeding 2,500 kilometres (1,553 miles). Although insect migration is well-documented, data on many species, including dragonflies, remains limited, and this paper presents the first migration data on any Western Hemisphere dragonfly species.

The globe skimmer dragonfly (*Pantala flavescens*) is renowned as one of the most remarkable insect migrants, holding the widest cosmopolitan range of any dragonfly species. Its range extends across all continents except Antarctica, including remote islands such as Amsterdam Island in the Indian Ocean and Easter Island in the Pacific. Interestingly, on Easter Island, *P. flavescens* has transitioned to a non-migratory lifestyle. This species undertakes migrations across both land and ocean, making it a captivating subject of study. The globe skimmer's annual multigenerational migration covers approximately 18,000 kilometres (about 11,200 miles), with individual dragonflies flying more than 6,000 kilometres (3,730 miles), making it one of the longest-known migrations among insects.

2. LIFE CYCLE OF DRAGONFLIES

Egg stage: The life cycle of a dragonfly begins when the female lays her eggs either directly in or near a body of water, usually during or immediately after mating. Depending on the species, dragonfly eggs can be deposited on aquatic plants, within wet mud or directly into the water. The eggs are typically tiny and often difficult to see with the naked eye. The incubation period for dragonfly eggs varies, lasting anywhere from one to five weeks. Environmental factors such as temperature and water conditions can influence the duration of this stage. In some cases, the eggs may remain dormant during unfavourable conditions, hatching only when the environment becomes suitable for the nymphs' survival (Khelifa et al., 2017).

Nymph: The nymph stage is the longest and most critical phase of the dragonfly's life cycle. This stage is entirely aquatic, with nymphs living underwater, often in ponds, lakes, or slow-moving streams. Dragonfly nymphs are predatory and feed on small aquatic organisms such as tadpoles, mosquito larvae, and even small fish. As they grow, nymphs undergo multiple molts, shedding their exoskeletons up to 14 times. This process allows them to grow larger with each molt (Khelifa et al., 2017). Depending on the species and environmental conditions, the nymph stage can last anywhere from several months to several years. During this time, nymphs are highly efficient hunters and play a crucial role in maintaining aquatic ecosystem balance by regulating the population of other aquatic organisms.

Adult: The transition from nymph to adult, known as the emergence event, marks the beginning of the dragonfly's adult stage. Once the nymph reaches its final molt, it climbs out of the water onto a plant or rock, where it sheds its exoskeleton and expands its wings. The adult dragonfly will rest for a few hours to allow its wings to harden before taking flight. As adults, dragonflies are aerial predators, feeding on a variety of flying insects, including mosquitoes, flies and even smaller dragonflies. This makes them beneficial for controlling insect populations, especially nuisance species(Khelifa et al., 2017). Mating occurs mid-air, and in some species, the female will lay eggs while still attached to the male. The adult lifespan of a dragonfly varies, typically ranging from a few weeks to several months, depending on species and environmental conditions.

3. CAUSES FOR DRAGONFLY MIGRATION

There are several reasons for migration:

1. Resource Availability: One of the primary drivers of dragonfly migration is the need to exploit seasonal and spatial variations in resources. Dragonflies rely on abundant prey such as mosquitoes and other small flying insects, which flourish at certain times of the year and in specific habitats. In the spring, many dragonfly species migrate northward, tracking the gradual blooming of plants and the emergence of insect populations that provide a reliable food source. As the weather warms and ecosystems flourish, dragonflies move to new regions where prey is plentiful (May. 2013). Conversely, in the autumn, they return to southern or warmer areas, where temperatures remain suitable for their survival during winter. In these overwintering habitats, food resources remain available, and the insects avoid the cold conditions of the northern latitudes, which are inhospitable for both them and their prey.

2. Breeding and Reproduction: For many migratory dragonflies, certain geographic locations provide ideal conditions for breeding, which may differ from their feeding grounds. These locations often have the right combination of habitat features, such as water quality, vegetation, and temperature, which are crucial for the survival of their larvae. Migration to or from breeding grounds allows the species to maintain reproductive success, ensuring that larvae develop in conditions where they have access to abundant food, fewer predators, and favorable temperatures (Anderson, 2009). For example, some dragonflies migrate to cooler northern regions during the summer months, where larvae can thrive in temporary ponds that are free from fish predators, and then return to warmer climates for overwintering.

3. Climate and Environmental Factors: Dragonfly migration is closely tied to environmental cues such as temperature, humidity, and daylight duration. Changes in these factors signal the onset of seasonal transitions, prompting migratory behavior. For instance, decreasing temperatures and shortening days in autumn trigger dragonflies to leave colder regions before winter sets in, as their ectothermic physiology makes it difficult for them to survive in freezing temperatures. Similarly, increased humidity or rainfall in certain regions can create temporary wetland habitats that are ideal for breeding and feeding, attracting dragonflies to migrate toward those areas. Wind patterns also play a significant role, as dragonflies often ride favorable wind currents to conserve energy during their long migrations across large distances, including over oceans or deserts (Ware et al., 2022).

4. Avoiding Competition: Migration also helps dragonflies mitigate intraspecific and interspecific competition within their habitats. By dispersing across wide geographic areas, they reduce overcrowding in resource-rich environments, ensuring that they have access to sufficient prey, suitable breeding sites, and optimal living conditions. In densely populated areas, competition for food and breeding sites can become intense, leading to diminished survival rates. By migrating to new areas, dragonflies can find less crowded habitats where competition is lower, thus improving their chances of survival and reproduction (Ware et al., 2022). This dispersal also reduces the pressure on local ecosystems, preventing overexploitation of resources and maintaining ecological balance within different habitats across their migratory routes.

4. GENERAL TYPES OF INSECT MIGRATION

1. True migration: Monarch butterflies are true migrants in which multiple generations makes a forward and return journey across oceans and continental land masses in search of overwintering and breeding sites. Green darner dragonfly also true migrants that take three generations to reach the great lakes in North America from Mexico, bridging across aquatic and terrestrial habitats

2. Emigration: Emigration in which there is a mass movement of insect 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.

3. Irruptive migration: This occurs in rare events like sudden rains in deserts that results in an overabundance of host plants for caterpillar and nectar for adults. A large swarms of the painted lady butter fly exploit such a plethora of newly available resources.

4. Nomadic migration: In nomadic migration no regular pattern or route is fallowed and breeding sites are ephemeral. Nomadic migrants, like desert locust, move aways from their home range, but do not follow predetermined paths (Satterfield et al., 2020). At times, not all individuals of an insect population migrate, this also known as partial migration

5. DRAGONFLY MIGRATION: A COMPLEX AND ADAPTIVE BEHAVIOUR

Identifying dragonfly migration is often challenging due to the variability in migratory behaviors across species. While some dragonflies form large, conspicuous swarms that fly together in the same direction for extended periods, many others migrate as individuals or in small groups, making their movements less noticeable (Glotzhober, 1991). The most obvious migratory events involve swarms, which have been reported in numbers reaching the millions, such as those described by Russell et al. (1998). These mass swarming events are a crucial aspect of migration, as they reflect the species' adaptive response to environmental changes. However, not all migrants travel in large groups. Many may go unnoticed as they move individually or in small clusters, particularly when flying along coastlines or natural landmarks (Dumont, 1977; Sprandel, 2001). During the fall, dragonflies can often be observed in directional flight, gathering at key geographic points such as Cape May, New Jersey, and Point Pelee, Ontario, where southward-directed landmasses act as staging areas for migration (Corbet, 1984). These gatherings may be confused with non-migratory feeding aggregations, which occur during the same period.

Migration serves an adaptive function, allowing individuals and populations to relocate from habitats that have become unsuitable to more favorable environments. The deterioration of an initial habitat could be due to declining temperatures, food availability, or other ecological factors. However, practical constraints mean that migration is often defined behaviorally, relying on observations of sustained directional flight and reduced responsiveness to stimuli like food or reproduction sites (Kennedy, 1985; Dingle, 2006). Even with these criteria, identifying migratory behavior can be challenging. It is still unclear how many North American dragonfly species are regular or irruptive migrants. Russell et al. (1998) discussed this issue and provided a list of 18 reliably reported migrant species, although others, like *Sympetrum vicinum* (Autumn Meadowhawk), may be making seasonal refuge flights rather than true long-distance migrations (Corbet, 1999).

Some species have well-documented long-distance migration patterns, including *Anax junius* (Common Green Darner), *Tramea lacerata* (Black Saddlebags), *Pantala flavescens* (Wandering Glider), *Pantala hymenea* (Spot-winged Glider) and *Sympetrum corruptum* (Variegated Meadowhawk). These species are recognized for their ability to travel vast distances as part of their regular life cycle (Dumont and Hinnekint, 1973; Dumont, 1977; Corbet, 1999). Additionally, genera like *Pantala*, *Tramea*, *Sympetrum* and *Libellula* from the family Libellulidae, as well as *Anax*, *Aeshna* and

Epiaeschna from the family Aeshnidae, are commonly cited as migratory (Dyatlova & Kalkman, 2008; Haritonov and Popova, 2011). These genera demonstrate a variety of migratory behaviours, with some species engaging in annual migrations as an essential part of their life cycle.

The distinction between regular migration and irruptive movements is significant. Annual migration suggests that these behaviours are a regular, adaptive component of the species' life cycle. In contrast, irruptive migrations may occur sporadically and appear to lack adaptive significance. This has been observed in *Libellula quadrimaculata* (Four-spotted Skimmer), a well-known European migrant. Dumont and Hinnekint (1973) hypothesized that mass migratory swarms of this species might arise following large emergences triggered by delayed spring weather. These migrations, which occur approximately every 10 years, may not be driven by environmental necessity. Instead, the authors proposed that they could result from non-adaptive movements, initiated when individuals are influenced by the sight of others flying or stimulated by internal irritation from high parasite loads, particularly trematodes. Haritonov and Popova (2011) also described irruptive movements of *L. quadrimaculata* in Siberia, further illustrating the complexity and variability of dragonfly migration.

6. MOVEMENTS OF DRAGONFLY

Trivial flight: Trivial flights encompass short-term movements associated with specific and observable tasks, such as hunting, thermoregulation, predator evasion, seeking mates, locating oviposition sites, and defending individual territories. This category also encompasses the maiden flight, which occurs immediately after emergence. Rather than a single event, the term "maiden flight" refers to the entire sequence of take-offs and landings during the initial maturation phase, preceding active hunting. Additionally, trivial flights include daily movements between reproductive and feeding habitats, as well as flights to night and weather shelters and back. Although these movements may span several kilometers, classifying them as a distinct type of "commuting flights" is not entirely appropriate (Kharitonov and Popova, 2010).

Irregular mass migration: Irregular (sporadic) mass migrations occur when a large number of individuals are expelled from their habitats or when excess population is "dumped" without the intention of colonizing new territories. These migrations are observed mainly in numerous and widespread species, particularly those inhabiting eutrophic lentic reservoirs. Unlike regular migrations that cover the entire distribution range, sporadic migrations are irregular and may be linked to cyclic climatic changes, such as fluctuations in humidity. Notably, in certain temperate regions of Eurasia, including West Siberia, these migrations tend to occur at **10-year intervals.** ***Libellula quadrimaculata***, a dragonfly species, exhibits particularly pronounced sporadic migrations. During such events, many individuals participate, sometimes comprising the majority of the population. Once migration begins in one local population, other populations may join, forming enormous flocks. For instance, in **Kokchetav Province** in 1981, we observed a migrating flock of ***Libellula quadrimaculata*** consisting of approximately **100 million insects** or **30 tons of living biomass.**

Seasonal meridional migration: During seasonal meridional migrations, adult organisms move from their region of origin to new areas for reproduction. The return migration is then carried out by their offspring. These remarkable journeys span hundreds to thousands of kilometers. While relatively rare, this phenomenon is observed in a few species, including *Pantala flavescens, Hemianax ephippiger, Sympetrum fonscolombei, Anax junius*, and others. In the southern part of West Siberia, such migrations are infrequent and are marked by occasional appearances of temporary local populations of A. parthenote, likely composed of migrants from the south.

Seasonal interstational migration: These movements occur between the sites of emergence and the feeding habitats, often referred to as 'refugia'. They are typically associated with seasonal changes, such as the drying up of reservoirs or other periodic alterations in conditions at the emergence sites. The distances covered during these migrations vary widely, ranging from hundreds of meters to tens or even hundreds of kilometers. Often, these movements involve seasonal shifts from hot valleys to mountainous regions. Reproductive diapause sometimes accompanies these migrations, leading to varying durations of stay in the 'outruns,' even within the same species. Migrating individuals may form loose flocks and often fly in tandems. This migration pattern is characteristic of certain species within the genera

Sympetrum and *Sympecma*, as well as in *Hemianax ephippiger, Selysiothemis nigra* and other dragonflies. In the forest-steppe of West Siberia, dragonflies frequently migrate between reservoirs and isolated forest patches, returning to their reproduction sites.

Dragonfly flight models: Dragonfly, fascinating flying insects exhibit four distinct flight modes.

Counter Stroking: During normal hovering flight, dragonflies employ a counter-stroking technique. Their wing pairs move in a figure-of-eight pattern within a nearly vertical stroke plane. Each wing beats independently, even at substantial angles of attack. The surrounding flow field exhibits unsteady aerodynamic patterns. When tethered, dragonflies experience transient lift peaks that can be 15 to 20 times their body weight. Over a full wing stroke, a tethered dragonfly generates sustained lift two to three times its body weight, with wing lift coefficients (CL) exceeding 2.3 in one study and 6.1 in another. Interestingly, these studies highlight the inadequacy of aerodynamic models based on steady flow. Such models underestimate lift values required to counteract the insect’s weight. The pronounced angles of attack during hovering flight led to boundary layer separation, rendering steady-state modelling techniques ineffective (Salami *et al.,* 2019).

Phased- stroking: During forward or cruising flight, dragonflies can achieve speeds of up to **100 times their body length per second.** The hindwing of a dragonfly leads the forewing by a phase angle shift (denoted as “g”) ranging from **54 to 100 degrees**. The interaction between the dragonfly’s wings is highly efficient and produces greater thrust compared to a single-flapping wing. Their approach involves identifying natural landmarks on the wings of the *Polycanthagyna melanictera*, selys dragonfly. The researchers investigated both turning maneuvers and forward flight modes. Revealed that dragonflies exhibit significant changes in wing shape (chordwise) and curvature (camber) during free flight, which have implications for aerodynamic modeling (Salami *et al.,* 2019).

Synchronised-stroking: Synchronized stroking—Accelerated flight During accelerated flight, dragonflies often synchronize their wing pairs so that there is no phase difference (g ¼ 0). This allows a sufficient thrust and lift so that they can accelerate for ‘‘brief periods,’’ enabling them to obtain velocities of 13.4 m/s. However, it requires a substantial amount of power and can only be sustained for short time intervals. For that reason, dragonflies only accelerate during prey pursuit or take-off, when a large thrust force and high lift are required (Salami *et al.,* 2019).

Gliding: Gliding mode is characterized by the forewings and hindwings having no relative motion. Dragonflies are capable of gliding 40 chord lengths in one complete wing beat. This is the simplest mode of flight and the easiest to measure and analyze. The dragonfly expends very little effort in this mode. They generally glide more often in hotter weather. This is because they run the risk of overheating during active flapping flight. The free gliding flight of *Sympetrum sanguineum* and *Calopteryx splendens* dragonflies was filmed by Wakeling and Ellington. Their films showed that dragonflies glide within a vertical plane and do not turn while gliding(Salami *et al.,* 2019).

Wing Modifications in Migratory Dragonflies: Migratory dragonflies, particularly *Pantala flavescens*, exhibit significant adaptations in their wing morphology, enabling them to cover vast distances during migration. These modifications are critical for enhancing flight efficiency, manoeuvrability, and endurance, key factors for successful long-distance travel.

One of the primary adaptations is in the length of their forewings and hindwings. The forewing of *P. flavescens* measures around 38 mm, while the hindwing is slightly shorter at 34.5 mm (Johansson, 2009). This elongated wing structure aids in reducing the energy required for flight, allowing for sustained periods of gliding and minimizing the need for continuous flapping, crucial during migratory journeys.

The wing area plays a pivotal role in generating lift and ensuring maneuverability. The forewing has a surface area of 330 mm², while the hindwing, with a larger area of 458.6 mm², offers greater lift (Johansson, 2009). This larger hindwing surface allows migratory dragonflies to glide efficiently, conserving energy over long distances. The expanded wing area also aids in maintaining altitude and maneuvering in various wind conditions encountered during migration.

An essential feature of the hindwing is the anal lobe, located about one-fourth of the way from the base. This structural adaptation enhances gliding efficiency, helping the dragonfly optimize its aerodynamic performance. By adjusting the angle of the anal lobe, dragonflies can improve flight stability and control, which is vital during extended migratory flights.

Another critical adaptation found in migratory dragonflies is the presence of enlarged thoracic setae tiny hair-like structures that sense air currents. The setae in migratory species are twice as large as those in non-migratory dragonflies. These enhanced sensory structures allow migratory dragonflies to better detect changes in wind and airflow, helping maintain stability and adjust their flight patterns accordingly during long journeys.

Additionally, dragonflies possess a unique wing structure along the leading edge of their wings, called the pterostigma. This small, weighted area helps stabilize the wings during flight by reducing vibration and preventing fluttering. The pterostigma acts as a counterbalance, ensuring that the wings remain steady, even in turbulent air, thereby conserving energy and maintaining flight efficiency.

7. FLIGHT MECHANISM

Major flight motor neurones

1. Elevator motor neurones: The largest motor neuron cell bodies in the ganglia are dvm1 and dvm6, typically measuring 60–65 µm in diameter in toluidine-blue stained preparations. Both neurons share similar dendritic structures, although the axons of dvm6 originate slightly posterior to those of dvm1. A common feature is the presence of one prominent process that extends posteriorly and another laterally toward the ganglion midline. However, this pattern is sometimes obscured by the swelling of one process over the other. Key structural features of flight motor neurons include: (a) Staining of the depressor motor neuron, pm1, and elevator motor neuron, dvm6, in the mesothoracic ganglion, though the cell bodies are out of focus. (b) Several dvm3 motor neurons are stained in the metathoracic ganglion, along with one dvm7 motor neuron, viewed from the ventral surface. (c) A dorsal view of stained mesothoracic elevator dvm1 motor neurons on one side. (d) A detailed view of the mid-region of a metathoracic ganglion, where pm1 depressor motor neurons and dvm1 elevator motor neurons are stained on one side, with dvm neurons stained on the other. Major branches of pm1 run parallel, and fine branches from all neurons cross the midline. Scale bars indicate 100 µm. The five cell bodies of dvm7 motor neurons are less clustered than those of other motor neurons that innervate common muscles. Located posterior to nerve 3, they are positioned near and medial to the pm1 cell bodies. While not enough dvm7 motor neurons were stained to draw definitive conclusions about their dendritic structure, they typically resemble the depressor motor neurons, pm1, whose axons also project into nerve 3.

2. Depressor motor neurones: The motor neurons of dvm3 have cell bodies located contralateral to the majority of their dendritic processes, axons, and target muscles. Positioned on the edges of the ganglia, anterior to nerve 1, twelve neurons, each measuring 40–45 µm in diameter, were filled in a single metathoracic ganglion. Some of these neurons may have innervated dvm4, as distinguishing between dvm3 and dvm4 motor neurons was not achieved. A major dendritic process extends across the ganglion, connecting the axon to the midline, where a narrower process leads to the cell body. Additional secondary processes branch from the major transverse process, extending posteriorly and slightly medially or laterally. In certain preparations, four pm1 motor neurons were filled, with cell bodies measuring 50–60 µm in diameter. These neurons are closely packed along the edges of the ganglion, posterior to nerve 3. Each neuron has one major process that extends toward the midline and another directed anteriorly within the ganglion (Simmons, 1977). Dragonflies exhibit exceptional flight abilities, largely due to their specialized musculature. Their flight is powered by muscles attached directly to the base of each wing, enabling them to control wing shape and angle with precision. As members of the order Odonata, dragonflies utilize a direct flight mechanism, where the muscles connect to the wing base sclerites. This direct mechanism allows for remarkable flight maneuvers, granting dragonflies the flexibility to operate all four wings independently. They can fly in various directions, including upwards, downwards, forwards, backwards, and side to side. Migratory dragonflies, in particular, achieve a flight frequency of approximately 38.01 Hz. Among their key muscles, the elevator muscle (dorso-ventral muscles) controls the upstroke, while the depressor muscle (dorso-longitudinal muscles) manages the downstroke. These adaptations contribute to the dragonfly's agility and versatile aerial capabilities (Bomphrey et al., 2016; Wootton, 2020).

8. ADAPTATIONS OF DRAGONFLIES FOR FLIGHT AND MIGRATION

1. Morphological Adaptations: Dragonflies possess several key morphological adaptations that enhance their flight efficiency and maneuverability:

Their wings are uniquely structured to be light-weight yet robust, allowing for precise control during complex aerial maneuvers. This adaptability is crucial for their survival in various environments. The muscles attached to the base of each wing are vital for flight dynamics. These muscles enable dragonflies to adjust the shape and angle of their wings, significantly contributing to their agility and ability to perform intricate flight patterns. The exoskeleton of dragonflies is made of chitin, providing essential protection without adding significant weight. This lightweight structure is fundamental to their aerial capabilities, allowing them to maintain agility during flight.

2. Physiological Adaptations: In addition to their morphological features, dragonflies exhibit several physiological adaptations that support their migratory lifestyle:

Before embarking on long flights, dragonflies accumulate fat reserves. These energy stores are crucial for sustaining them throughout their migratory journeys, particularly when food sources may be scarce. The dragonfly nymphs develop quickly, transforming into adults at an accelerated rate. This rapid growth ensures that they can exploit favourable environmental conditions, enhancing their survival prospects. Dragonflies synchronize their reproductive cycles with favourable environmental conditions, laying eggs in suitable aquatic habitats. This timing helps ensure the survival of their offspring, contributing to population sustainability. They possess specialized structures that help maintain water balance, allowing them to thrive in both terrestrial and aquatic environments. This adaptability is essential for their survival in diverse habitats.

3. Navigation and Orientation: Dragonflies utilize various cues for navigation and orientation during their migratory flights:

The position of the sun and other celestial bodies serve as navigational aids. Dragonflies can determine their direction and the time of day based on these celestial references, which are crucial during long migrations. Their exceptional vision plays a significant role in locating prey, avoiding obstacles, and identifying suitable habitats. The compound eyes of dragonflies provide a wide field of view, enhancing their spatial awareness. Dragonflies are capable of detecting chemical cues in their environment, aiding them in locating food sources, breeding sites, and suitable resting spots. This ability to interpret olfactory signals enhances their overall foraging and reproductive success. These collective adaptations enable dragonflies to exhibit remarkable survival skills and flight capabilities during migration, underscoring their evolutionary success in diverse ecosystems (Cao et al., 2018).

Nocturnal migration of dragonflies: Dragonflies are typically known for their long-range migrations during the daytime (Valley, 2004). However, recent observations indicate that these insects also migrate at night, particularly when crossing over the sea. During nocturnal migrations, dragonflies display different behaviours compared to their daytime flights. This study provides compelling evidence of dragonfly migration over the sea occurring primarily at night. Diurnally migrating insects often visually orient themselves to coastlines to prevent drifting out to sea, and they may search for suitable stopover sites to refuel before embarking on long over-water journeys (Russell & Wilson, 1996; Russell et al., 1998). In contrast, nocturnal migrants at high altitudes have limited visibility of landscape features, allowing them to fly over water without adjusting their orientation. Notably, the migrations observed were frequently associated with fog, which obscured landscape detection.

The observed flight duration was approximately 9 to 10 hours, suggesting that if dragonflies behaved similarly over the sea as they do on land, they could cover distances of 150 to 400 km in a single night. This estimation aligns with previous findings from various researchers indicating that dragonflies can migrate thousands of kilometers over consecutive nights (Corbet, 1980; Samways & Osborn, 1998). Weather fronts significantly influence the horizontal displacement of migratory insects, including dragonflies, particularly in tropical and subtropical regions. Corbet (1999) noted a correlation between the arrival and departure of migratory dragonflies on oceanic islands and the passage of weather fronts, ruling out the possibility of significant transport by wind.

During nocturnal migration, dragonflies were generally observed flying below 1000 meters, with concentrations occurring around 200-300 or 500 meters above sea level. These altitudes are considerably higher than those typically seen during daytime migrations, where flights are often only a few meters off the ground (Russell et al., 1998). The altitudes observed in this study were similar to those recorded for nocturnally migrating moths and other insects crossing the sea (Drake et al., 1981). This behavior mirrors that of other nocturnal migrant insects in cool weather conditions (Feng et al., 2004; Reynolds et al., 2005). The airspeeds of downwind-oriented dragonflies, measured during their nocturnal high-altitude migrations, ranged from 3 to 7 m/s, comparable to estimates from diurnal migrations with tailwind assistance (Srygley, 2003).

An increase in airspeed as the wind direction shifted from tailwind to headwind was observed, consistent with predictions from Pennycuick's (1978) model of maximum range velocity, particularly in a mixed population of migrants dominated by *P. flavescens* during late summer return migrations. The observed decrease in airspeed with increasing tailwind velocity has been documented both within and across individual dragonflies (Srygley, 2003). Additionally, the ability of dragonflies to compensate for headwind drift during upwind migrations has not been previously reported. This increase in airspeed during upwind flight may be attributed to an increase in wingbeat frequency at lower ambient temperatures found at higher altitudes.

In 2003 and 2004, researchers noted a significant increase followed by a decline in dragonfly catches using a searchlight trap on Beihuang Island in the Bohai Gulf. The dominant species captured was *Pantala flavescens* Fabricius (Odonata: Libellulidae), indicating a seasonal pattern of nocturnal migration across the sea in China. Simultaneous radar observations revealed that these dragonflies typically flew at altitudes of up to 1000 meters during their nocturnal migrations (Srygley, 2003; Valley, 2004). They were often found concentrated around 200-300 or 500 meters, coinciding with temperature inversions (Wolf et al., 1986).

In early summer, dragonflies adjusted their flight direction in response to downwind conditions, leading to varied displacement directions at different altitudes. However, by late summer, they adeptly compensated for wind drift, including headwind conditions, maintaining a consistent southwest trajectory despite changes in wind direction. Based on radar data and hourly catches from the searchlight trap, dragonflies were estimated to fly for approximately 9-10 hours at speeds of about 5-11 meters per second, enabling them to cover distances of 150-400 kilometers in a single flight. It is believed that these dragonflies originated in Jiangsu province and migrated to northeast China, where they took advantage of seasonal paddy fields in early summer. Their offspring likely migrate southward during late summer and autumn (Feng et al., 2006).

9. CONCLUSION

The migration of dragonflies, particularly species like *Pantala flavescens*, underscores the intricate interplay between environmental factors and evolutionary adaptations that enable these insects to thrive across vast distances. Their migratory patterns not only facilitate the redistribution of nutrients and biomass in ecosystems but also demonstrate a remarkable capacity for adaptability through diverse flight mechanisms and physiological strategies. As research continues to uncover the complexities of dragonfly migration, such as the influence of environmental cues and the role of nocturnal behavior it becomes increasingly clear that these insects are not just transient visitors but vital components of the ecological fabric. Understanding their migratory dynamics is essential for appreciating their ecological roles and for informing conservation strategies aimed at preserving the health of ecosystems they inhabit. Continued investigation into their migratory behaviors will enhance our knowledge of insect ecology and contribute to broader efforts in biodiversity conservation.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that generative AI technologies such as Large Language Models, etc. have been used during the writing or editing of manuscripts. This explanation will include the name, version, model, and source of the generative AI technology and as well as all input prompts provided to the generative AI technology.

Details of the AI usage are given below:

1. chat gpt

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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