

The aerodynamics and behavior of Odonates in flight

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Abstract

The aerodynamics and flight behavior of odonates, commonly known as dragonflies and damselflies, represent an extraordinary fusion of biological adaptation and engineering efficiency. Odonates exhibit remarkable flight capabilities, including hovering, gliding, agile turns, and even backward flight, facilitated by their two independent pairs of wings. This study explores the unique aerodynamic mechanisms that enable such versatility, including differential wing-phase motion, lift generation, and drag optimization. Dragonflies, in particular, employ asynchronous wing beats, generating high lift and thrust efficiency by creating multiple interacting vortices, while damselflies primarily exhibit synchronous wing motions for energy-efficient gliding. The biomechanics of odonate flight are examined, with an emphasis on muscle articulation, wing structure, and the role of leading-edge vortices (LEVs). Behavioral aspects such as territorial defense, predation strategies, and mating displays are also analyzed, highlighting how flight mechanics adapt to ecological functions. Understanding odonate aerodynamics not only enriches our knowledge of evolutionary biology but also inspires advances in biomimetic engineering and micro aerial vehicle (MAV) design. This interdisciplinary study provides insights into the intersection of biology, physics, and robotics, emphasizing the relevance of nature-inspired solutions for modern technological challenges.

Keywords: Aerodynamics, Behaviour, Wings, Flight, Evolution.

Introduction

Odonates, which include both dragonflies and damselflies, represent one of the two modern-day representatives of Palaeoptera, an evolutionary lineage that is widely believed to have diverged from the remaining endopterygote insects at some significant point during the complex evolutionary journey of primitive hexapods. Over time, they have diversified into an impressive total of more than 6000 extant species that occupy a wide range of ecological niches. These niches include numerous aquatic habitats, where Odonates often serve as dominant predators in their ecosystems, as well as riparian zones where they may fall prey to larger predators (Córdoba-Aguilar *et al.*, 2023) ^[1]. As a consequence of their adaptability, Odonates can be found across the globe, in every zoogeographic region, thriving in environments that range from sea level to altitudes reaching as high as 5000 meters. Delving into the specifics of their anatomy, from the fine details of their teeth and spines to the intricacies of their internal viscera, Odonates possess a well-formed and distinctive set of morphological and biological characteristics that clearly set them apart from other groups of insects. In terms of classification, Odonates are organized into twenty-five families, which all descend from a total of nine ancestral lineages. The largest of these families is Libellulidae, which is impressive in its own right, boasting over 1000 valid species. Following closely behind in size is the family Gomphidae, which consists of more than 800 species. On the opposite end of the spectrum are the smallest families, namely the non-obligatory synonym Calopterygidae, and the even smaller, unique periglacial dwelling family Megapodagrionidae, both of which contain approximately 90 species each. These two families, which are characterized by having a lower number of species, trace their lineage back to five or six original ancestral Odonate

lineages. Notably, eight species belonging to a ninth descendant family of the 90 Calopterygidae species found globally inhabit the mountainous regions of southern Africa, serving as a testimony to the unique biogeographical history of these Gondwanan lands. Additionally, there have been discoveries surrounding relict American Odonates, adding another layer of interest and complexity to the study of these remarkable insects (Beaune & Sellier, 2021) ^[2]. Some claim that dragonfly adults tend to be more widely distributed than the nymphs and larvae, while the nymphs make up the bulk of the odonates found at a site. Many species tend to exhibit extremely limited movements from their natal site on either their own or different populations (Orr *et al.*, 2021) ^[43]. The classification of Odonata may thus seem complex and possibly confusing, but they are a fascinating group, and to be able to distinguish the different families is very much part of the experience of studying odonates, and the efforts to revise and clarify our knowledge can only add to that experience (Perron & Pick, 2020) ^[4].

Importance in Ecosystems

Odonates are important both as predators and as prey for various kinds of animals, so the elimination of one "top" site from the food web will be felt throughout the entire food web. Furthermore, Odonates are biological indicators and therefore, an Odonate species has the potential to monitor the ecological health of its habitat areas (Dijkstra & Schröter, 2020) ^[5]. The habitat of an ecosystem can range from a few cubic centimeters of small forest ponds to hundreds of square kilometers of agricultural land. The elimination of such a habitat system will have numerous and diverse implications at different levels of biological systems: from molecular to ecological levels.

There are several examples of interactions within ecosystems in which Odonate species are involved. Some typical examples include a common kaki tree potentially attacked by three different insect pests, the control of which by Odonates will vary depending on the species of Odonate. However, due to the ecosystem effect as a whole, they all contribute to the increase of the final kaki yield. Additionally, several reports indicate that continuous demolition of natural ecosystems can have detrimental effects on the composition and structure of the species. Thus, the loss of Odonate species will also have a detrimental impact on biological, ecological, and social systems. From a single cell to the entire ecosystem, numerous biochemical processes are carried out, most of which ultimately deal with the flow of energy and/or cycling of nutrients through various components of the energy/nutrient budget of ecosystems. Odonates are primary predators and have incredible colonizing behavior. They occur in almost every type of water, whether polluted or clean (Lekevičius, 2022) [6]. They can adapt these ecosystem types of food chains and food webs using aquatic and terrestrial life as part of various trophic levels. Conserving the Odonate habitats will also conserve the integrity of an ecosystem. Through this perspective, the presence of Odonates reveals whether the ecosystem is polluted or clean, allowing their use as a monitoring system. Overall, the presence or absence of Odonates can be used to predict and conserve different ecosystem and environmental conditions around the globe (Sahu *et al.*, 2023) [7].

Anatomy and Morphology of Odonates

Odonates are one of the oldest living species of insects and are known to possess certain unique morphological features. The adult Odonates consist of a maximum of 10 body segments, of which 3 are distinct regions: the head, thorax, and abdomen. The head comprises a pair of compound eyes, a necklace-shaped structure, a short pair of antennae, three ocelli, three pairs of mouthparts, and long antennal structures. The thorax of Odonates is the locomotor region and hence has three pairs of legs and two pairs of wings. The abdomen is the copulatory region and is moderately elongated (Bybee *et al.*, 2021) [8]. The Odonates' wings are elongated, membranous, and traversed with a fine network of veins that are strongly interconnected, giving them a rigid structure and thus eliminating the need for a thick cross vein, which is common in many insects. The legs are heterodont, organs of prehension, and hence are bristled and have a long digital spine connected to the tibiotarsus. Although highly specialized organs, their wings are more highly specialized than the legs, creating unique flight paths (Nel & Piney, 2023) [9]. The flexible raptorial structure allowing complex movement in turning is highly developed in the Odonates. The abdomen comprises membranous cuticular enlargements that are the copulatory organs, along with glandular structures, penial claspers, cerci, and paraprot. The lamellar structures shed water upon emergence from water. Based on these features, Odonates are the most aerially adapted hunters, with elongated, unique, and highly specialized veins that contribute to a diversity of flight paths, allowing them to fade in and nab their prey (MacLeod *et al.*, 2022) [10].

The venation and veinlets in the middle of these four wings help in the quick flutter to stabilize during wing beats. This flexibility of the wings extends to their central margin, with

their wing beat motion during hovering—more likely, damselflies flutter, while dragonflies have steady wing beats (Lu *et al.*, 2023). A dragonfly wing has veins and cross-veins, which contribute to enhancement during sudden forces, supporting them in performing a variety of swift angular maneuvers (Deregnacourt *et al.* 2021) [12].

Wings and Wing Venation

The aerodynamics and behavior of odonates in flight are our main concern in this article. Most animals fly with wings, but few maintain six degrees of freedom in flight instead of controlling a combination of different wingbeat patterns and body attitudes (Koehnsen *et al.* 2023) [13]. Odonates are capable of such complex flight maneuvers due to their unique wing and body structures (Zhu *et al.* 2022) [14]. In this section, we will discuss the wings of odonates in terms of their morphology and wing venation to elucidate how these structures play crucial roles in odonate flight (Singh *et al.* 2022) [15].

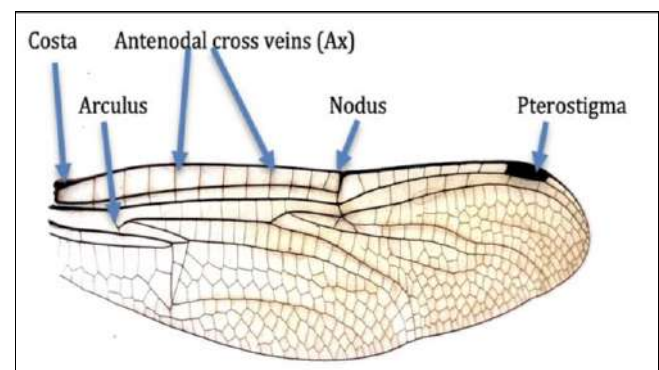


Fig 1: Forewing of Anisoptera

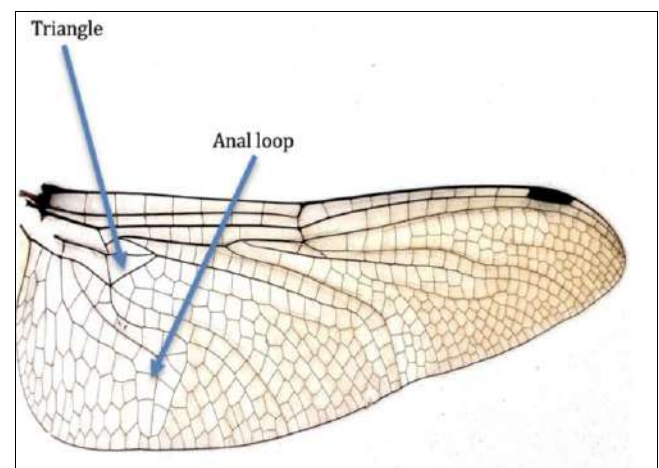


Fig 2: Hindwing of Anisoptera

Wings and Wing Venation Odonate wings are flat, which is a common characteristic of flight in insects (Fabian *et al.* 2022) [16]. These two pairs of wings beat independently and are capable of different wingbeat patterns. The forewings (Fig.1) are larger than the hindwings (Fig.2) but are of similar shape (Josse *et al.* 2023) [17]. All odonate wings, including those of both Anisoptera and Zygoptera, share the typical venation that characterizes Paleoptera. The odonate wings have two general types of venation: primitive venation and special venation (Rosová, 2020) [18]. The orientation of the wing veins provides a combination of strength and flexibility for the wings, resulting in a bending

stiffness that is perpendicular to the plane of the wings (Table 1). Paleopterous insects, including odonates, keep the wings horizontal while holding their bodies parallel to the ground, which results in the wings being twisted approximately $\pm 45^\circ$ (Karthika *et al.* 2021) ^[19]. In addition, the asymmetric forewing configuration of odonates enables a differential twist angle, which further enhances the angle of attack of both the forewings and the flapping plane upwards. This adaptive morphology also allows the hindwings to beat out of phase with the larger forewings to reduce aerodynamic drag and lift-producing vortices. In addition, the wings also provide additional veins, and the nodes from which they originate increase their structural strength (Krishnan & Devasia, 2024) ^[20].

Studies have shown that the large amount of venation causes the wing to become heavier, but it also provides several aerodynamic advantages. In the case of dragonflies, the longitudinal cross veins between large longitudinal veins increase the strength of the wing, thereby making the wing rotation resistant, simplifying the wing flapping cycle, and

maximizing the wing rotation angle (Yang *et al.*, 2023) ^[21]. Dragonflies and damselflies are closely related, differing from each other in wing shape and venation. The primitive Zygoptera are lighter and have wing venation with a high angle of connectivity compared with the Anisoptera (Béthoux *et al.* 2021) ^[22]. The high angle of connectivity observed in the venation of Anisoptera leads to increased rigidity, resulting in a further reduction of the weight of the wings. Some Anisoptera possess pterostigma in the forewings and lack it in the hindwings. Long pterostigma affects the wing shape. Species in the Libellulidae family possess a pterostigma that is approximately 27% of the wing's length, while most species in the Lestinae family have a pterostigma that is about 42% of the same. Despite this, all species have the same monitoring environment. It is known that there are significant differences in venation, body size, wing attributes, and ecology between the Lestidae and Libellulidae and between the Anisoptera and Zygoptera (Table 2). This is because the species have different evolutionary ages (Prokop *et al.*, 2023) ^[23].

Table 1: Major longitudinal veins in Odonates

Vein	Dragonflies (Anisoptera)	Damselflies (Zygoptera)	Function
Costa (C)	Runs along the leading edge of both wings	Runs along the leading edge of both wings	Provides structural support
Subcosta (Sc)	Located just below the Costa, extending partway through the wing	Located below Costa, but weaker	Supports leading edge
Radius (R)	Divides into Radius anterior (RA) and Radius posterior (RP)	Similar, but less prominent branching	Strengthens wing, carries forces
Media (M)	Divides into Media anterior (MA) and Media posterior (MP)	Less pronounced than in dragonflies	Helps maintain wing shape
Cubitus (Cu)	Splits into Cubitus anterior (CuA) and Cubitus posterior (CuP)	Similar structure, but weaker	Provides flexibility and rigidity balance
Anal Veins (A1, A2, etc.)	Forms the distinctive anal loop in hindwings	Present, but no large anal loop	Supports the wing base

Table 2: Key structures and their differences

Structure	Dragonflies (Anisoptera)	Damselflies (Zygoptera)	Function
Pterostigma	Present, thickened, short	Present, longer and thinner	Aids in wing stability
Nodus	Located at about 1/3 wing length from base, offset in fore and hindwings	More aligned in both wings	Strengthens the wing at a key flexion point
Discoidal Cell	Triangular, divided into two parts (triangle & supratriangle)	Simple quadrilateral	Important taxonomic feature
Anal Loop	Large, forming a "boot-shaped" structure in hindwings	Absent or very small	Provides extra lift in dragonflies
Arculus	Located near the base, where main veins branch	Located near the base, simpler structure	Supports main veins

Wing Morphology and Its Influence on Flight Performance

Biological significance of wing variations. Wing shape and size Odonates have evolved a diversity of morphologies to satisfy a range of ecological constraints and pressures. Terrestrial Odonate wings display a broad spectrum of wing shapes or aspect ratios. Larger aspect ratios result in greater wing elongation, which not only improves straight-line forward speed but also may increase maneuvering ability (Table 3). The wings of adult dragonflies and damselflies are constructed via hemimetabolous development and have thick antenodal veins that may modulate wing flexibility, which in turn affects wing deformation during flight. Wing deformation One of the most striking aerodynamic adaptations in evolving terrestrial Odonates is wing

deformation and flexibility. Insects that have evolved stiffer, more rigid wings move relatively slowly through still air, even in conditions of mimicry where other Odonates have wings of larger aspect ratios that highly inflate and are energetic to flap. Aspects of wing deformation caused by the action of the flight motor against the main veins and wing membrane by indirect thoracico-coxal incepted wings at their wing root and thus the wing tips, independent of the main veins being furled or only partially furled or longitudinally arched, are distinct from the relatively straight-to-curved patterns of wing displacement of small nominal reduction mechanisms that aid in flight, such as the setal fringe around the entire wing margin of some basal insect groups. For these reasons, the wings of Odonates are good models for studying thrust production.

Table 3: Wing Morphology and Its Influence on Flight Performance

Feature	Dragonflies (Anisoptera)	Damselflies (Zygoptera)	Effect on Flight Performance
Wing Shape	Hindwings broader at the base than forewings	Forewings and hindwings similar in shape	Dragonflies have better lift and maneuverability, while damselflies have more synchronized, gliding flight.
Wing Loading	High (stronger, faster flight)	Low (lighter wings, more delicate flight)	Dragonflies can generate more thrust for fast, sustained flight; damselflies are slower but more energy-efficient.
Wing Coupling	Independent wing movement	Synchronous wing movement	Dragonflies can hover and change direction quickly, while damselflies have a more rhythmic, fluttering flight.
Discoidal Cell	Triangular, divided into two parts	Simple quadrilateral	Influences aerodynamics and structural rigidity of the wings.
Pterostigma	Present, thickened, stabilizing structure	Present, thinner and longer	Helps with wing control and stability in both groups.
Anal Loop	Well-developed in hindwings, forming a "boot" shape	Absent or very small	Provides additional lift and control in dragonflies.
Flight Capabilities	Strong, fast, agile, can hover, fly backward, and glide	Weaker fliers, mostly gliding and hovering	Dragonflies excel in predation and territorial defense, while damselflies are more adapted to slow, precise movement.
Crossvein Density	High, forming a dense network	Lower, more open venation	Dragonflies have more structural reinforcement, allowing powerful wing strokes.

Flight Strategies and Maneuvers of Odonates

Odonate flight is highly agile, and they engage in advanced flight strategies. The main strategy of flight with Odonates is hovering, used primarily for hunting, in addition to mating and perching. Glides are used for evading attacks occurring from below. Odonates can perform extreme rapid yaw turns up to about 800°/s with a time constant of the order of 5.8 ms. They can also perform rapid pitch rotations of 400 – 3,600°/s to evade frontal attacks. Odonates can adopt different flight strategies when choosing what and when to saccade. The placement and function of sensory organs reveal a strong association with the approach style of predators to potential prey.

In summary, it is shown that through adaptations in physiology, perceptual systems, and behavioral strategies, Odonates manage to catch a wide variety of food sources from various environments. These differences reflect the

different ecological niches and resources of prey that these Odonates have evolved to catch. When analyzed closely, these flight behaviors highlight the delicate balance between the evolution of mating strategies and the successful capture of a variety of different-sized prey resources. A blade wing shape results in high efficiency and increased turning performance. A highly cambered wing with gently rounded leading and trailing edges is likely to give a good lift-to-drag ratio but poor turn performance. Also, they may fly in a sinuous or evasive flight path to escape a predator, complemented with reversals and jumps.

The aerodynamics of how Odonates fly and the turning capacity of their wings demonstrate that different species are highly adapted to their respective habitats (Table 4). Flight at higher wing stroke amplitude is used for rapid water hunting and allows partial mitigation of problems

associated with glare. All strategies take into consideration that prey is captured using the best combination of visual and sensory feedback and mechanics. The species with high wingbeat frequencies or a propensity to catch prey high in the sky have strong ascending abilities. Different wingbeat frequencies may also result in unique areas of the sky being searched to find suitable prey types. It is apparent that some species have more than one technique for catching small prey. Some species also change from an upside to a

horizontal down swoop hunting strategy. A change in sex ratio and condition is what is likely to elicit a response from a dragonfly to switch hunting style to suit its needs. Few other dragonflies will change their hunting style during an outbreak. It is also likely to be expensive energetically to catch gnats, and it may consequently be the more dominant females that do this. Of the same species but different sex, females are likely to catch more and consequently contain more lipids for egg production.

Table 4: Flight strategies and maneuvers of Odonates

Flight Strategy / Maneuver	Dragonflies (Anisoptera)	Damselflies (Zygoptera)	Function / Advantage
Gliding & Soaring	Can glide for short distances, using broad hindwings for lift	Rarely glides, relies on continuous wingbeats	Energy conservation during long flights
Hovering	Excellent hovering ability due to independent wing movement	Can hover briefly but less stable	Essential for prey capture and territorial displays
Backward Flight	Can fly backward with precise control	Rarely observed, less efficient	Helps in evading predators and adjusting position mid-air
Fast Forward Flight	Speeds up to 50 km/h (31 mph), powerful wing strokes	Slower flight, generally fluttering	Dragonflies excel in rapid pursuit of prey
Turning & Banking	High maneuverability, sharp turns using asymmetric wing beats	More gradual turns, less agile	Dragonflies are better at chasing and avoiding threats
Wing Synchronization	Forewings and hindwings beat independently	Forewings and hindwings beat in sync	Independent wing movement allows greater control in dragonflies
Territorial Displays	High-speed chases, hovering confrontations	Slow, hovering, or fluttering displays	Used for mating competition and defending hunting grounds
Mating Flight	Males perform aerial acrobatics, guarding females after mating	Tandem flight before and after copulation	Ensures reproductive success by preventing rival interference

Flight Mechanics and Biomechanics of Odonate Flight

Odonates, despite a fossil record dating to approximately 300 million years ago that shows the same basic architecture as those living today, are masters of powered flight. Efficient in the aerial and aquatic phases of life, their abilities have likely contributed to the large number of genera and species that exist today. Special adaptations for the aerial phase allow many species to capture their prey and avoid becoming prey themselves. How odonates soar, hover, and pivot so adeptly are questions that can have multiple answers. One of the most studied aspects of odonate flight performance is their muscle. Up to 13% of a dragonfly's total body mass comprises the "direct flight muscles, muscles of the legs used for perching, stabilizing, and capturing prey as well as reproductive organs" that grossly dominate muscle volume. As they account for a greater portion of the total mass of a dragonfly when compared with the thoracic skeleton and enjoy direct control by its nervous system, wings are important components of the tail structures. Wing movements are accomplished primarily through the many muscles acting upon the thorax. For instance, in one experiment, it was found that the neural engine controlling flight muscles can exchange up to 30% of information about changes in airflow during the upstroke flight, during the downstroke flight, and not at all when at

rest when feeding. It is the interconnected ability to move multiple parts of the body and/or wings in sequence that allows odonates to exhibit the range of behaviors that they showcase today.

Odonates flap their wings during a stereotyped stroke pattern at relatively low frequencies compared to dipterans, typically 30 Hz for dragonflies and 50 Hz for damselflies. Dipterans become range limited at about 250 Hz, and as frequency goes up, stroke amplitude goes down. Odonates also have rather narrow stroke amplitudes. Odonate cumulative muscular energy expenditure has been measured at 5.3 mJ/kg with a mean power of 408 W/kg. This is much lower than many other insects (Rüppell & Hilfert-Rüppell, 2020) [24]. The structure of odonate wings and the way that they move assist in generating lift and thrust. The lifting force, also known as "lift," consists of two components: 'added mass' and a force that arises from the wing's inclination relative to the main airflow. The former was produced as the wing pushed the air in front of, behind, and towards the middle from either side. Drag is the counter result to lift, and there are two types of drag: profile drag and induced drag. The forces generated by the wings during the upward and downward flaps are generally not equal. Thus, the pattern is often categorized into outstroke, downstroke, backward stroke, and upstroke.

Thrust is the physical force created by the engine or propulsion system of a flying machine; lift is the physical force created by the odonate's wings. This distinction between the two really creates odonate flight that differs strongly from both fixed-wing flight and helicopters. Just like other winged insects, the interaction of the wings is very important to odonate flight. For instance, some studies have shown that the forewings and hindwings of beetles work in reverse in the wings of odonates. During flight dynamics, the left-right wings' lifting strength is usually not proportional.

Most flights are sustained using energy from muscle contraction, and odonates can attain high sustained speeds. Cluster glides are powered by potential energy developed over the odonate's daily diel activity period, and odonates can re-plunge to regain altitude. Lift is usually well in excess of the weight of the animal (Nakata *et al.*2020) [25]. The gravitational force is the main force resisting forward movement and setting the cruising speed. Lift and horizontal force vary with the angle of attack, allowing animals to maintain altitude while varying forward speed and coefficients by adjusting their wingbeat kinematics. Flapping wing strokes can forcibly move and interact with the surrounding fluid, analogous to propeller flow fields in water, water jets, and ship waterlines. The wings, via their hinges, bodies, and legs, transmit forces and torques in these kinds of flows to the body and legs, where muscles must counteract them, often propelling the animal through the environment. In general, the more flexible the limb and the faster the muscle response, the more maneuverable the animal will be (Biewener *et al.*2022) [27]. The flexibility of odonate wings is likely to help with collision avoidance, inter-male communication, and rapid reflexes needed for predation. Their wing flexibility is also likely to be more energy efficient for creating lift, or a superior lift-to-drag ratio with less energy, than if they had stiffer wings (Korkmaz *et al.*2023) [28]. The high lift coefficients needed to stay in the air are created via clever wing kinematics and compliance of the wings themselves. Most odonates perform rapid aerial hand-cleaning when taking off from plant structures and the water. Open wings allow for much greater stroke amplitudes and hence greater propulsive forces, so it is possible that the wings are most effective at removing water when outspread (Ruiz *et al.*2023) [30].

Wingbeat Kinematics

Odonates, a fascinating group of insects, are capable of impressive dynamic movements. By skillfully flapping their four wings in unison, they can fly forwards, backwards, change direction rapidly, and even hover in place with remarkable agility. Since insect wings are functioning within a viscous environment, the intricate motion of the wing tips generates a complex vortex that effectively transfers momentum to the surrounding air. This detailed process and its implications is what explains the aerodynamics of flapping flight, allowing us to infer wing movement through various parameters such as force output and body accelerations. Additionally, the intricate wingbeat patterns of these insects are described by a range of kinematic parameters. These parameters include wingbeat amplitude and stroke angle, stroke plane, the phase of

dorsoventral displacement, mean frequency, as well as the phase itself, all of which can vary dramatically among different species. For instance, in smaller dragonflies and damselflies, the amplitude of wingbeat might range between 78° and 97°, and the frequency can vary from 20 to 80 Hz during hovering mode. Notably, this frequency is approximately 4 to 5 times that of their taxiing speed. Furthermore, when considering stroke angles in moths, one might observe ranges between 48° and 163° at a 15-degree downstroke over the course of an eighth of the period, contributing to their remarkable flight characteristics (Lehmann & Wehmann, 2020) [31].

The phenomenon of wingbeat kinematics stands out as a crucial factor that could play an influential role in the evolution of territorial behaviors among these species (Sikandar, 2024) [32]. It also serves as an explanation for the complex aerial displays that they perform, which are often a mix of artistic flair and functional necessity. Notably, the variation in wingbeat kinematics observed in individual species with unnerve systems shows a correlation with various elements, such as wingbeat frequency, and it is found to be marginally associated with wing length, sternonotum angle, and the gender of the individual (Liu *et al.*, 2021) [33]. This correlation indicates that insects tend to adjust their wingbeat kinematics in response to their specific morphological characteristics, aiming to optimize their flight performance within those constraints. Several factors must be considered when evaluating the kinematics of wingbeats, as they can significantly influence the results. These factors may include tethering during observation, the presence of marks on the wings, the overall shape and aspect ratio of the wings, as well as the differences within populations. Such considerations are critical for a thorough assessment of the kinematic patterns that occur in wingbeats (Kihlström *et al.*, 2021) [34]. It is highly probable that conducting detailed studies on each distinct species will yield refined insights, leading to sub-orderings of substantial evidence that pertain to taxonomic classifications such as families, sub-families, or possibly even down to the genus and species levels. Such investigations could pave the way for a deeper understanding of the evolutionary trajectories and ecological adaptations present in the world of flying insects (Meresman *et al.*2020) [35].

Lift and Drag Forces

The flight of odonates, similar to that of any other insect species, can be described simply as the resistance faced by their body and wings as they move through the air, particularly in a backward direction. Indeed, while there are two primary forces contributing to the lift experienced by odonates, the interplay between these two forces is highly significant, which makes it reasonable to consider them collectively when discussing flight optimization and mechanics (Hågvar, 2024) [36]. Lift is generated on the wings of the odonates to effectively counterbalance their weight and facilitate unimpeded motion through the air. The distinctive structure of their tails and wings ensures that when a water drop departs from their body, it is subsequently carried by the water after the odonates connect their tail to the water surface. This interaction is intriguing, as these water droplets not only maintain a connection to the

environment but also assist the wings in performing their supportive function during flight (Novella Fernandez, 2024)^[37]. Furthermore, in addition to relying on the presence of these water droplets, the flight mechanics of odonates are greatly enhanced by their rapid wing beats, which create variations in air pressure both beneath and above the wings. The intricate anatomy of these wings is characterized by a shape resembling triangular bodies located at their tips, a design that contributes significantly to their impressive aerial capabilities (Moore & Khan, 2023)^[38].

Odonates, a group of insects that include dragonflies and damselflies, possess unique adaptations that enable them to alter the angle of attack during their vertical flight, as compared to when they are flying horizontally (Guthrie, 2024)^[39]. For instance, at the conclusion of a wave flight, or when executing a sharp turn, the angle of attack effectively increases, primarily due to the upward motion of their wings. This increase in the angle of attack results in an enhancement of lift, allowing these insects to maneuver efficiently in the air. Moreover, there is an important aerodynamic aspect to consider: the parasitic drag acts on the head ends of the odonates. This particular force is responsible for aiding in their sharp turns, which also contributes to an increase in the angle of attack. Remarkably, odonates can almost bring their speed down to zero during such maneuvers. When they do this, they lose roughly fifty percent of their stored potential energy, which they subsequently convert into kinetic energy by dropping down (Jouault *et al.*, 2022)^[40]. This conversion is crucial for their ability to gain speed rapidly again after a maneuver. When flying, odonates that have their wings laid back, which are typically long and strong, can stall if they fail to respond adequately to the vertical movements of their wings. In a horizontal flight or forward motion, these insects tend to maintain either a positive angle of attack or, at times, a neutral, or zero, angle of attack. Additionally, the outstanding quickness and ability to make sharp turns that characterize their flight are attributable to their remarkably high coefficient of lift. It is important to note that when one mentions the term "lift," it fundamentally refers to the opposing force of gravity. To maintain flight, the difference between the gravitational force acting on the odonate and the lift generated must exceed the velocity at which they are traveling. When an odonate is hovering or floating in place, it is capable of slightly bending its wings, harnessing the force generated by lift to rise upwards and initiate movement. During the vertical release of one odonate from another, they create disturbances in the air around them, facilitating a rapid descent that enables them to take off smoothly. Furthermore, the lateral force exerted on these insects is crucial; it plays a significant role in controlling their vertical flight, as well as assisting with directional changes during horizontal maneuvers. The lift generated during the flight of these remarkable insects is fundamentally linked to the intricate shape and structure of their wings, which are specifically designed for effective air movement and maneuverability in their aerial environment (Orr *et al.*, 2021)^[43].

Comparative Aerodynamics with Other Insects

When considering the flight characteristics of various insects, particularly those in relation to the Odonates, it becomes clear that their flying abilities are quite unique and

distinct. Odonates, which include dragonflies and damselflies, possess flight traits that set them apart from many other insect groups (de *et al.* 2021). For instance, Lepidopterans, which are another prominent and well-known group of insects, are characterized by their relatively slow wing beats and low wing loadings, which generally indicate a much lower flight efficiency compared to Odonates. Furthermore, Lepidopterans demonstrate a remarkable capability for long-distance migration, a trait enabled by their ability to support a substantial portion of their body weight on their forewings through an intricate coupling of the wing hinge system. This adaptation allows them to achieve consistent and prolonged flight with relative ease. In contrast, Odonates possess wings that are robustly structured, which leads to different flight dynamics. Their wings, unlike those of Lepidopterans, are not as lightly sclerotized and typically feature distinct shapes that enhance their aerial maneuverability (Orr *et al.*, 2021)^[43]. Bumblebees and short-tongued bees, which also represent a different category of insects, demonstrate highly efficient lift mechanisms as well. These fascinating insects can articulate their wings with five degrees of freedom, while their bodies possess three degrees of freedom, granting them exceptional aerodynamic versatility and agility in the air (Askew, 2021). This evolutionary trend reflects a broader principle in nature; similar traits arise in different groups as they respond to comparable environmental pressures and adapt accordingly. The study of these adaptations offers valuable insights into the evolutionary mechanisms that drive the remarkable diversity seen within the insect world, particularly in the context of flight (Huang *et al.* 2020)^[45].

Technological Applications and Biomimicry

One of the most fascinating aspects of Odonate flight is how closely tied every wingbeat's kinematic behavior is to the aerodynamic phasing at play (Table 5). An understanding of the underlying aerodynamics will not only elucidate the flight capabilities of Odonates, reducing the reliance on direct observations, but will also present new principles upon which the vehicles of tomorrow can be designed to be more efficient (Yu *et al.*, 2022)^[46] (Li *et al.*, 2024)^[47].

There are reports of attempts at creating biomimetic designs inspired by the leading-edge vortices of both preferences and dragonfly wings. Researchers have also started to investigate whether a micro air vehicle inspired by dragonfly flight could be useful in delivering pollen within commercial greenhouses (Othman *et al.* 2023)^[49]. These attempts provide a glimpse of the potential for change in different kinds of agriculture, conservation biology, mosquito control, and surveillance that can arise from studies of coupled kinematic and aerodynamic behavior of dragonflies. They have also reported that the shape and motion of the damselfly body in flight are designed to maximize the 'bao' that is generated to compensate for gravitational forces. However, a drive for more realistic flights of this micro air vehicle will require a deeper understanding of the full temporal and three-dimensional behavior of vortices evolving in the wake of these wings over time. As a part of cutting-edge science, which sees biology feeding into technology, there will also be a number of associated ethical obligations and implications to consider well in advance (Ji *et al.*, 2022).

Table 5: Technological Applications and Biomimicry of Odonate Flight

Aspect	Technological Application	Biomimicry Inspired by Odonates	Potential Benefits
Independent Wing Control	Micro Air Vehicles (MAVs), drones	Dual-wing drones with asynchronous movement	Enhanced maneuverability and stability in turbulent air
Hovering & Backward Flight	Autonomous aerial robots	Insect-inspired hovering drones	Precise control for search-and-rescue operations
High Agility & Maneuvering	Military and reconnaissance UAVs	Dragonfly-inspired quadcopters	Rapid turns, high-speed chases, and mid-air stability
Energy Efficiency in Flight	Bio-inspired aircraft design	Wing synchronization patterns in damselflies	Improved fuel efficiency and endurance in aircraft
Lift & Thrust Optimization	Flapping-wing robots	Dragonfly-like vortex interactions for lift	Increased payload capacity with minimal energy consumption
Aerodynamic Stability	Wind-resistant drones	Biomimetic wing flexibility and shape adaptation	Better performance in unstable or windy conditions
Collision Avoidance	AI-controlled flight systems	Dragonfly-inspired neural flight control	Faster real-time adjustments in navigation systems
Vision-Based Tracking	AI-guided targeting in defense	Dragonfly-like motion tracking and predictive flight	Enhanced object detection and interception capabilities
Flexible Wing Structures	Adaptive wing morphing technologies	Bioinspired wing materials that change shape in flight	Increased flight adaptability for various environments

Conclusion

There is still much to be learned about Odonate biology, especially with respect to behavior, population dynamics, and interaction with the environment. Future research could focus on several key areas: detailed kinematic analysis of aerial maneuvers with respect to eliciting behaviors, monitoring for power use via video overlay of stereophotogrammetric data and modeling, and interpretative modeling with respect to the forces generated by the wings and the direct effect on the movement response; the potential relationship between Odonate flight behavior and habitat; how habitat change, specifically those due to climate change such as pond desiccation or changes in water level and temperature, affects flight performance and physiology; Odonate wing kinematics across the breadth of the order and testing for functionality and trade-offs; timing of dragonfly flight appearance within a flight season as an indicator of environmental stress; and flight escape responses in *Onychogomphus uncatatus* after the onset of food deprivation.

Future collaborations may use modern physics and kinematics to help naturalists make detailed and repeatable measurements of Odonate behaviors that may otherwise be clouded in ecological theory. An interdisciplinary approach merging ecology with biological or engineering physics through a common interest in behavior could be achieved through laboratory or fieldwork. We advocate an open-minded approach to test both functional and ecological theories on animal behavior and explore any results such research may yield. Future work is a hot topic of behavioral reaction as a basis for Odonate habitat choice in an intact natural system. Dedicated knowledge of Odonate behavior and performance could help conservationists devise strategies to preserve and conserve populations, understand the ecological impacts of local species extinctions or declines, and promote a pilot program to determine if ecological indicators are good markers of pulsed resource use. Long-lived adults perform many of the necessary

ecological functions, and therefore, a complete examination of the behavior may be most interesting to conservation research in the long term.

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