

Article

A Support-Based Approach to Flight and Vertical Locomotion in *Apis mellifera* Revealed by High-Speed Imaging

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Abstract

Honeybee (*Apis mellifera*) flight and vertical locomotion were investigated using high-speed imaging and schlieren flow visualization. Free-flight recordings were analyzed to extract wingbeat frequency, projected stroke amplitude, wingtip trajectories, and membrane deformation. The wingtip trajectory exhibited a pronounced asymmetry between upstroke and downstroke, suggesting a dominant role of the downstroke in thrust production. Significant membrane deformation was observed near stroke reversal, indicating strong wing flexibility and dynamic modulation of wing shape during flapping. A novel support-based framework was introduced to characterize vertical locomotion through the support polygon formed by leg contact points and the displacement of its centroid relative to the body. This movement function quantified changes in support distribution and revealed adaptive leg-contact strategies during wall climbing. Schlieren visualization provided qualitative evidence of wingtip vortex formation, although finer wake structures remained difficult to resolve. These findings provide new experimental observations of honeybee flight kinematics and introduce a quantitative framework for analyzing vertical locomotion using support redistribution metrics.

Keywords: *Apis mellifera*; honeybee; flight kinematics; wingbeat dynamics; high-speed imaging; schlieren imaging; unsteady aerodynamics; wake structures; insect flight

1. Introduction

Insect flight is a cornerstone of terrestrial ecosystem functioning, enabling critical processes such as pollination, dispersal, and species interactions. Among these, pollination represents one of the most significant ecological services, directly supporting the reproduction of a large proportion of flowering plants and contributing substantially to global food production. Insect-mediated pollination is a fundamental ecological process that underpins the reproduction of approximately 75% of globally important crop species and nearly 90% of wild flowering plants, making it essential for both biodiversity and food security [1,2]. Among pollinators, *Apis mellifera* (Figure 1) is one of the most economically and ecologically significant species due to its high foraging efficiency, generalist behavior, and adaptability to diverse environmental conditions [3,4]. Honeybees are capable of foraging over several kilometers, enabling effective pollen transfer across large spatial scales and contributing to ecosystem connectivity and resilience [5,6]. Honeybee flight enables effective foraging across several kilometers,

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supporting pollen transfer and maintaining ecosystem connectivity. Consequently, understanding the mechanisms underlying insect flight, especially in pollinators such as honeybees, is essential not only for advancing fundamental biological knowledge but also for addressing broader ecological and agricultural challenges.



Figure 1. *Apis mellifera* photographed in urban setting.

Honeybee (*Apis mellifera*) flight is characterized by high wingbeat frequencies (~226–240 Hz) and relatively low stroke amplitudes (~87–90°), distinguishing it from many insects that rely on larger strokes to generate lift [7,8]. High-speed kinematic analyses further reveal that take-offs typically involve at least 15 wingbeats, with stroke amplitudes exceeding 100°, wingtip velocities sufficient for thrust generation, and maximum forewing–hindwing angles exceeding 50° [7]. By contrast, other bee species, including bumblebees (*Bombus* spp.) [9], carpenter bees (*Xylocopa* spp.) [10], and members of the Euglossine tribe [11] hover with shallow strokes (<130°) separated by rapid reversals [8]. Honeybees beat their wings at roughly 230–240 Hz, enabling efficient flight and lift generation [12].

The hinged (or flexible) wing system exhibits chordwise deformation, with the wings maintaining positive camber throughout the stroke, thereby enhancing thrust rather than lift [13]. Altshuler et al. [8] demonstrated that the kinematics of honeybee (*Apis mellifera*) hovering generate prominent aerodynamic force peaks at the beginning, middle, and end of each stroke, indicating that additional unsteady mechanisms, beyond simple translational lift, are important, especially around stroke reversals.

When ascending or hovering in low-density air, honeybees increase stroke amplitude by ~30–50% without changing wingbeat frequency, boosting wingtip velocity and net aerodynamic force. Quasi-steady models indicate that lift depends mainly on wingtip velocity, while drag is influenced by both velocity and angle of attack. By modulating wingtip speed while preserving wing angle patterns, bees maintain an efficient lift-to-drag ratio across flight conditions [7].

Building on insights from honeybee kinematics, comparative studies in bumblebees (*Bombus* spp.) provide additional perspective on aerodynamic performance, including

adaptations to hovering with heavy payloads and the effects of flapping amplitude and frequency on vertical force and power consumption [14,15].

Flow visualization studies using smoke-line techniques in free-flying bumblebees demonstrate that insects exploit leading-edge vortices to generate aerodynamic forces [16]. Bumblebees shed both tip and root vortices, without a clear aerodynamic link between left and right wings, suggesting reduced aerodynamic efficiency but increased independent wing control, highlighting behavioral flexibility [17,18]. Turbulent conditions further induce more variable and extreme wing kinematics, showing active responses to body instabilities [19]. Advances in motion tracking, including Fast Lock-On (FLO) and virtual stereo systems, allow high-resolution monitoring of wingbeat frequency, wing motion, and flow fields in free-flying honeybees, enabling integration with particle image velocimetry (PIV) for airflow characterization [20].

Experimental studies of free-flying bumblebees in wind tunnels confirm the exploitation of leading-edge vortices for lift generation and the shedding of both tip and root vortices, a flow topology distinct from other insects that may favor control independence between left and right wings [16]. Recent computational studies have extended these insights to compressible, rarefied flows, demonstrating that rarefaction can improve lift coefficients while higher Mach numbers reduce lift due to pressure variations. The presence of slip boundaries subtly affects vortex formation, and acoustic signatures are highly dependent on the Mach number due to shock interactions [21].

Bumblebees also adjust their wing kinematics in response to load carrying, increasing stroke amplitude with load size, although metabolic rate is more strongly tied to wingbeat frequency and the bee's loading history rather than immediate load [22,23]. In cluttered environments, flight performance is influenced more by behavioral strategies, such as path sinuosity and collision avoidance, than by acceleration capacity, with larger bees navigating obstacles more cautiously [24]. Together, these findings demonstrate that bee flight involves a highly tuned interplay between wing kinematics, unsteady aerodynamics, environmental context, and behavioral adaptation, enabling hovering, ascending, load carrying, and maneuvering in complex environments while maintaining efficiency and control. Although flight and walking are often studied separately, honeybees routinely transition between aerial locomotion and surface attachment during foraging, landing, and take-off. Understanding both wing-driven flight dynamics and support redistribution during surface locomotion provides a more comprehensive description of honeybee movement strategies across different locomotor modes. For this reason, the present study examines both free-flight kinematics and vertical walking behavior.

Despite progress, the coupled relationship between wing kinematics and surrounding flow in free-flying honeybees remains incompletely characterized, particularly under realistic flight conditions. The present study addresses this gap by combining high-speed kinematic analysis with flow visualization to understand the aerodynamic mechanisms underlying honeybee flight.

Therefore, the objectives of the present study are threefold: (1) to extract and analyze the principal kinematic parameters of *Apis mellifera* flight from high-speed recordings obtained under near-natural conditions; (2) to investigate the associated flow structures using schlieren visualization; and (3) to develop a support-based framework for quantifying vertical locomotion through the evolution of the support polygon and support centroid displacement. By combining flight kinematics, qualitative flow visualization, and locomotion analysis within a single experimental framework, the study aims to provide a more comprehensive characterization of honeybee motion.

2. Materials and Methods

The present study focuses on *Apis mellifera*, one of the most extensively studied pollinating insects and a species characterized by high wingbeat frequencies and highly repeatable flight behavior. Its relatively small size and rapid wing motion make it a suitable model for investigating the relationship between wing kinematics, wing deformation, and flow structures using high-speed imaging techniques. Therefore, *Apis mellifera* was selected as the experimental subject for the present investigation.

A series of high-speed recordings of *Apis mellifera* were acquired and analyzed using two complementary visualization approaches: high-speed imaging under natural illumination and schlieren flow visualization. For the natural-light recordings, experiments were conducted outdoors in order to preserve near-natural flight conditions. Individual bees were gently captured, introduced into the measurement volume, and immediately released, allowing for spontaneous free-flight behavior. Each recording corresponded to a different specimen of the same species, an approach considered appropriate given that the objective of the study was to characterize general flight dynamics at the species level rather than individual-specific behavior.

A total of 20 individual honeybees were recorded, yielding 20 flight sequences and approximately 500 analyzed frames for each flight phase. Recordings were performed over 5 experimental days. Each sequence corresponded to a different specimen and was analyzed independently.

High-speed image sequences were recorded using a high-frame-rate camera (Phantom VEO 710L (Vision Research, Inc., New Jersey, USA) used at its highest frame rate of 7500 fps for the highest 1280×780 pixels resolution), enabling the capture of rapid wing kinematics and body motion. The experimental configuration for natural-light imaging is shown in Figure 2.

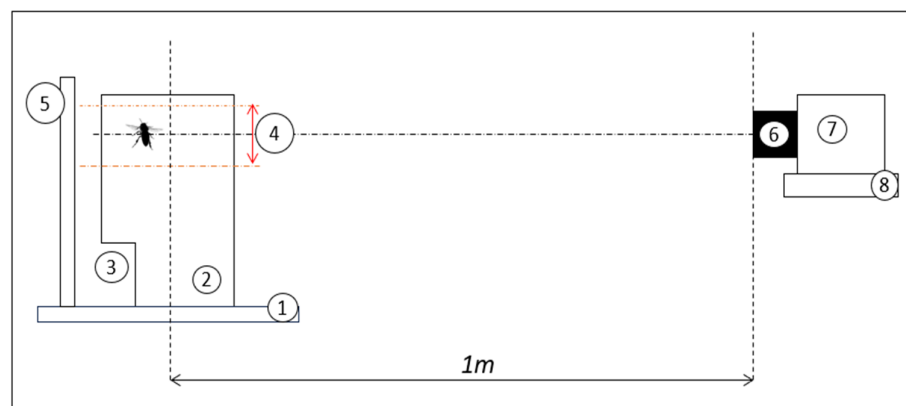


Figure 2. Natural light setup for high-speed recordings: 1—table top, 2—transparent tank, 3—lateral opening, 4—zoomed-in test area, 5—white screen, 6—camera lens, 7—CMOS high-speed camera, 8—camera tripod.

The experimental setup consisted of a tabletop support (1) on which a transparent test chamber (2) was placed. The chamber was equipped with a small lateral opening (3) through which individual bees were introduced. Once inside, the bees exhibited spontaneous upward flight and exited through the open top of the chamber, which was intentionally left uncovered to avoid confinement effects. The upper region of the chamber was monitored using a zoom lens (5) attached to a high-speed camera (6). The camera was mounted on a tripod (7) and positioned above the chamber to capture detailed images of the bee during the ascent phase of flight. The camera and camera lens used in this setup is the same as the ones used for the schlieren imaging presented in Table 1.

Complementary schlieren imaging was employed to visualize density gradients in the airflow induced by wing motion, allowing qualitative assessment of wake structures and unsteady aerodynamic features. The schlieren setup (Figure 3), consisting of the equipment found in Table 1, was configured to enhance sensitivity to small refractive index variations associated with the bee-generated flow field. The schlieren setup was implemented in both Z-type (Figure 4a) and single-mirror configurations (Figure 4), the latter providing increased image magnification of the insect while maintaining comparable resolution.

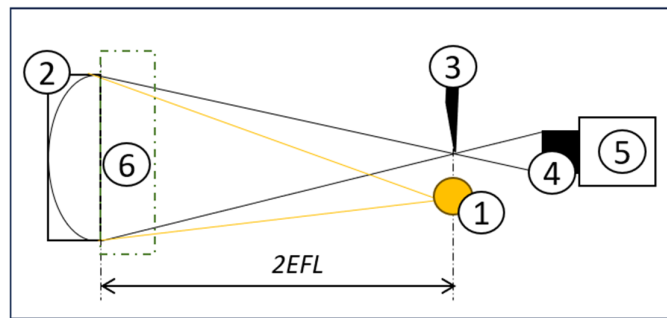
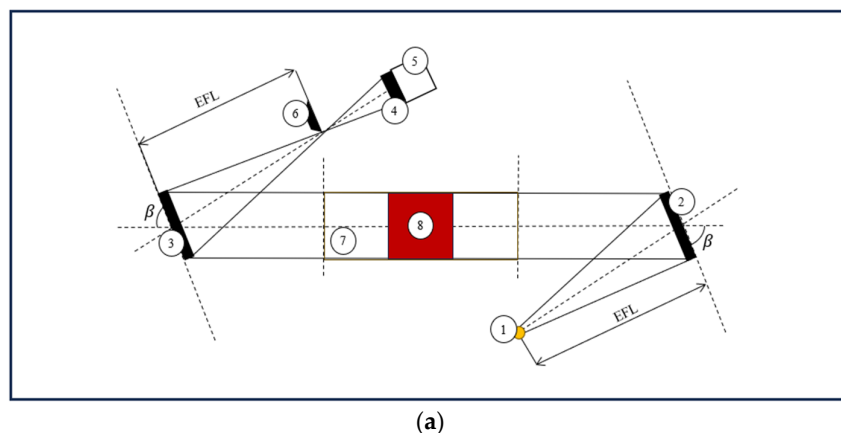


Figure 3. Single-mirror schlieren setup: 1—light source, 2—parabolic mirror, 3—knife edge, 4—camera lens, 5—high-speed camera, 6—test area.



(a)



(b)

Figure 4. (a) Z-type schematics of the setup: 1—light source, 2—1st parabolic mirror, 3—2nd parabolic mirror, 4—camera lens, 5—high-speed camera, 6—knife edge, 7—test area, 8—transparent tank, β —mirror offset angle, (b) laboratory photograph of the Z-type setup, similar to the one found in [25].

Table 1. Schlieren setup equipment.

Component	Model Specifications	Key Parameters	Notes
Parabolic mirrors	Al-plated	EFL = 1524 mm	Used in Toepler-single mirror
	From Edmund Optics [25]	Diameter = 254 mm $\lambda/8$	Used in Z-type/shadowgraph
Light Source	LS-S1 [26]	Output diameter 0.5 mm	Laser-pumped, Wavelength 440–750 nm
High-speed camera	Phantom Veo 10L [27]	Max. resolution 120×820 at max. 7500 fps	Used at different recording speeds
Camera lens	Tamron Nikon [28]	70–200 mm F/2.8, MACRO	Used with adjusted zoom and diaphragm opening
Knife-edge	Anti-reflective black metal sheet	-	Mounted on tripod

Wingbeat frequency was determined by analyzing the temporal periodicity of wing motion across successive frames. Characteristic wing positions, corresponding to stroke reversal points, were identified, and the time interval between consecutive occurrences was used to define the flapping period. The image sequence used for this process is found in Figure 5.

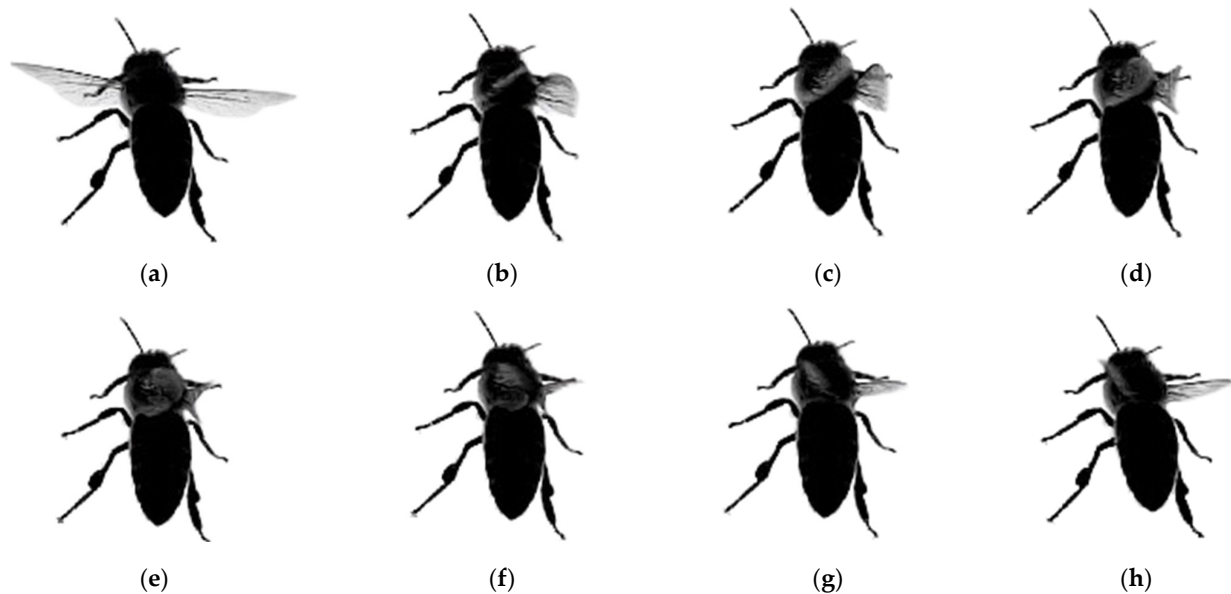


Figure 5. Fast upwards flight of the *Apis mellifera* (from (a–h)).

Wing membrane deformation in the XZ plane (Figure 6) was analyzed in MATLAB by tracking 30 points distributed along the membrane contour in each frame. For each selected frame, 30 points were manually placed along the visible wing membrane contour, extending from the wing root to the wingtip. The points were approximately evenly distributed along the contour to capture the overall membrane shape and local curvature. The resulting coordinates were subsequently imported into MATLAB, where a parametric spline was fitted to reconstruct the membrane profile.

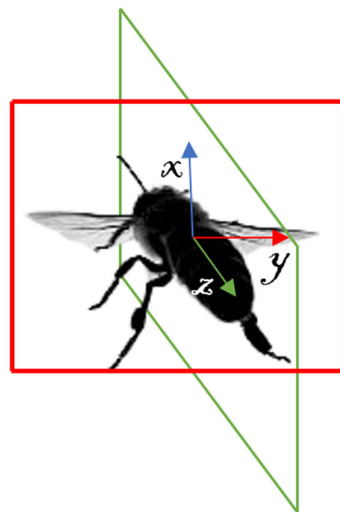


Figure 6. Reference plane and axis system considered for the present study.

The recording of the upwards flight was also used to compute the rotation angle of the wings at the end of the upstroke and the beginning of the downstroke.

The projected stroke amplitude of the bee during free flight was derived from measurements in the XZ plane. All kinematic quantities were extracted from a single-camera view and therefore represent projected two-dimensional measurements. Out-of-plane wing motion, variations in stroke-plane orientation, and three-dimensional wing deformation could not be resolved. Consequently, the reported stroke amplitudes, wingtip trajectories, and deformation metrics should be interpreted as projected quantities rather than true three-dimensional values.

The movement function for the vertical walk of the bee was computed following the next work logic. The movement pattern was characterized through a support-based approach, where the instantaneous support centroid was computed from the convex hull of the leg contact points. The displacement of this centroid relative to the body center was defined as a movement function, reflecting the redistribution of support during locomotion. This quantity captures the combined effect of leg placement, contact timing, and stance asymmetry, providing a compact descriptor of locomotor dynamics.

For each frame k , the body center was obtained via centroid tracking and consistently mapped onto the corresponding frame used for leg contact point identification. The position of the body center can thus be defined as:

$$b^{(k)} = (x_b^k, y_b^k) \quad (1)$$

While for the contact points:

$$p_i^k = (x_i^k, y_i^k) \quad (2)$$

Only values for contacting legs were kept, which defined:

$$c_i^{(k)} = \begin{cases} 1 & \text{leg in contact} \\ 0 & \text{not in contact} \end{cases} \quad (3)$$

The support polygon was built for all valid contact points:

$$\Omega^{(k)} = \text{convex hull of } p_i^k \quad (4)$$

The centroid of support was constructed:

$$c^{(k)} = \frac{1}{m_k} \sum_{i: c_i^{(k)}=1} p_i^k \quad (5)$$

Body-centered coordinates were applied:

$$\bar{c}^{(k)} = c^{(k)} - b^{(k)} \quad (6)$$

The movement function described in Equation (7) was computed.

$$M^{(k)} = \|\bar{c}^{(k)}\| = \sqrt{c_x^2 + c_y^2} \quad (7)$$

All image sequences were post-processed using MATLAB 2020a (MathWorks, Natick, MA, USA) [29]. Kinematic parameters, including wingbeat frequency, stroke amplitude, and wingtip trajectories, were extracted using frame-by-frame analysis and image-based tracking techniques. Preprocessing steps included contrast enhancement and noise reduction to improve feature detectability, particularly in schlieren recordings where low signal intensity was observed.

3. Results

3.1. Kinematic Extraction from Natural Light High-Speed Imagery

The kinematic analysis comprised the extraction of key flight parameters, including wingbeat frequency, projected stroke amplitude, wingtip trajectory, leading-edge (LE) displacement, wing twist characteristics, asymmetry between upstroke and downstroke phases, and body–wing coordination. Here, several flight regimes were analyzed: upwards (nearly vertical movement), horizontal forwards flight, backwards flight, extreme maneuvering and vertical walk.

High-speed image sequences were processed using MATLAB. Prior to analysis, frames were subjected to contrast enhancement and noise reduction to improve the visibility of wing edges and body contours, particularly in recordings with low-signal intensity. A calibration procedure was performed based on a known reference length within the field of view to convert pixel measurements into physical units. Wing and body features were identified using frame-by-frame analysis. The wingtip and leading-edge positions were tracked either manually or using semi-automated image processing techniques, depending on image quality. The body axis was defined by connecting the head and abdomen centroids, providing a reference frame for evaluating wing motion relative to the body.

3.1.1. Wingbeat Frequency

The analysis for the wingbeat was conducted over ten consecutive flapping cycles for both horizontal and vertical flight conditions to ensure representative and consistent measurements. For clarity, the wingtip trajectory is illustrated in Figure 7 for a single representative flapping cycle. While the analysis was performed over ten cycles, the trajectory obtained by superimposing all cycles appears more dispersed, primarily due to the horizontal component of the flight, which introduces cycle-to-cycle variability and spatial offset of the wingtip path. As shown in Figure 7, the wingtip trajectory exhibits a non-elliptical and asymmetric loop, characterized by a larger excursion during one phase of the stroke and a more compact return path. This asymmetry is consistent with forward flight conditions, where the downstroke contributes more significantly to thrust generation, while the upstroke follows a reduced or modified trajectory. The implications of these findings are further elaborated in Section 4 (Discussion).

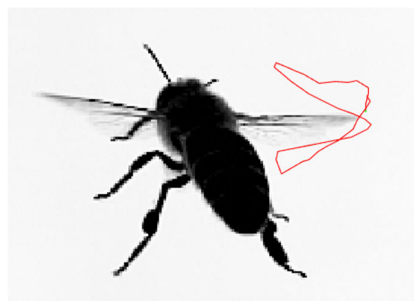


Figure 7. Wingtip tracking over a single flapping cycle.

3.1.2. Membrane Deformation

A limited number of frames were first processed manually to identify the membrane shape and ensure consistent point placement. These annotated frames were subsequently used to support automated tracking in the remaining sequence. The tracked coordinates were fitted using a cubic parametric spline interpolation implemented with MATLAB's *spline()* function. No smoothing was applied, and the resulting spline was constrained to

pass through all selected contour points. The reconstructed curve was subsequently used to quantify the projected membrane deformation. A short sequence of the membrane deformation with emphasis on the downstroke twist is depicted in Figure 8.



Figure 8. Sequence depicting the projected wing twist of the downstroke for the *Apis mellifera*, recorded at 7500 fps. The membrane twist is detected both manually (red points and green spline) and automatically (overlaid yellow spline).

The automated spline reconstruction was used to facilitate contour visualization and consistency across frames. Quantitative deformation parameters were calculated from the manually selected contour points and the corresponding spline fit. No separate quantitative validation of the automated tracking procedure was performed.

Because the wing membrane adopted a strongly curved, near-arc-shaped profile during the upper stroke phase, a direct two-point angular definition of twist was not considered sufficiently representative. Instead, the projected twist was quantified from the membrane contour (Figure 9). In MATLAB, multiple points were selected along the visible wing contour in each frame, and a parametric spline was fitted through these points. The resulting curve was used to determine geometric descriptors of deformation, including the maximum distance from the endpoint chord, the arc-to-chord ratio, and an equivalent projected twist angle.

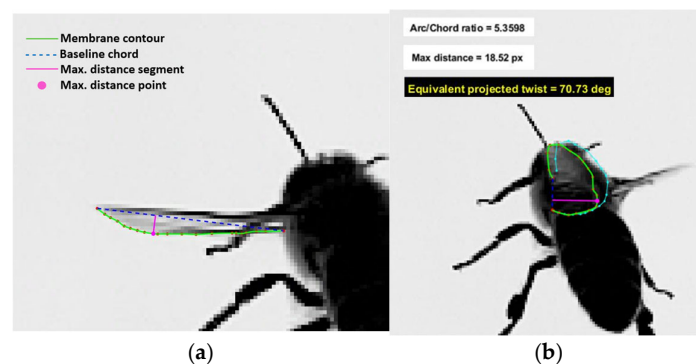


Figure 9. Contour-based quantification of projected wing deformation. (a) Membrane contour extracted from high-speed images using manually selected points and spline fitting (green), together with the corresponding endpoint chord (blue dashed line). The maximum deviation from the chord

is shown (magenta), providing a measure of membrane curvature. (b) Representative output illustrating the computed deformation parameters, including arc-to-chord ratio, maximum distance, and equivalent projected twist angle, derived from the fitted contour geometry.

3.1.3. Projected Stroke Amplitude

The projected stroke amplitude was determined through image-based analysis. This involved measuring the angle between the thorax axis and the leading edge (LE) of the wing in each frame. In addition, the angle between the thorax and abdomen axes was evaluated to account for body articulation during flight. All angular measurements were defined as positive for both upstroke and downstroke phases. The stroke amplitude was then calculated as the maximum angular excursion of the leading edge relative to the body axis, corresponding to the highest angles attained on either side (left and right) of the thorax axis. Annotated frames for this method can be found in Figure 10. The leading edge (LE) was employed as a geometric proxy for wing orientation, recognizing that local deformation may affect its instantaneous position. Owing to the single-view imaging configuration, all measurements correspond to projected quantities. The stroke amplitude was defined as the total angular excursion of the wing relative to the thorax axis, determined as the difference between the maximum and minimum LE angles over a flapping cycle. The analysis was conducted over ten consecutive flapping cycles for both horizontal and vertical flight regimes, enabling a consistent comparison between flight modes.

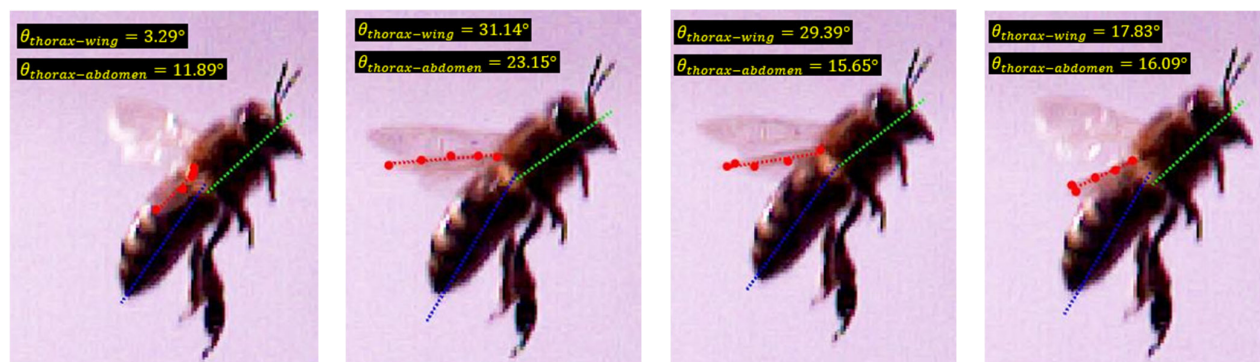


Figure 10. Stroke amplitude with angles measured for thorax-LE and thorax-abdomen axis.

3.1.4. Vertical Walk Case

The walking behavior of *Apis mellifera* on a transparent vertical surface was analyzed using high-speed image sequences. The recordings were acquired with the insect facing the camera, allowing clear visualization of leg placement and contact points. Selected frames were manually annotated in MATLAB by identifying the body center and the tarsal contact points of each leg (left and right fore, middle, and hind legs). Frames without clearly identifiable contacts were excluded from the analysis. The tracked coordinates were used to compute kinematic and geometric parameters, including leg-to-body distances, left-right spread, number of contacting legs, and support polygon characteristics (centroid and area), enabling a quantitative assessment of leg positioning and contact dynamics during locomotion. Several frames from the output analyzed image sequence can be found in Figure 11.



Figure 11. Sequence of manually annotated frames illustrating leg contact tracking of *Apis mellifera* during wall locomotion. The body center is indicated in yellow, while the contact points of the six legs (LF, LM, LH, RF, RM, RH) are marked in red. The sequence highlights the temporal evolution of leg placement and contact configuration used for subsequent kinematic analysis.

The support polygon was obtained from manually identified tarsal contact points of *Apis mellifera* during wall locomotion. For each analyzed frame, the body center and the contact positions of the six legs (left and right fore, middle, and hind) were marked in MATLAB. Frames with insufficient visibility were excluded. The instantaneous support region was then defined as the convex hull of all valid contact points, forming a polygon that represents the area over which the insect is mechanically supported. From this polygon, geometric properties such as area and centroid position were computed. This representation is relevant because it provides a quantitative measure of how the insect distributes its support during locomotion. Changes in the support polygon reflect variations in leg placement, contact patterns, and symmetry, offering insight into stability, load distribution, and coordination of the legs. In particular, the size and position of the support polygon relative to the body center can be used to infer how the insect maintains balance and adapts its stance on a vertical surface. Figure 12 presents a few positioning instances for a better understanding and result visualization.

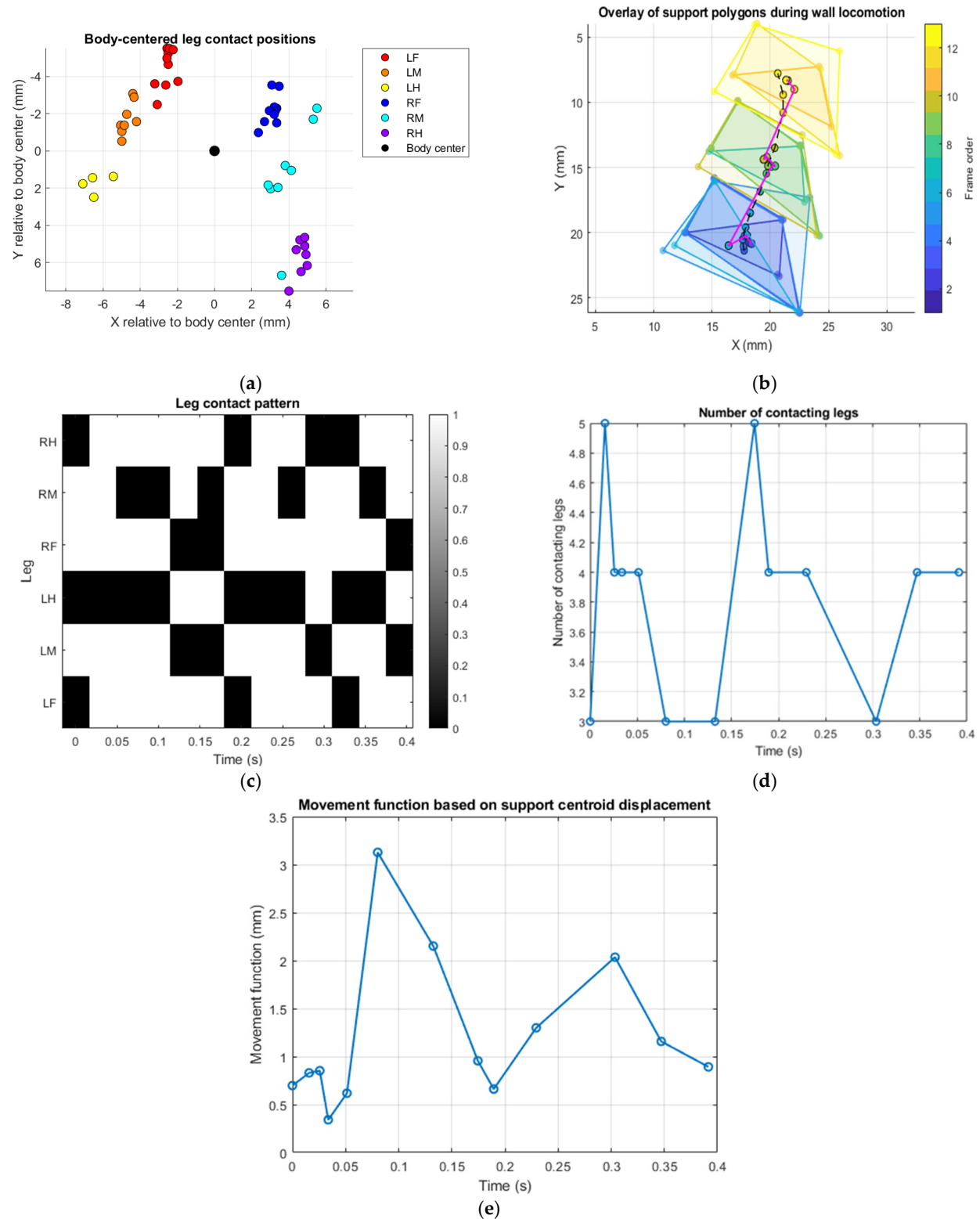


Figure 12. (a) Leg contact map, (b) support polygons relative to body center, (c) leg contact pattern, (d) number of contacting legs and (e) Movement function based on support centroid displacement.

3.2. Schlieren Visualization

Schlieren imaging was employed to provide qualitative insight into the flow field generated by the flapping wings. While distinct flow structures were not consistently resolved, the technique enabled visualization of density gradients associated with the unsteady motion of the wings.

Schlieren images were acquired at 7500 fps in free flight. Taking into account the maximum magnification allowed by the current system (equipment described in Table 1) in the Z-type configuration, the images show the flight and the body plume of the bee, but the images do not clearly depict any distinguishable aerodynamic elements.

Sample images obtained with the Z-type system are presented in Figure 13 in order to highlight the strong reflectivity of the bee wings.



Figure 13. Schlieren stills from the Z-type schlieren imaging campaign depicting the reflectiveness of the bee wing.

A single-mirror schlieren configuration was employed to enhance the effective magnification of the observed flow structures. However, compared to the Z-type arrangement, this configuration presents a reduced test area, as precise optical alignment is required to minimize aberrations. The limited spatial extent of the system, combined with the free motion of the specimen within a larger volume, occasionally resulted in overlapping visualizations within the schlieren field.

Despite these constraints, the setup was capable of revealing small but distinct wingtip vortices (Figure 14). The observation of additional flow features was limited by the highly refractive nature of the bee wings under schlieren conditions, which introduced glare and optical disturbances. This can be contrasted with observations reported for butterflies, where the opaquer wing structure led to clearer schlieren images [30]. Furthermore, the vortices generated by butterflies are typically larger and more easily distinguishable, due to their greater wingspan and lower flapping frequencies.

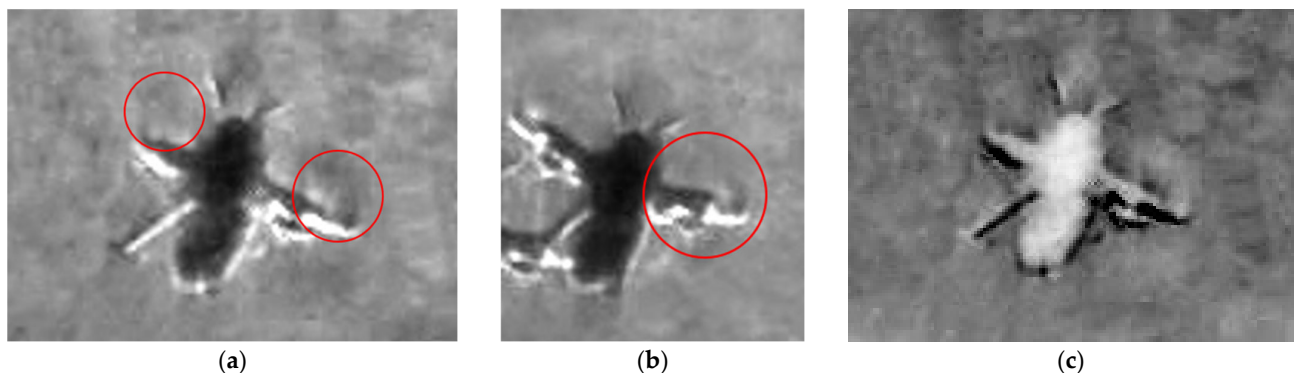


Figure 14. Single-mirror schlieren image of the bee in vertical, free flight with attached wing vortex and wing glare for both frames (a) and (b) and (c) negative of (b) for better vortex isolation where glares and body contours become black, and the flow is highlighted in white.

3.3. Comparative Perspective with Butterfly Flight

The flight characteristics observed in *Apis mellifera* differ substantially from those previously reported for *Iphiclides podalirius* [30], reflecting distinct aerodynamic strategies associated with their morphology and ecological roles. Honeybee flight is characterized by high wingbeat frequencies and relatively small stroke amplitudes, producing a nearly continuous generation of aerodynamic forces through rapid wing oscillations. In contrast, *Iphiclides podalirius* employs a low-frequency, large-amplitude flapping motion in which force production is concentrated within specific phases of the wingbeat cycle. High-speed schlieren observations of the butterfly revealed pronounced wing cupping, clap-and-fling interactions, and persistent vortex structures during stroke reversal, indicating a stronger reliance on unsteady aerodynamic mechanisms for lift enhancement and maneuverability.

The differences extend beyond wing kinematics to the overall motion mechanics of the body. In the honeybee, body orientation remained comparatively stable during free flight, with trajectory control primarily achieved through rapid modulation of wing motion. Conversely, *Iphiclides podalirius* exhibited substantial thoracic pitching and body reorientation during maneuvering, suggesting a stronger coupling between body dynamics and aerodynamic force generation. Previous trajectory reconstructions of the butterfly demonstrated that changes in body attitude contribute directly to flight-path control, whereas the honeybee relies predominantly on high-frequency wing-driven corrections. This distinction reflects two alternative solutions to aerial locomotion: a high-frequency stabilization strategy in the honeybee and a body-assisted maneuvering strategy in the butterfly.

Despite these differences, both species exhibited evidence of flexible wing deformation and the formation of coherent flow structures associated with force production. Schlieren imaging revealed wingtip vortices in both insects, indicating that unsteady vortex-dominated aerodynamics remain fundamental across a wide range of Reynolds numbers and wingbeat frequencies. The observed membrane deformation in *Apis mellifera* near stroke reversal may therefore serve a functional role analogous to the wing cupping observed in *Iphiclides podalirius*, although the underlying kinematic mechanisms differ considerably. Together, these observations highlight how insects with contrasting morphologies and flight styles achieve aerodynamic efficiency through different combinations of wing flexibility, body motion, and vortex control. These flight characteristics are described in Table 2.

Table 2. Comparative overview of flight kinematics, body motion, and aerodynamic mechanisms observed in *Apis mellifera* and *Iphiclides podalirius*.

Parameter	<i>Apis mellifera</i>	<i>Iphiclides podalirius</i>
Wingbeat frequency	~230 Hz	~5–15 Hz
Stroke amplitude	Moderate (~90–120°)	Large
Flight style	Rapid, continuous force generation	Intermittent, large-amplitude force generation
Dominant control mechanism	Wing kinematic modulation	Body and thorax reorientation
Body pitching	Limited	Pronounced
Wing deformation	Present near stroke reversal	Strong wing cupping and deformation
Schlieren observations	Wingtip vortices	Wingtip vortices, clap-and-fling structures, attached flow on cupped wings
Maneuverability strategy	High-frequency corrections	Thorax-assisted maneuvering

To provide a broader biomechanical context for the present observations, the flight characteristics of *Apis mellifera* were compared with those previously observed in *Iphiclides podalirius* using high-speed imaging and schlieren visualization. Although the two species differ substantially in morphology, wingbeat frequency, and flight style, both rely on unsteady aerodynamic mechanisms and wing flexibility to generate aerodynamic forces and maintain maneuverability. Figure 15 summarizes the principal differences in locomotion strategy, highlighting the contrasting roles of wing kinematics, body motion, and aerodynamic force generation in the two species.

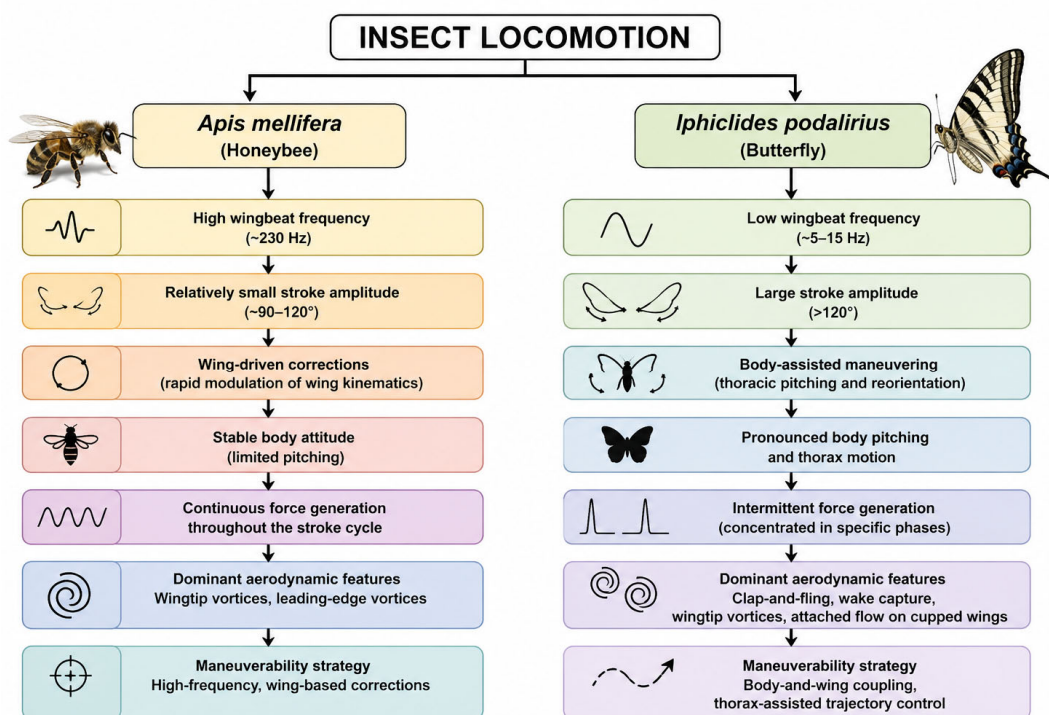


Figure 15. Comparative overview of locomotion strategies in *Apis mellifera* and *Iphiclides podalirius*.

In summary, the comparison highlights two distinct locomotion strategies, with *Apis mellifera* relying primarily on high-frequency wing-driven control and *Iphiclides podalirius* employing stronger body–wing coupling and thoracic-assisted maneuvering to achieve flight stability and agility. Despite their contrasting flight mechanics, both species demonstrate how wing flexibility, unsteady aerodynamics, and motion control can be integrated through different biomechanical strategies to achieve efficient and maneuverable flight.

4. Discussion

The present study combines high-speed kinematic analysis with qualitative schlieren visualization to investigate the flight dynamics of *Apis mellifera* under near-natural conditions. The results highlight both the complexity of honeybee wing kinematics and the challenges associated with resolving the associated flow structures at this scale.

A limitation of the present study is the use of a single-view imaging configuration. While this approach enabled detailed observation of wing motion, the extracted kinematic parameters correspond to projected quantities in the imaging plane. Three-dimensional effects, including out-of-plane wing motion and stroke-plane variations, could not be quantified. Therefore, the reported wingtip trajectories and deformation measures should

be interpreted as qualitative or projected descriptors of wing behavior. Future work should employ stereoscopic or multi-camera imaging to reconstruct the full three-dimensional kinematics.

4.1. Kinematic Asymmetry and Flight Efficiency

The extracted wingtip trajectories suggest a non-elliptical and asymmetric pattern, particularly evident during forward and upward flight. This asymmetry, characterized by a larger excursion during one phase of the stroke and a more compact return path, is consistent with previous observations that honeybees rely on unsteady aerodynamic mechanisms to generate both lift and thrust [8]. In particular, the enhanced contribution of the downstroke to propulsion, coupled with a modified upstroke, suggests an adaptation toward forward thrust generation rather than purely vertical lift.

Such behavior aligns with the findings of Altshuler et al. [8], who demonstrated that honeybee flight is dominated by short-amplitude, high-frequency strokes, with force production peaks occurring at stroke reversals. The present observations further support the notion that even small deviations in trajectory shape can significantly influence aerodynamic force balance, especially in free-flight conditions where body motion and environmental disturbances are present.

4.2. Membrane Deformation and Aerodynamic Implications

The contour-based analysis of wing deformation highlights the importance of chordwise flexibility in honeybee flight. The observed near-arc-shaped membrane configuration during the upper stroke phase indicates that simple rigid-wing assumptions are insufficient to describe the aerodynamics of the system. The use of spline-based reconstruction allowed for a more representative quantification of deformation, capturing features such as maximum curvature and arc-to-chord ratios.

This behavior is consistent with previous studies demonstrating that wing flexibility enhances aerodynamic performance by maintaining favorable camber and delaying flow separation [13]. In the present case, the deformation observed during stroke reversal likely contributes to the modulation of effective angle of attack and the stabilization of leading-edge vortices. However, due to the single-view imaging configuration, the extracted deformation remains a projected quantity, and out-of-plane effects cannot be fully resolved.

4.3. Stroke Amplitude Modulation and Body–Wing Coordination

The analysis of projected stroke amplitude indicates that honeybee flight involves significant modulation of wing excursion relative to the body axis. The inclusion of thorax–abdomen angle measurements further highlights the role of body articulation in shaping the effective stroke plane. This coupling between body orientation and wing motion suggests that honeybees actively adjust their posture to optimize aerodynamic force production.

The observed coordination between body axis variation and wing motion supports the hypothesis that flight control in insects is achieved through integrated body–wing dynamics rather than purely wing-driven mechanisms. Such coupling has been reported in other bee species and is associated with stabilization strategies and maneuverability in unsteady environments [19].

4.4. Support-Based Movement Pattern in Vertical Locomotion

A key contribution of the present study is the introduction of a support-based movement function to describe vertical walking behavior. By defining the instantaneous support polygon as the convex hull of the contacting legs and computing its centroid

relative to the body center, the analysis provides a compact representation of locomotor dynamics.

The resulting movement function, expressed as the displacement of the support centroid from the body center, captures the combined effects of leg placement, contact timing, and stance asymmetry. Variations in this quantity reflect the continuous redistribution of support required to maintain stability on a vertical surface. Unlike classical gait analysis, which relies on periodic step cycles, this approach emphasizes the dynamic adaptation of support geometry, which is particularly relevant in constrained or non-horizontal environments.

The contact patterns and number of supporting legs indicate that the bee does not strictly adhere to a canonical tripod gait during vertical locomotion. Instead, the observed behavior suggests a more flexible support strategy, characterized by variable contact configurations and continuous adjustment of leg positions. This is consistent with the need for enhanced stability when interacting with vertical substrates, where gravitational loading and adhesion constraints differ significantly from horizontal locomotion.

4.5. Schlieren Visualization and Limitations in Flow Detection

The schlieren imaging results provide qualitative insight into the flow field generated by the flapping wings, although the visualization of distinct aerodynamic structures remains limited. In the Z-type configuration, the dominant features observed were related to body-induced density gradients and strong optical reflections from the wings, which obscured finer flow details.

The single-mirror configuration, while offering increased magnification, revealed small but identifiable wingtip vortices. However, the detection of additional flow structures was hindered by the highly refractive nature of the bee wings, which introduced glare and reduced image contrast. This limitation is intrinsic to the optical properties of the insect and the sensitivity of schlieren techniques to refractive disturbances.

In contrast, previous schlieren studies on butterflies have reported clearer vortex structures, attributed to the opaquer nature of their wings and their larger characteristic scales [30]. Additionally, the larger wingspan and lower flapping frequencies of butterflies result in more pronounced flow features, which are easier to resolve using optical techniques. The relatively small size and high-frequency motion of honeybee wings likely produce vortices of smaller spatial and temporal scales, approaching the resolution limits of the current setup.

5. Conclusions

This study presents a combined kinematic and flow visualization analysis of *Apis mellifera* flight under near-natural conditions, highlighting key aspects of wing motion, deformation, and locomotor behavior. High-speed imaging enabled the extraction of detailed kinematic parameters, revealing asymmetric wingtip trajectories, modulation of stroke amplitude, and a strong coupling between body orientation and wing motion. These findings support the view that honeybee flight relies on unsteady aerodynamic mechanisms and coordinated body–wing dynamics to achieve efficient force generation and maneuverability.

The contour-based analysis of wing membrane deformation demonstrated the importance of flexibility in shaping aerodynamic performance, particularly during stroke reversal phases. In addition, the introduction of a support-based movement function for vertical locomotion provides a compact geometric descriptor of support redistribution during locomotion for describing how insects redistribute support through leg

coordination, offering a compact and physically meaningful descriptor of walking dynamics on constrained surfaces.

Schlieren imaging provided qualitative insight into the flow structures generated by the flapping wings, with limited but identifiable evidence of wingtip vortices. However, the visualization of finer aerodynamic features was restricted by the small spatial scale of the flow and the optical properties of the insect wings.

Several methodological limitations should be acknowledged. The use of single-view imaging constrains the analysis to projected quantities, limiting the reconstruction of fully three-dimensional wing kinematics and deformation. Furthermore, the reliance on manual and semi-automated tracking introduces potential user-dependent variability, particularly in frames with reduced image clarity. The schlieren technique, while effective for detecting density gradients, proved sensitive to optical disturbances and was not sufficient on its own to fully resolve the complexity of the flow field at this scale.

Future work should therefore focus on integrating complementary measurement techniques, such as particle image velocimetry (PIV) or tomographic methods, to obtain quantitative flow field data and improve spatial resolution. Additionally, extending the support-based locomotion framework to larger datasets and combining it with force estimation or adhesion measurements could provide deeper insight into stability mechanisms and control strategies in insect locomotion.

Overall, the results contribute to a more comprehensive understanding of honeybee flight and locomotion, bridging kinematic analysis and flow visualization, and offering perspectives relevant to both biological research and the development of bio-inspired aerial and climbing systems.

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