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How aphids fly: Take-off, free flight and implications for short and long distance migration

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Abstract

1. An introduction to high-speed photography and its entomological impact is provided, emphasizing the importance of high frame rates and high resolution.

2. The take-off and free flight of *Drepanosiphum platanoidis* and *Myzus persicae* were studied in still air using high-speed photography in HD.

3. The wing tip and body posture were tracked to show how they are displaced during each wingbeat cycle. The important structural elements of the wing are described.

4. The wingbeat is driven by a reinforced leading edge, the pterostigma and costa. The remainder of the coupled fore- and hindwing acts as a single aerofoil that deforms during flight, due to sparse venation and a lack of cross veins.

5. During flight, aphids use a 'near clap and fling' mechanism with a body pitch close to 90°. Rapid acceleration about the thoracic lateral axis into wing reversal generates enough lift for take-off, typically within the first or second wingbeat.

6. Unique footage shows that aphids demonstrate a high degree of flight control and manoeuvrability in the lab, occasionally using forward and inverted flight, two flight modes that are otherwise poorly known.

7. While research into the impact of turbulent convection is needed, we posit that the strength of atmospheric forces presents a formidable challenge to aphid migrants. Above the flight boundary layer, migrating aphids may not easily oppose upwardly moving air, although if used, 'frozen flight' may cause them to descend on average.

8. We evaluate five devices for insect flight research.

KEYWORDS
body pitch, clap and fling, *Drepanosiphum platanoidis*, forward flight, frozen flight, high-speed photography, inverted flight, *Myzus persicae*, Phantom T4040, wingbeat

INTRODUCTION

The study of aphid migration lacks a complete understanding of the aerodynamic significance of flight behaviour, which includes wing displacements and postural changes of the body, legs and antennae. Flight behaviour clearly has a key role to play in driving primary and secondary virus and bacterial transmission into crops, an important topic that needs to be addressed for effective sustainable food production. Wootton (1996) provides the only interpretation of the aphid wingbeat cycle, albeit based on a poor quality video taken by J.S. Kennedy many years previously. Further research to quantify lift and thrust properties is needed to explain how aphids take off and fly, and how they accomplish short and long distance migrations, a topic that has preoccupied aphidologists for decades (Fereres et al., 2017; Loxdale et al., 1993; Parry, 2013; Taylor, 1965). Although some progress on flight behaviour and kinematics has been made within the

Heteroptera (Betts, 1986a, 1986b; Wootton, 1996), very little equivalent research has been conducted for aphids. This is surprising given the group's agricultural significance and ubiquity.

The title of this paper, 'How aphids fly', is inspired by the reference to a 16 mm film made in 1953 cited in Jensen (1956) entitled 'How locusts fly'. While there is an absence of a mechanistic understanding aphid flight, in terms of the drag, lift and thrust components (Sane, 2003), other areas have been well studied and include the analyses of functional anatomy of, and relationships between body size, wing loadings, wing venation, morphology, lipid metabolism and wing muscle structure, which together provide a useful foundation (Byrne et al., 1988; Cullen, 1974; Dixon, 1974; Dixon & Kindlmann, 1999; Franielczyk-Pietyra & Wegierek, 2017; Hassall et al., 2021; Kidd, 1991; Yao & Katagiri, 2011).

As a contribution to the special issue 'Advances in insect biomonitoring for agriculture and forestry', we provide a historical summary of the development of high-speed photography (HSP) and its role in research entomology. We then summarize the study of aphid flight behaviour to show that aphids are neither clumsy fliers, nor passive agents of the wind, but instead exceptional flying insects that are in control of their trajectories and movement within still air. We conclude with a summary of how HSP can inform biomonitoring.

A brief history of the emergence of HSP and its use in insect flight research

Dawson (2018) provides an excellent summary of the activities of Marey, Anschutz and von Ledenfeld that saw major advancements in the 1880s using a chronophotographic technique. Marey's 'chambre chronophotographique', akin to a cine camera, recorded images at 60 frames per second (FPS) but was easily surpassed by Lucien Bull's invention at the turn of the century. Bull's stereoscopic spark drum camera captured a muscid fly in 3D at more than 2000 FPS (Bull, 1904). Yet despite Bull's achievements and their limited use, stroboscopes would routinely be used to estimate wingbeat frequencies decades later (Wang, 2005; Williams & Chadwick, 1943; Wootton, 2020). From 1953, Torkel Weis-Fogh used HSP films in conjunction with stroboscopes and a drum camera to understand locust flight, although exact details of the frame rates are scant (Weis-Fogh, 1956; 1976). The capability to record images in excess of 10,000 FPS was achieved in 1959 when a recording of mosquito wing movements using a Fastax WFI high-speed camera at 16,000 FPS was made by UK Ministry of Defence at Porton Down (Propellants, Explosives and Rocket Motor Establishment, 1959). From the 1960s, HSP went from strength to strength. For example, Werner Nachtigall synchronized three cameras operating at 8000 FPS to record two blow fly species *Phormia regina* (Meigen) and *Calliphora vicina* Robineau-Desvoidy (Nachtigall, 1966). Nachtigall's use of HSP in entomology was closely followed by Weis-Fogh, whose contribution is significant, because he not only discovered resilin, the elastic energy store that powers the downstroke, but also the mechanism of lift generation (Weis-Fogh, 1960) that became known as the 'clap and fling',

captured in his study of the tiny parasitoid *Encarsia formosa* using a Hitachi HIMAC at 7150 FPS (Weis-Fogh, 1973). This laid the foundation for several world class research groups to emerge, including Charles P. Ellington at Cambridge, who demonstrated the use of a leading edge vortex on the downstroke, rejecting steady state dynamics (Ellington, 1984; Ellington et al., 1996), and Robin Wootton at Exeter, who has made major contributions to the understanding of flight in hemipterans and wing deformability in insects more generally (Wootton, 1981, 1996, 2020).

Current capability of HSP for kinematic and behavioural studies

Prior to the development of HSP, measurement of turning angles was not precise (Ellington, 1984); however, this limitation has been resolved by the current tranche of high-speed, high definition (HD) cameras (Appendix A), following 60 years of technological progress. Advancements in the capability of Phantom TMX 7510™ cameras, with 1.75 million FPS at 1280 × 32 pixel resolution, have led to the development of cameras with faster FPS, such as the iX Cameras Inc i-SPEED 727™ with 2.45 million FPS at 1280 × 800 pixels. Given insect research ideally requires HD to resolve complex wing movements, achieving a balance in tradeoffs among frame rate, resolution and aperture is an ever-moving target. For example, at 1280 × 800 pixels, FPS in the TMX 7510 drops to 76,000, while at HD 1344 × 978 pixels in the i-SPEED 727, there is a reduction to 20,000 FPS. Arguably, however, these lower FPS levels remain well in excess of those typically required since insect wingbeat frequencies range from 10 to 1000 Hz and are easily catered for by cameras that operate at 1000 (Farisenkov et al., 2022; Fang et al., 2023) to 5000 FPS (Ellington, 1984; Hürkey et al., 2023). Although full HD is desirable, the wider field of view offered by HSP also allows flight paths to stay within frame for longer.

Capability to record free flight in aphids using HSP

As stated by Kennedy and Booth (1963), observing aphids in free flight offers the most realistic way of observing natural flight behaviour, including turning angles and postural changes that are hampered by the use of flight mills (Ellington, 1984). Under laboratory conditions, a free flying alate aphid beats its wings at 100–200 Hz (typically <150 Hz for most species) and travels at speeds of 0.41–0.70 m/s when unassisted by strong convection or laminar flow. Herein, it is important to acknowledge differences in performance relative to differences in environmental stimuli, species, size and age (Cullen, 1974; Hardie & Powell, 2002; Hassall et al., 2021; Kennedy & Booth, 1963; Moore & Miller, 2002; Tercel et al., 2018; Thomas et al., 1977). At 76,000 FPS, more than 600 images are generated per wingbeat at 120 Hz, which represents an order of magnitude larger than that required by biologists for most experiments. Further, for *Forcipomyia* spp. (Diptera: Ceratopogonidae), which have the fastest wingbeat

frequency of any insect at 1046 Hz (Sotavalta, 1953), more than 70 frames are possible per wingbeat, which still allows for considerable insight into their flight behaviour. In this paper, we use descriptive and semi-quantitative methods, inspired by Nachtigall (1976) and Weis-Fogh (1976), to analyse HSP recording of take-off and free flight in two species of aphid with contrasting alate strategies and flight capabilities to increase understanding of flight behaviour in this economically important insect group.

METHODS

We analyse take-off and free flight in *Drepanosiphum platanoidis* (Schrank) and *Myzus persicae* (Sulzer) captured in seven HSP MP4 videos (Bell, 2023). We make no claim that these recorded flights constitute a formal, standardized experiment, since we imposed no control on the environment, the status of the aphids or the photographic arena. Yet, we believe that these images will be scientifically useful to lay the foundations for forthcoming full kinematic models of aphid flight.

Aphids

Drepanosiphum platanoidis (Schrank), the sycamore aphid, feeds on *Acer* spp, a monophyletic group of trees ancestral to Asia, but present in Europe for the last 30 million years (Gao et al., 2020). *Drepanosiphum platanoidis* has a growing global distribution and is now found on the west coast of Canada and in Australasia, where sycamore and maple trees are found. As one of the larger aphids (body length: 3.2–4.3 mm; body mass: 0.6–1.8 mg), *D. platanoidis* varies in size with generation, with a 1.8-fold greater wing loading in large summer migrants (wing length $\approx$5.25 mm) than small spring migrants (wing length $\approx$3.9 mm; Dixon, 1969). The summer generation has an exceptionally long adult life span of about 3 months and retains the ability to fly throughout (Dixon, 1969; Haine, 1955).

Myzus persicae (Sulzer), the peach potato aphid, is a medium sized aphid (body length: 1.8–2.1 mm; fore- and hindwing lengths: 3.08 and 1.89 mm, respectively; body mass: 0.33 mg; Byrne et al., 1988). The aphid is extremely polyphagous and a global pest, capable of feeding upon nine host plant species within a lifetime (Mathers pers comm.; Mathers et al., 2017). *Myzus persicae* utilizes both sexual (holocyclic) and permanent parthenogenetic (anholocyclic) reproduction, as well as possessing a strong migratory urge (Bell et al., 2015; Hemming et al., 2022). Unlike *D. platanoidis*, *M. persicae* has a limited adult flight period of up to 5 days, depending on temperature (fundatrigeniae: 3.61 days; alienicolae: 2.36 days), due to wing muscle autolysis, (Johnson, 1953; Woodford, 1968).

We sourced *D. platanoidis* locally from sycamore trees at the Rothamsted Research estate, UK (51.8089° N, 0.3566° W) from August to October 2023, while *M. persicae* was derived from a sugar beet culture infected with beet yellows virus, a circulative but non-propagative virus that does not affect flight muscles, only the gut and accessory salivary gland (Brault et al., 2010).

High-speed camera

After comparison with other available HSP cameras, we selected the Phantom™ T4040, due to its superior resolution and higher frame rate, with only small trade-offs in resolution (Appendix A). We operated the camera at 9350–13,000 FPS and 4.2-Mpx resolution (2560 × 1664), with aspect ratios ranging between 2048 × 1280 and 2560 × 1664 pixels. Videos were captured using the Phantom Camera Control software (PCC) as Cine RAW files that were subsequently converted to MP4 for analysis and viewing in slow motion. Time is recorded in milliseconds (msec) and embedded in the MP4 files. Filming at high FPS and in HD requires specialist flicker-free high-speed illumination lighting: we used two GSVitec™ MultiLED MX that each produced 12,000 lx of white light. Although we recorded multiple videos for the two species over several weeks, two and five remained in focus and were biologically useful for *M. persicae* and *D. platanoidis*, respectively (Bell, 2023).

Analysis

To understand flight behaviour, we tracked the tip of the wing between the terminating veins R_s and M_1 (Figure 1). To visualize lift generation, we tracked the centre of the mesothorax that carries the forewings and midlegs and compared the trajectory relative to the horizontal plane. Tracking to indicate periods of acceleration, deacceleration, rotation, supination, pronation and displacement was performed in Tracker (https://physlets.org/trackerv6.1.5). Body and wing calculations for body pitch and wing stroke plane are as per Weis-Fogh (1956, Figure II, 2). Since we did not calibrate the setup, we do not directly refer to absolute speed values and distances, but relative measures.

DISCUSSION AND RESULTS

How aphids fly

Like many other insects, aphids use an oblique stroke plane that induces the wing to move faster relative to the air on the downstroke, exploiting non-steady aerodynamics during pronation and supination. This strategy generates sufficient rotational lift and thrust to take off and remain aloft (Dickinson et al., 1999; Ellington, 1984; Sane, 2003; Wootton, 1999), despite sparce venation, a lack of cross veins and corrugation, which would otherwise provide structural reinforcement (Wootton, 1996).

The wingbeats for *M. persicae* and *D. platanoidis* follow a 'near clap and fling' (Sane, 2003) during take-off and free flight (video 1: Bell, 2023). In the only other high-speed video of aphid flight that we are aware of, Wootton (1996) was unable to confirm whether or not the wings made contact; however, the videos presented here show very clearly a lack of contact between the wings. At the start of the first downstroke at take-off, the forewings in the two species are
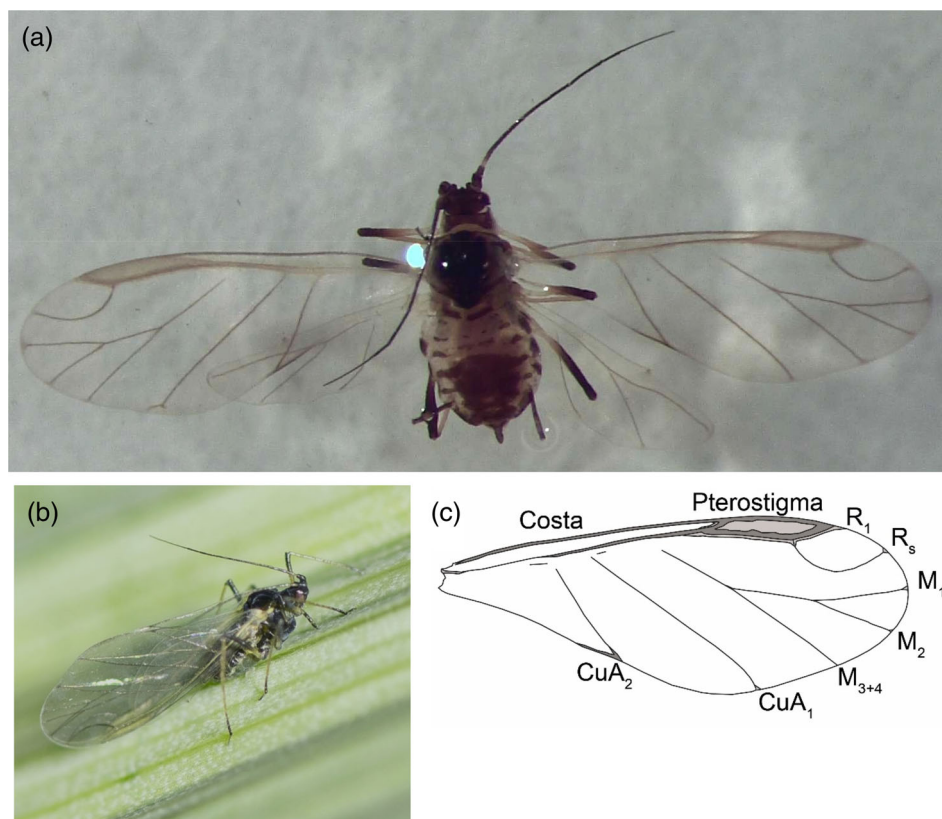
FIGURE 1 *Myzus persicae* forewing, hindwing and body (a), posture at rest (b) and annotated wing venation (c). The pterostigma and costa, both of which are reinforced with additional sclerotized chitin, represent the leading edge of the wing (Franielczyk-Pietyra & Wegierek, 2017). The function of the pterostigma is to dampen wing vibration amplitude (aeroelastic flutter), by positioning its large mass concentration in a forward position, leading to greater potential flight speed, due to increased wing efficiencies (Norberg, 1972; Song et al., 2020). The costa–pterostigma, the leading edge that is responsible for driving the up- and downstroke, is highly correlated with fundamental frequency (wingbeats per second), and may sometimes generate enough energy to be loud enough to also represent the dominant frequency (Hassall et al., 2021; Sueur et al., 2005). The cross veins, which would act as structural reinforcements, are missing. The connections between CuA_1, CuA_2, M_{3+4}, M_2, and M_1 to the costa are absent, indicating these are 'false' veins that likely receive no haemolymph. The cup-shaped radial vein R_s and the concealed R_1 may also lack any connection, but this needs further investigation. Compared with all other winged insects, with the exception of thrips, aphids lack thoracic accessory pulsatile organs, the so-called additional 'hearts' that pump haemolymph into 'true' wing veins (Salcedo & Socha, 2020); this is likely due to the presence of 'false' veins that may only act as reinforcement elements, rather than 'true' haemolymph-receiving wing veins (Franielczyk-Pietyra & Wegierek, 2017). Generally across aphid species, wing length is expected to be inversely related to wingbeat frequency (Mercer, 1979). Wing illustration of *M. persicae* originally drawn by Kelly Jowett for Hassall et al. (2021) but adapted for this paper.

positioned very close together, but do not touch, in a strategy that is argued to generate aerodynamic benefits (Sane, 2003). For *D. platanoidis*, the wings are then driven downward at a stroke angle of 30°, which begins the creation of a leading edge vortex that generates lift (Figure 2). The subsequent upstroke returns as an arc, initially rather shallow, at a stroke plane of 54°, and accelerating through a steeper angle of 16° relative to the vertical axis that most likely generates much of the thrust component along with a smaller amount of lift. The wing then returns to the point of pre-pronation to finish the upstroke. In *M. persicae*, there is a steeper first downstroke plane (66°), perhaps as a function of the shorter wing length relative to the body, which becomes increasingly shallower and more arced through downstrokes 2–4. The supination that induces wing rotation at the start of the upstroke becomes more pronounced in the 4th upstroke than the 1st (Figures 3 and 4). In the second upstroke, sufficient lift

was generated for take-off at the midpoint, shortly after wing rotation (Figure 5). The time ratio between downstroke and upstroke indicates a slower upstroke progression.

Among insects, hemipterans uniquely possess both indirect (asynchronous) and direct (synchronous) flight muscles. Indeed, a study of *Brevicoryne brassicae* (L.) and *Macrosiphum rosae* (L.) concluded that the main power-producing flight muscles comprise the indirect asynchronous, fibrillar myofibrils (i.e., dorsal longitudinal, tergosternal and oblique dorsal muscles) that drive the two pairs of coupled wings, whereas less than 10% of the power for flight is produced by the direct flight muscles (basalars and subalars; Cullen, 1974).

Although not observed in our study, aphids are known to change their mass and, therefore, their speed by ejecting honeydew before take-off. For example, the sycamore aphid *D. platanoidis* that excretes up to 84 μg of honeydew (≈5% of total body weight; Mercer, 1979).
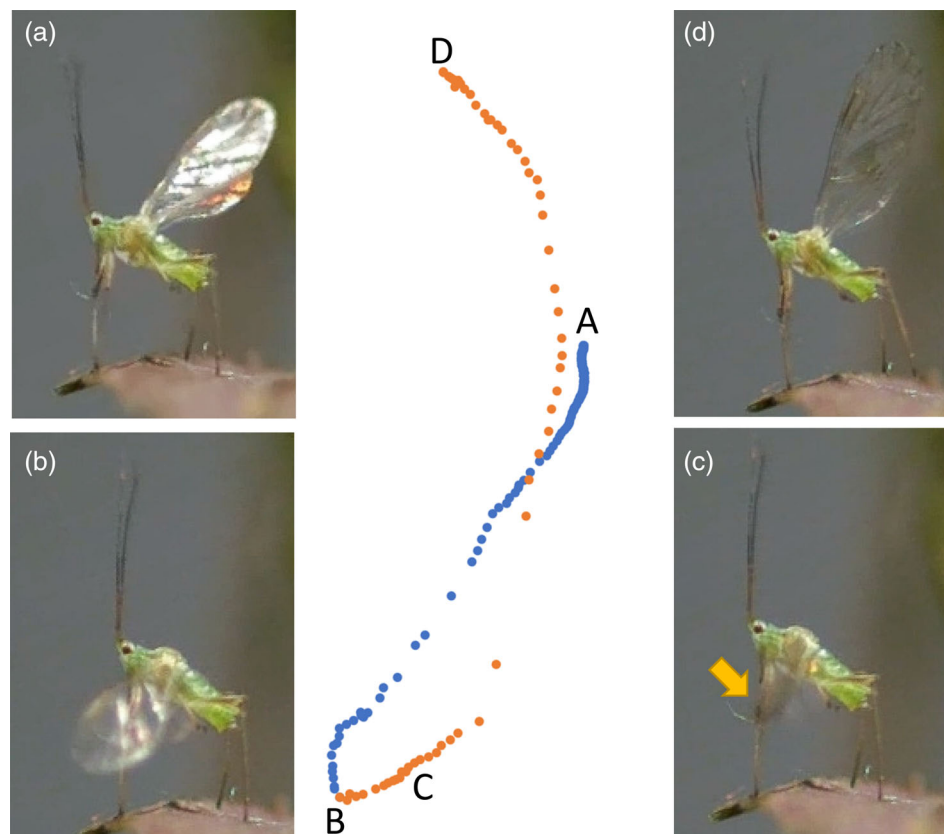
FIGURE 2 A dot plot of *D. platanoidis* wing tip trajectories at key stages through the first wingbeat cycle prior to take off (inset), accompanied by plates at their reference position along that trajectory (a–d). The tip of the wing between the terminating veins R_s and M_1 (Figure 1) was tracked, using cartesian coordinates (coloured dots) through frames 1–225 at >25 msec; blue dots indicate the downstroke (stroke plane: 30°) that generates most of the lift, and orange dots indicate the upstroke (stroke plane: 9°) that generates most of the forward thrust. Downstroke time was 2.8 times slower than upstroke time. (a) The start of the downstroke with wings in a semi-erect position (frame 0; 0 msec). In the region of the thoracic lateral axis, the wing then passes through a rapid phase of acceleration, indicated by the seven well-spaced blue dots. (b) At the onset of the upstroke, soon after a deceleration phase, the wing begins to twist, ready for stroke reversal (frame 168; 19 msec). (c) Stroke reversal, when the whole wing is under active torsion and supination with considerable pressure changes about its surface. The camber of the wing is reversed, such that the distal part of the forewing has swung under the leading edge and the hindwing has been displaced beyond the first pair of legs (yellow arrow) and transverse ventral bending (curvature) of the wing along its length is also visible, due to extreme rotational and aerodynamics forces. The relatively high energy induced during this reversal and ventral bending process may be sufficiently loud enough to become the dominant frequency (Hassall et al., 2021; Sueur et al., 2005). Though difficult to observe due to the speed of movement, the costa–pterostigma falls slightly forward of the *z* axis, perpendicular to the thorax (frame 181; 20 msec). (d) End of upstroke, with wings in an erect position ready for pronation (frame 227; 25 msec). The wing has travelled through a rapid phase of acceleration soon after C to where the upstroke crosses the downstroke pathway. This phase may have generated enough lift for the rear tarsus to rise from the leaf surface. When reset for the next wingbeat, the wing follows a larger arc, because the forewings are re-positioned much higher over the thorax than the first downstroke during take-off (videos 2a and b, Bell, 2023).

During take-off, aphids must overcome the leaf boundary layer that can reach 10 mm in thickness, depending on wind speed, size, shape and surface density of trichomes of the leaf (Cahon et al., 2018). For most aphid hosts, leaf boundary layers are unlikely to be an issue because trichomes are small or non-existent, as was true in our study (Reynolds *pers comm*.). The longer trichomes of nettles and foxgloves, for example, may present a unique challenge, where aphids may need to generate more lift or climb to an elevated position to avoid boundary layer effects; this topic requires further research.

Most aphid flights, regardless of distance/duration, are diurnal and always employ an active flapping mode, with no gliding (Loxdale et al., 1993; Parry, 2013; Wootton *pers comm*). Once airborne, aphid flight duration may last between just a few seconds to several hours, as appetitive flight (trivial or station-keeping, moving between hosts no more than a few hundred metres) or long distance migration over tens or even hundreds of kilometres (Fereres et al., 2017; Loxdale et al., 1993; Parry, 2013; Taylor, 1965). These flight modes are distinguished by whether movement remains within the flight boundary layer (FBL; appetitive flight) or not (migration). Aphid flight within the FBL extends up to a height of 10 m, depending on weather (Taylor, 1974). Here, aphids can actively contribute to their own lift and control their speed and direction of movement, as required (Kennedy & Thomas 1974; Taylor, 1974). Aphids within the FBL may not travel far. For example, in a mass release of 30,000 radioactive
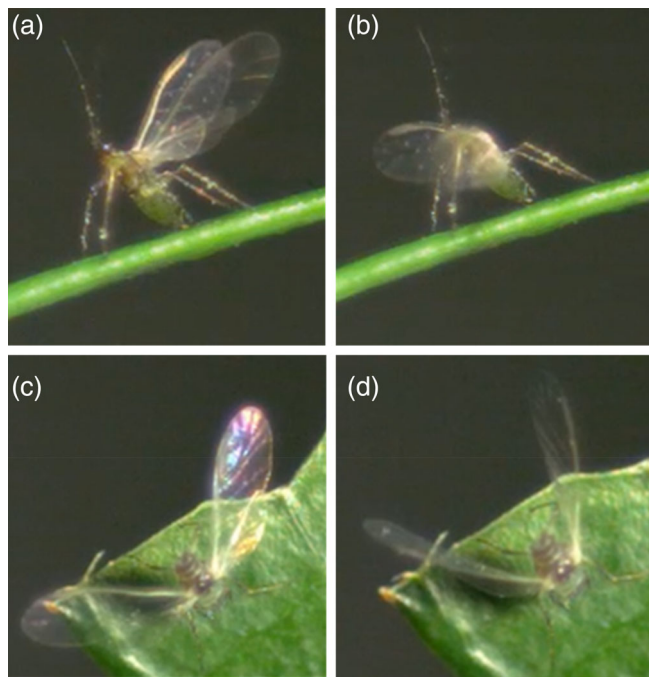
FIGURE 3 First wingbeat downstroke in *M. persicae* from lateral (a,b) and dorsal (c,d) perspectives. (a) Body pitch at 53° relative to the leaf stem at the start of first downstroke. (b) and (c) Completion of the first downstroke before wing reversal. (D): Supination, clearly showing transverse bending of the leading edge that is under torsion, and camber reversal of the distal part of the wing, as shown in Figure 2c (videos 3a and b, Bell, 2023).
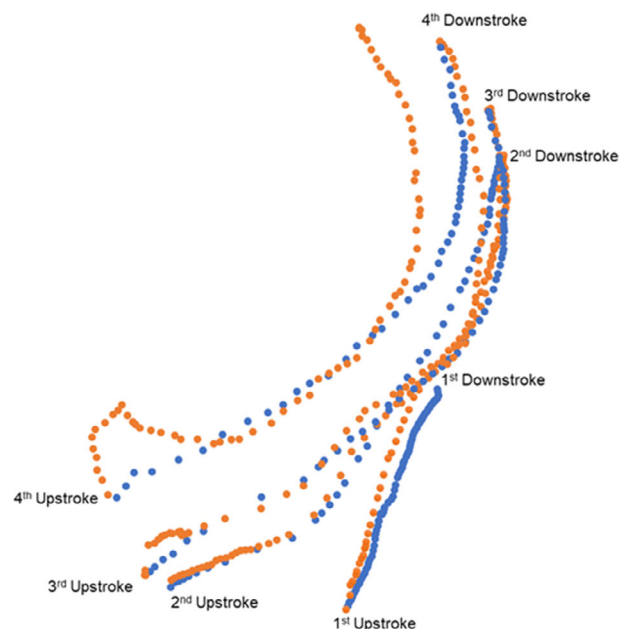

FIGURE 4 Dot plots of *M. persicae* wing tip trajectories during the first four down- and upstrokes, based on cartesian coordinates (Figure 3a,b). The tip of the wing, between the terminating veins R_s and M_1 (Figure 1), was tracked through frames 1–505 at 54 msec, where blue dots indicate the downstroke and orange dots represent the upstroke. The stroke plane increases from a shallow angle on the first downstroke (22°) and upstroke (20°) to steeper and more arced angles for subsequent upstrokes (29–33°) and downstrokes (35–39°). The first downstroke took the longest time to complete of all wing movements (9 msec), followed by more rapid movement in the subsequent three downstrokes (6, 6 and 5 msec), while subsequent upstrokes were generally slower than downstrokes (8, 7, 7 and 7 msec). Extrapolation of this sequence of wingbeats from time to frequency gives 74 Hz, which is slower than average during free flight (>100 Hz; Hassall et al., 2021). A stronger wing reversal phase appears to emerge at the start of the upstroke, particularly in the third and fourth upstrokes (video 3a, Bell, 2023).

M. persicae, Harrewijn et al. (1981) concluded that most individuals would have landed only 121 m from the take-off point, assuming that these individuals remained in the FBL.

Previous work has shown that, to take off, aphids typically orientate themselves directly into gentle winds of up to 1.2 m/s (Kennedy & Thomas, 1974); however, our HSP videos show that aphid flight is also possible in still air, seemingly without an orientation preference. For higher altitude flight used for migration, aphids undoubtedly require convection and turbulence to lift them above the FBL; here wind speeds can reach 80–110 km/h (Taylor, 1974; Wainwright et al., 2017). The widely held view for *D. platanoidis* is that small (size and mass), faster alatae may be better adapted for migratory flight than larger, slower individuals with higher wing loading, due to greater body mass and length of fore and hindwings (Byrne et al., 1988; Dixon, 1974; Kidd, 1991).

Implications for short and long distance migration

We found that aphids adopt an erect body posture during flight that induces a close-to-vertical stroke plane (Figure 4), consistent with observations by Johnson (1958) and Wootton (1996), albeit with shallower body pitches (65° and 30–50°, respectively), which may allow for greater flight duration, as argued by Mercer (1979) for *D. platanoidis* (body pitch: 30–50°). The erect body posture arises as a

consequence of slower flight speeds, leading to a more horizontal stroke plane (Ellington, 1984). Ristroph et al. (2013) showed that steep body pitches assist in flight stabilization, as shown for the woolly aphid (*Eriosoma lanigerum* (Hausmann)) and this remains true for larger insects when combined with hind leg extension, especially in turbulent air (Combes & Dudley, 2009).

The consequences of a horizontal stroke plane for aphid migration may be a compromise in control of upward flight capability, given a possible reduction in lift, particularly under turbulence. Reynolds and Reynolds (2009) argued that aphids are 'neutrally buoyant', later refined by Wainwright et al. (2017), who suggested that upwardly flying small insects do not keep pace with the air flow, but slow their ascent at a rate proportional to the updraft strength. Although undetectable in a single wingbeat (Figure 5), we posit that given the small degree of self-generated lift during aphid flight, overall flight control ability in convective, turbulent atmospheric conditions will be heavily compromised. This hypothesis is consistent with what has been observed for fruit flies, which experienced increased travel times and
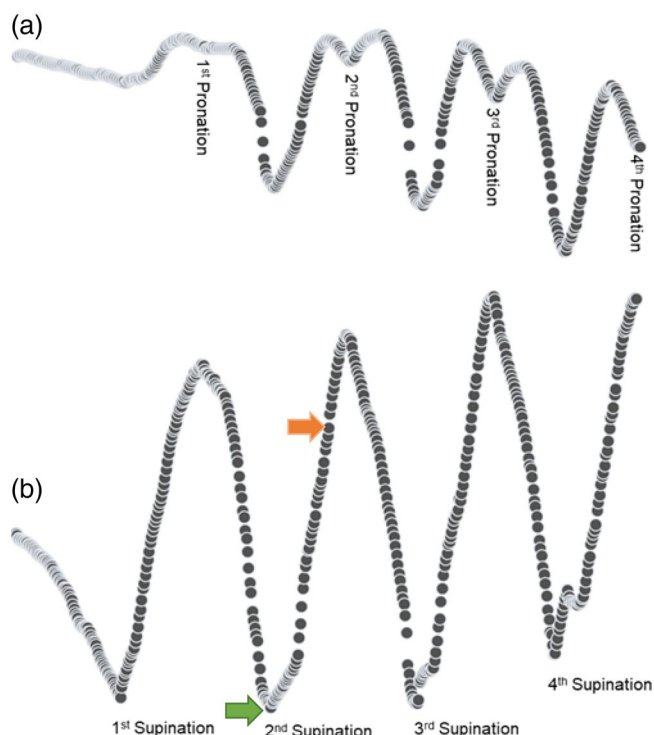
FIGURE 5 The first four down- and upstrokes for *M. persicae*, plotted as cartesian coordinates for horizontal (a) and vertical (b) movement of the wing tip (*y*-axis) against time (*x*-axis). The depth of pronation increases with each wingbeat (a,b), generating more power for the following stroke, and supination becomes more complex, in terms of wing reversal, with each upstroke. There is a small increase in wingbeat amplitude for the second, third and fourth wingbeats compared to the first, and there is a notable increase in acceleration from the second half of the downstroke to the second quarter of the upstroke, indicated by the greater spacing of the dots. At the bottom of the second downstroke, the back legs raise off the ground (green arrow) and by the midpoint of the second upstroke, *M. persicae* is already airborne (orange arrow; video 3a, Bell, 2023).

FIGURE 6 *D. platanoidis* during free flight with an increasingly high body angle from the horizontal with negligible changes in the centre of mass. (a) 47°; (b) 60°; (c) 78°; (d) 81°. With a body angle of 81° (vertical = 90° from the horizontal axis, *x*) shown in d, the stroke plane of 73° is almost horizontal (horizontal = 90° from the vertical axis, *z*) and may compromise upward movement, without assistance from external forces (convection, turbulence, light headwinds). During flight in still air, the aphid did not deviate from the horizontal plane (videos 4a and b, Bell, 2023).

higher energetic costs during turbulent convection (Ortega-Jiménez & Combes, 2018).

The question remains as to whether aphid movement is active or passive—more specifically, do aphids alter their behaviour to mediate movement, such as descent, or is movement an involuntary function of the strength of upward moving air and change in atmospheric conditions? Considering the possibility of active behavioural changes to initiate a descent, a control mechanism worth further consideration is an adjustment of body position. Given that we found this mediates a positive change in front leg elevation at the bottom of the downstroke (Figure 6); then, for example, during weak convection currents, aphids may depress their legs to induce a change in body pitch into forward flight, leading to greater control of downward movement. However, this may only be of negligible impact, even in the weakest of turbulent convection flows, but more research is needed. Another strategy for leaving upwardly moving air may be so-called 'frozen flight', as a state of immobilization that potentially allows aphids to fall at terminal velocities of between 0.82 and 1.78 m/s (Thomas et al., 1977).
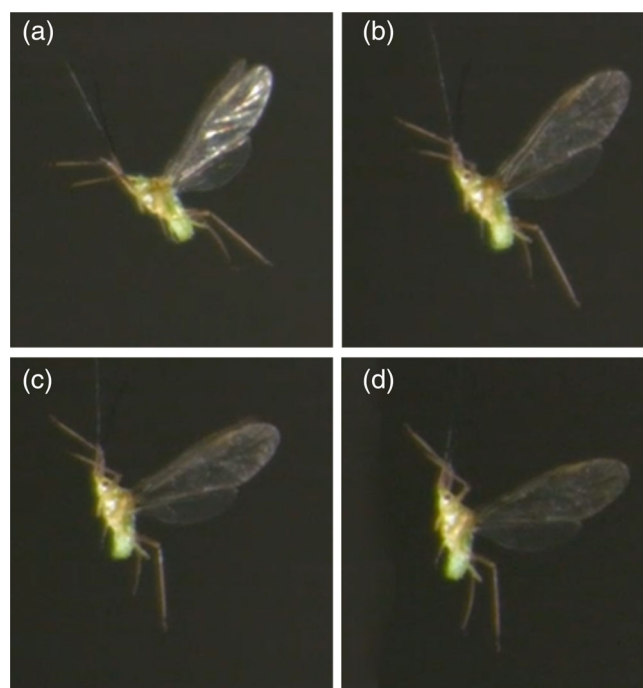
Limits of the study and future challenges

While many factors may have limited our study, we restrict our discussion to weather and atmospherics, natural conditions and flight time. We made no attempt to recreate natural conditions, such as representative light wavelengths and intensities, or conducive temperatures, humidity and atmospheric pressure. Hence, we did not observe flight behaviour under likely field-realistic atmospheric conditions. The still air in which we filmed the aphids is a rare phenomenon and unlikely to benefit migrant aphids that are more likely to move upwards beyond the FBL under turbulent convection in sunny conditions. However, HSP capture of aphids in flight in unstable air represents a major challenge, due to depth of field constraints, even under laboratory conditions. Thus, there is clearly a need to capture realistic aphid flight behaviours under simulated turbulent convection (Ortega-Jiménez & Combes, 2018). We suggest that tomographic particle image velocimetry, combined with use of multiple cameras and some focal serendipity, may deliver new insights into appetitive and migratory flight behaviours.

We restricted filming of aphids to the upper side of a leaf; however, the more likely take-off location on a plant is from the underside of a leaf, with only an occasional leap to the upper surface, as exhibited in a limited group of aphids (*Drepanosiphum, Eucallipterus*
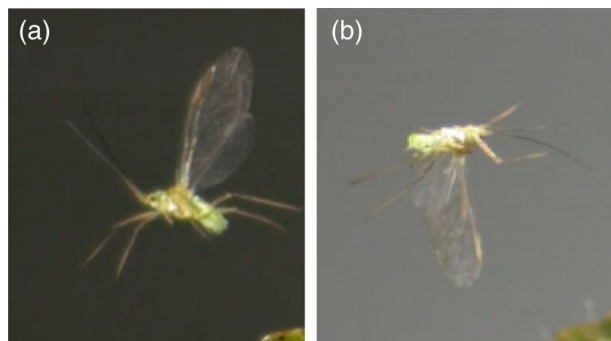
FIGURE 7 (a) *D. platanoidis* forward flight, at 68–80 msec. During this phase, no upward lift was detected, but there was evidence of a slightly downward movement, equivalent to about the width of the eye (<200 μm; video 4a, Bell, 2023). (b) Ventrodorsal flight, which does not appear to impact flight performance, although the change in centre of mass, where the wings, legs and antennae become closer to the ground, may induce a downward trajectory; this flight mode may only be used briefly, for distances <1 m (video 5: Bell, 2023).

and the Phyllaphidinae; Haine, 1955). While we show that aphids fly well during inversion (Figure 7b), indicating a capability to compensate for a range of take-off scenarios, we suggest further research to capture aphid behaviour on the underside of the leaf is needed to confirm whether alate aphids also roll into position by either turning their bodies or using a self-righting strategy into forward flight following vertical descent. It should be noted that as well as position on the leaf, host plant quality and aphid generation also affect rates of take-off (Dixon & Mercer, 1983). Although it is unclear whether HSP capture aphid flight behaviour well in the natural environment, the range of portable camera options currently available (Appendix A) make it more possible than ever before.

Our recordings of aphid flight were short bursts over milliseconds (msec), limiting our estimation of take-off speeds, changes in performance over time, such as wingbeat amplitude and maximum flight time duration, making it difficult to link our results with previous measurements (David & Hardie, 1988; Haine, 1955; Hardie & Powell, 2002; Kennedy & Booth, 1963; Mercer, 1979; Nottingham et al., 1991). Thus, it is our ambition to capture much longer duration flights using HSP to improve understanding of short and long distance migration behaviour to inform sustainable agriculture of the role of aphid flight in disease transmission.

Contribution of HSP to biomonitoring

HSP captures the flight performance of small insects in the lab that cannot be observed at the same resolution or frame rate by any other means. Consequently, HSP is essential to inform biomechanical models that require insight on kinematics as well as estimations of lift, thrust and drag. The energetic cost of flight can then be calculated under still and turbulent air, getting science ever closer to understanding the distances flown by aphid migrants (Parry, 2013).

Hassall et al. (2021) captured the harmonics of aphid flight yet was unable to indicate where on the wing higher frequencies were being generated. HSP can assist, capturing wing displacement while elucidating the impact of structural components (Rajabi & Gorb, 2020). Using HSP, we hope resolve whether wing harmonics are species specific and therefore whether they can be used to identify aphids in the field.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All videos have been made publicly available on Zenodo. Bell, J.R. (2023) How aphids fly: take off, free flight and implications for short and long distance migration. Zenodo. https://doi.org/10.5281/zenodo.10250517.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix A. Comparison of High-Speed Cameras for Entomological Research.

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