Tomographic particle image velocimetry of desert locust wakes: instantaneous volumes combine to reveal hidden vortex elements and rapid wake deformation

Richard J. Bomphrey1,*, Per Henningsson1, Dirk Michaelis2 and David Hollis3

1Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK
2LaVision GmbH, Anna-Vandenhoeck-Ring 19, D-37081, Göttingen, Germany
3LaVision UK Ltd, Grove Technology Park, Grove, Oxfordshire OX12 9FF, UK

Aerodynamic structures generated by animals in flight are unstable and complex. Recent progress in quantitative flow visualization has advanced our understanding of animal aerodynamics, but measurements have hitherto been limited to flow velocities at a plane through the wake. We applied an emergent, high-speed, volumetric fluid imaging technique (tomographic particle image velocimetry) to examine segments of the wake of desert locusts, capturing fully three-dimensional instantaneous flow fields. We used those flow fields to characterize the aerodynamic footprint in unprecedented detail and revealed previously unseen wake elements that would have gone undetected by two-dimensional or stereo-imaging technology. Vortex iso-surface topographies show the spatio-temporal signature of aerodynamic force generation manifest in the wake of locusts, and expose the extent to which animal wakes can deform, potentially leading to unreliable calculations of lift and thrust when using conventional diagnostic methods. We discuss implications for experimental design and analysis as volumetric flow imaging becomes more widespread.

Keywords: biomechanics; biomimetics; locust; aerodynamics; Particle Image Velocimetry; flight

1. INTRODUCTION

Our knowledge of how animals move through fluids has long been reliant upon theoretical work with experimental studies using animals trailing behind owing to the challenging proposition of directly observing fluid flows that are small in scale and highly time dependent [1]. This is particularly important in the realms of insect flight where those difficulties are at their most severe. The most established flow diagnostic technique for animals moving through fluids is particle image velocimetry (PIV). Recent increases in the power of financially viable lasers have contributed to an acceleration in our descriptive and quantitative understanding of the flows induced by beating wings, single-camera PIV and twin-camera stereo-PIV techniques that have been used to date yield either two-component or three-component vectors arranged on a two-dimensional plane through the animal’s wake (2D-2C, or 2D-3C). A particle-tracking technique has successfully been used to capture measurement volumes in water and applied to the hydrodynamics of fish swimming [2,3] but reconstructions of the three-dimensional wake structure of animals flying in air necessarily rely on the post hoc reconstruction of a pseudo-volume by stacking transverse (i.e. normal to the wind or water tunnel freestream) flow field planes that have not been captured simultaneously. If the ratio of wind tunnel speed to sampling frequency is very small, then plane-stacking may be reasonable because the displacement between successive imaging events is small and, between them, the wake will have had little time in which to deform. We can, therefore, be reasonably confident that the pseudo-volumetric data given by a stack generated under those conditions is a realistic representation of the animal’s wake. Sophisticated advection-based modeling has proved somewhat successful in artificially increasing the sampling rate of PIV data [4], but as wind tunnel speed increases, or if sampling frequency is relatively low, then the planes to be stacked become

*Author for correspondence (richard.bomphrey@zoo.ox.ac.uk).
more distant in time and space. Larger intervals decrease both spatial resolution in the stacking dimension and confidence in realistic inter-plane connectivity and cross-correlation analysis. Any further analysis based on derivatives of fluid displacement depends heavily on major assumptions that may not necessarily be valid under these experimental conditions. The most important of these assumptions is that there are no elements of the vortex wake that are missed because of inadequately low spatio-temporal resolution; the second most important assumption is that the wake has not deformed between consecutive slices in the stack. We tested these assumptions by measuring volumetric flow fields in the near wake of six desert locusts (Schistocerca gregaria), using the emergent volumetric imaging technology, tomoscopic PIV (tomo-PIV) [5,6], and generated the most detailed, time-resolved, description of a flying animal’s wake to date.

2. METHODS
We conducted high-speed (1 kHz), volumetric (3D-3C) tomo-PIV experiments on tethered locusts flying in a low-speed wind tunnel (figure 1). The wind tunnel test section is 0.5 × 0.5 × 1 m and was equipped with four high-speed cameras (Photron SA-3, Photron Europe Ltd., West Wycombe, UK) for this study, synchronized by a high-speed controller (LaVision GmbH, Germany).

The flow was seeded with olive oil particles from a particle generator driven by compressed air (LaVision UK Ltd). Laser illumination (10 mJ, Litron Lasers LDY301, Rugby, UK) was delivered via a custom light guide that included three mirrors and a cylindrical lens that expanded the beam in one axis only. A long fourth mirror reflected the light sheet back through the volume of interest to ensure forward scatter into every camera. Defocusing the beam following its divergence over the field of view (the hindwing trailing edges were approximately 50 mm from the illuminated volume) at a body position speed of 3.3 ms⁻¹, which is the equilibrium flight speed of locusts [8]. The mean environmental conditions were 24°C, 987 mb and 20 percent humidity. Each individual was granted a few minutes to acclimatize to flying in the wind tunnel, and acclimatization was assessed by observing their adoption of the complete flight posture as defined by Weis-Fogh [14]. This posture has been shown in previous studies to correlate with weight-supporting flight [8,12,14].

We recorded 1.3 s sequences (limited by the camera internal memory) triggered during tethered flights each corresponding to ca 25 consecutive wingbeats (mean 25.1, range 17–31). Three-dimensional flow field volumes were reconstructed using only the first 20 modes identified from proper orthogonal decomposition (POD) analysis. Reconstructions contained 73 per cent of the energy in the flow fields, the remaining energy was largely confined to the periphery of the volumes, where erroneous vectors become more common owing to deteriorating laser intensity outside the region of interest, resulting from the approximately Gaussian intensity distribution of the elliptical shaped illumination. The wingbeat frequency of each individual was also extracted from the POD analysis of the flow vector fields. The dominant frequency was used to generate a generic phase-averaged wingbeat of sequentially captured wake volumes for each locust in order to gauge intraspecific variation. For subsequent visualization, consecutive volumes were translated 3.3 mm based on the ratio of freestream convection speed to sampling frequency (displacement = 3.3 ms⁻¹/1000 s⁻¹).

3. RESULTS
3.1. Vortex wake structure of locusts
Figure 2 shows the phase-averaged vortex wake of a representative locust individual with Q-criterion iso-surfaces used to mark the presence of vortex cores.
Figure 2. The vortex wake of a desert locust (L6) reconstructed from a series of cuboidal fluid volumes captured immediately downstream and phase-averaged over 30 wingbeats. Within each small, instantaneous volume the long axis represents a true spatial dimension. Successive instantaneous volumes have been moved downstream, based on flight speed, such that the axis also represents a conversion of time to streamwise distance in accordance with the Taylor hypothesis. Iso-surfaces of $Q = 0.007$ are coloured by vorticity in the freestream axis ($\omega_x$, the direction of flight: right to left). The wake shown extends from the sagittal plane outboard to the right of the animal. See body text for further explanation of key structures.

(\(Q = 0.007\)). The \(Q\) value is the second invariant of the rate of deformation tensor and becomes positive when the Euclidean norm of the vorticity tensor becomes greater than that of the rate of strain and can be used to identify vortex cores [18]. The surface colours denote the vorticity component anti-parallel with the freestream ($\omega_x$). The structure is repeated to show two wingbeat periods: only the right half of the locust’s wake is shown as the animal flies from right to left. The wake shed from the fore- and hindwings of desert locusts is a complex arrangement of vortical structures dominated by strong tip vortices shed from the broad hindwings (figure 2; a). A smaller, transverse, vortex element—linked to the tip vortex—is shed more or less horizontally as circulation around the hindwing grows at the start of the downstroke (figure 2; b). That, in turn, connects to a root vortex that is clearly visible before it inflects inboard and joins the body at mid-downstroke (figure 2; c). The remainder of the hindwing downstroke wake is a single tip vortex showing strong positive loading on the wing that persists past the point of maximum ventral excursion and into the early stages of the upstroke (figure 2; d).

During the upstroke, the hindwing sheds a vertically oriented vortex element into the wake. The position behind the end of the downstroke tip vortex is indicative of the wing’s rearward sweep at a velocity faster than the freestream following supination and the tip’s subsequent dorsal progression being coincident with a rearward sweep at a speed matching the freestream (figure 2; e; cf. fig. 3.4, 3.6 of [13]). Between these vertical vortices generated by the contra-lateral wings, momentum is added in the direction of the freestream, producing thrust. The rearward sweep of the wing reaches its maximum posterior excursion before its maximum dorsal excursion [16], and this leads to an elegant arc of the trailing wingtip vortex at the end of the upstroke (figure 2; f). The negative loading experienced by the wing at this point continues past the maximum vertical excursion of the tip and then rapidly ceases following commencement of the downstroke.

The forewings also shed tip vortices during the downstroke (figure 2; g), although the fore and hindwing wakes differ in that there is no evidence for root vortices from the forewing. The forewing upstroke, too, shows evidence of negative loading, and a second tip vortex arc is clearly visible as the wingtip passes the highest dorsal point on its trajectory, giving rise to a pattern not dissimilar to that shown by measurements of locust wing tip trajectories [13,19] (figure 2; h).

3.2. Aerodynamic structures in relation to wing stroke kinematics and flight dynamics

Walker et al. [16] showed that, despite a rapid increase in angle of incidence (defined as the angle the chord makes with a horizontal plane) during the upstroke of both wings, the lift of attack (defined as the angle the chord makes with the local flow) remains negative. Indeed, during the upstroke, the angle of incidence can be as high as 40° or more for both wings, but the angle of attack always remains negative, and typically around $-10^\circ$ for both wings [16]. These negative angles of attack will inevitably lead to negative loading of the wings; so it came as no surprise to observe tip vortices present during the upstroke of opposite sense to the downstroke tip vortices (figure 2; f,a,g,h). That notwithstanding, the phase relationship between fore- and hindwings ensures that the interval in which negative loading is visible on both wings is typically very short because the forewing continues to produce positive lift when the lift from the hindwing becomes negative, and the hindwing begins to generate positive lift as the forewing completes its upstroke [15]. This accounts for the brevity of net negative lift production seen in force balance measurements [9], calculations based on flow measurements [12] and computational fluid dynamics simulations [15]. During the negative loading phases, the hindwings are elevated about the wing hinge greater than 60° above horizontal. Thus, much of the aerodynamic force will be directed laterally (and bilaterally symmetrically). The wings are also close to their maximum rearward excursion, and as such the downward component of the force (i.e. the negative lift) will be a significant contributor to the pitch-up moment observed at this stage of the wing stroke by Taylor & Zbikowski [9].

Periodic wing stroke kinematics give rise to corresponding periodicity in aerodynamic force generation. The
cyclical motion of the wing centres of pressure shifts the point of application relative to the body centre of mass, which in turn leads to modulation of pitch, roll and yaw torques. Because the longitudinal flight dynamics are already well-characterized \cite{9} and we have assumed symmetry in roll and yaw in this tethered flight experiment, we can use our data to understand the mechanistic basis of fluctuations in streamwise accelerations, vertical accelerations and pitch by correlating the timing of the shedding of aerodynamic structures with the measured forces and torques described previously. The majority of the downward-directed flow is induced during the hindwing downstroke (figure 3; a–d) with upward flow of small magnitude induced during the upstroke (figure 3; e). In contrast, backward-directed induced flow—augmenting the freestream velocity and contributing to thrust—occurs most intensely during the upstroke between the vertically aligned vortex structures (figure 3; e), although there is also a contribution to thrust throughout the downstroke. The period of the stroke cycle when drag is dominant is during pronation, i.e. the end of the upstroke and beginning of the downstroke (figure 3; a,f).

3.3. Short-lived root vortices in locust flight

The presence of upwash on the sagittal plane behind the thorax in the early stages of the downstroke was indicated in velocity transects described by Henningsson & Bomphrey (\cite{12}; fig. 3) but, perhaps surprisingly, in the early downstroke, there exists a distinct hindwing root vortex of strength comparable to that of the tip vortex. Given the relationship between diminishing chord length along the hindwing (a triangle to first approximation) and the increasing incident flow velocities outwards along the wing during the flapping motion (a function of radial distance from the wing hinge), it is quite possible that aerodynamic force builds at the tip first, and the more proximal areas later. This differential could introduce shearing of the flow between the higher induced velocities outboard and the slower moving air closer to the centreline of the animal, which ultimately rolls up into a coherent vortex.

Figure 4 shows the same phase-averaged locust wake (L6) but with the vorticity magnitude iso-surfaces coloured by vorticity either in the spanwise (figure 4a,c) or in vertical (figure 4b,d) axes. These visualizations of the flow are currently possible only by using a volumetric technique such as the one described here, and they highlight the structures that would be both well described (blue and red), and missed (green), by vertical and horizontal laser plane orientations, respectively, and a conventional two-dimensional or stereo-PIV approach.

3.4. Consistency in locust aerodynamics

Kinematic consistency between wingbeats is known to be very high in tethered desert locust individuals with correlation coefficients of fore and hindwing angles of incidence reaching 0.96 and 0.98, respectively \cite{16}. Consistency between individuals is also high, although variation in the trajectory of the forewing becomes apparent with inter-individual correlation coefficients of fore and hindwing angles of incidence reaching 0.84 and 0.95, respectively \cite{16}. Waller et al. \cite{16} also described higher variability in forewing angle of attack and camber than for the hindwing, both of which will lead to inconsistency in forewing force
production and corresponding wake strength. This is reflected in figure 5, where the wake is presented for all six locusts that were tested. The major features of downstroke tip vortices (orange/red) and counter rotating upstroke tip vortices (blue) appear in all cases. The strength of vorticity in the downstroke tip vortices varies somewhat between the strongest (figure 5; L6 and L9) and the weakest (figure 5; L3 and L5) but the greatest difference lies, as expected, in the strength of the forewing tip vortex, which is strong for L8, weak in L9, and entirely absent for L7, indicating variable aerodynamic activity of the forewing. (Specifically, colour variation reflects variation in vorticity in the axis of travel, while the absence of a core indicates that no vortex has been identified by the \( Q \)-criterion at the chosen threshold.) The spacing between the fore- and hindwing trailing vortices also differs between individuals, from almost merging (figure 5; L6) to being quite distinct (figure 5; L5, L8 and L9), reflecting variation in fore- and hindwing phasing. Note that the vortex wake shown in other figures is from locust L6. This is because L6 shows the most detail in terms of flow structure. Each of the others shows a reduced set of structures, yet exhibits no features that cannot be seen in the wake of L6. Furthermore, of all the locusts tested, L6 was the most consistent flier in terms of the correlation coefficients of the first two temporal POD modes (0.992 in both cases), had the largest mass (1.73 g) and high normalized lift (lift/weight = 1.48 calculated using an induced flow method described in [12]). The correlation coefficients for the first two temporal modes of each locust were always high (L3 (0.976, 0.973); L5 (0.976, 0.976); L6 (0.992, 0.992); L7 (0.826, 0.818); L8 (0.985, 0.982); L9 (0.991, 0.990)).

4. TOMOGRAPHIC PARTICLE IMAGE VELOCIMETRY

4.1. Volumetric wake imaging

Tomo-PIV allows us to optimize vector resolution in all three Cartesian dimensions. Moreover, it decouples the effects of sampling frequency and wind tunnel speed that can lead to the omission of vortical structures when during data processing.
stacking conventional two-dimensional or stereo-PIV planes. The likelihood of missing wake elements increases as the angle they make with the measurement plane decreases or if the wind tunnel speed is high enough that consecutive measurements are separated by convection distances that are comparable with, or greater than, vortex core diameters. Both of these factors are important in these locust flow field reconstructions and would be limitations of wake reconstructions built from conventional stereo-PIV data plane stacking. Specifically, the transverse vortex element linking the hindwing tip and root vortices formed during the acceleration phase of the downstroke would be undetectable because it is less than 10 mm in diameter (figure 2; b). Similarly, the tip vortices of the hindwing upstroke would be lost between successive sampling planes because they are oriented vertically and less than 6 mm in diameter (figure 2; e). The small size of these elements gives rise to just two or three adjacent vectors, which is insufficient to resolve their structure. The hindwing tip vortices formed during negative loading on the upstroke establish a portion of the wing stroke that contributes significantly to thrust, and the mechanistic basis of this would have remained unclear without the use of fully volumetric imaging. The power of the tomo-PIV technique was increased through the use of POD and phase-averaging, which was ideally suited to this analysis because of the high repeatability of locust wingbeats. Two wingbeats of time-resolved tomographic reconstructions are compared with the 20-mode POD, phase-averaged reconstruction in the electronic supplementary material showing the elimination of non-periodic features and the retention of detail in the vortex wake.

4.2. Wake deformation

Reconstructing the full wingbeat period from smaller, overlapping, instantaneous volumes reveals details of wake deformation. It can be seen from figure 6 that the vortex iso-surfaces do not always align. Perfect alignment could be expected only if the following three assumptions are met: (i) that the size and strength of the vortex core remains consistent from one instant to the next, with vorticity dissipating at a constant rate, (ii) that the induced velocities do not lead to translational propagation of the vortex core, and (iii) that the point of trailing vortex shedding—e.g. the wingtip—remains stationary or maintains a fixed velocity relative to the freestream. In reality, none of these assumptions is met. In the time-dependent case of insect wing motion shown here, deviation from seamless overlap of the adjacent volumes provides information about the nature of vortex dynamics and deformation of the wake as a whole. For instance, the mean angle of the iso-surfaces within each sampling block do not align with the overall gross angle of the trailing vortex of which it is part (figure 6). This discrepancy belies the difference between the angle at which that wake element is shed and the direction of its self-induced motion. Thus, a portion of the trailing wing tip vortex that is shed during the downstroke, and ostensibly horizontally, will travel ventrally as a result of the induced flow behind the animal. This translation causes an offset between iso-surfaces of the same structure in successive images. Similarly, the downward movement of the wing can have a corresponding effect. Hypothetically, the trailing vortex could again be shed largely horizontally, but the next image comes from a subsequent time interval when the wing has progressed further through the downstroke, and therefore sheds that portion of the vortex lower than the previous one. The aerodynamic loading on the wing and its direction of travel can combine additively to make the effect strong or weak but, if present, the result will be the ‘stepped’ effect in vortex core topography that can be seen in figure 6. As expected, the wake structure does not, therefore, comply with the Taylor hypothesis of frozen, homogeneous, turbulent wakes, which states that the temporal distribution of fluctuations in flow velocity matches the instantaneous spatial fluctuations [20] despite the conversion of time to streamwise distance being a prominent feature of the literature.

A hypothetical, and simplified, single loop wake topology behind a two-winged animal flying at low speeds is shown in figure 7. Here, a single vortex loop is shed from the two wing tips as they pull apart and the wings progress from a position held closely together, dorsally, to a position at the end of the downstroke that is swept forward (figure 7a). The loop is shown in profile in figure 7b; so it resembles a rectangle with rounded ends, and the elements of the loop that are shed first convect downwards and backwards relative to the animal. The result of this convective wake deformation is such that, by the end of the downstroke, the plane of the loop does not match the stroke plane angle, but has instead become horizontal. This arrangement is not dissimilar to the vortex wake dynamics measured behind a tethered tobacco hawkmoth [21].

The implications of changes in the wake geometry on the correct calculation of aerodynamic forces are significant, systematic and potentially dramatic, depending on the type of image acquisition and subsequent analysis that is employed. Figure 7c shows the hypothetical result of small-volume high-speed tomo-PIV—the
method we present here. The wake is divided akin to a loaf of sliced bread: each slice represents an instantaneous volumetric measurement that incorporates only the integrated time history between the shedding event and the measurement plane. The effect of time history is lessened by decreasing the distance between the animal and the illuminated volume. The contribution of each slice to instantaneous force generation can be calculated by applying standard aerodynamic theory to the unsteady, or quasi-steady, flow [22] and is illustrated throughout by dashed red arrows normal to the instantaneous plane of the loop element and corresponding vortex dipole. Figure 7d shows a single snapshot of the wake as would be captured by large-volume low-speed imaging at the end of the downstroke ($t = 6$). It becomes immediately obvious that calculation of a net impulse from the vortex ring once it has deformed during downstream convection can give rise to a misleading result. In this illustrative example, the contribution of the wing action to lift has been overestimated and the contribution to thrust has been eliminated altogether. The lack of thrust in this idealized case is the expected result if there is no net acceleration—i.e. thrust balances drag. The effect highlights a fundamental difference between stacking measurement planes or volumes captured at subsequent time intervals, and the image one might acquire from large volume wake imaging [2,3]. Large volume snapshots necessarily incorporate the history of the wake as it contracts, convects and deforms with time in much the same way that smoke streak visualization does [23–25]. Stacked transverse PIV planes and volumes, on the other hand, reconstruct composite wakes that show much less influence of time, and can be a closer representation of the loading on the subject animal provided that the sampling plane is close to the aerodynamic surfaces [1].

Linear interpolation between measurement planes to create pseudo-volumetric data from two-dimensional or stereo-PIV data—rapidly becoming a standard practice in studies of animals swimming and flying—is shown in this example to have a systematic angular error that underestimates lift and overestimates thrust in comparison with the small-volume high-speed stereo-PIV result (figure 7e—where the force vectors from each method are overlain). In this case, the direction of systematic error is reversed from that of the large-volume low-speed method and, in addition, the interpolated wake structure is misshapen and has sections missing (most notable between $t = 5$ and $t = 6$, and between $t = 0$ and $t = 1$, respectively). These two error types are dramatically reduced, although never completely eradicated, if the image acquisition rate is high relative to the wingbeat frequency (so-called ‘time-resolved’ PIV).

The stepped effect shown in figure 7c between vortex core iso-surfaces in successive small volumes captured at high frequency can be used to gauge the degree of wake deformation that might occur during a wing stroke period. We can assume with some degree of certainty that successive iso-surfaces belong to the same structure, and that the most likely reality is that they will align. With that a priori assumption, we can shift the small-volume high-speed flow fields in the vertical axis to estimate the structure that would be seen using large-volume low-speed imaging or smoke streaklines. Because the surfaces will never align perfectly while using this method, the result is a compromise, only indicative of the direction of deformation (cf. figure 7f). Nevertheless,
The method also highlights a potential source of error in existing studies that use velocimetry to derive forces—principally lift and thrust—using animal wake morphologies. Even in the single axis of deformation considered here, the locust wake deforms considerably over just the downstroke period. Errors of this type have been alluded to previously [1,12,27] but seldom discussed in detail, and never quantified. Tomo-PIV is an instrumentation and computation-intensive technique, even for small volumes, and will not be possible in all cases. Nevertheless, wake force estimates should be routinely considered in the light of potential flow morphology deformation and quantified wherever possible.

The work was supported by an EPSRC Career Acceleration Fellowship to R.J.B. and EPSRC grant EP/H004025/1 to R.J.B. The authors thank the Oxford Flight Group for useful discussions on a draft, and acknowledge support in kind from LaVision GmbH and LaVision UK Ltd.

REFERENCES


7 Elsinga, G. E. & Westerweel, J. 2011 The point-spread-function and the spatial resolution of PIV crosscorrelation

Figure 8. Grey vortex wake: phase-averaged vortex wake of a desert locust reconstructed from stacking successive wake volume acquisitions. The coloured wake, coloured by vorticity in the freestream axis, \(\omega_x\), has been subjected to vertical (z-axis) realigned of the volumes, based on the largest vortex structures found in each volume to indicate direction of wake deformation. The primary structure (the hindwing downstroke trailing vortex: yellow/red) tilts from an original angle of 32° (representative of the angle at which it was shed) down to just 20° to the horizontal, raising concerns over impulse calculations from measurements of deforming wakes.

Figure 8 shows the result of vertically aligning adjacent wake volume iso-surfaces from the wake of a desert locust. At first glance, the effect appears to be relatively minor, but if we coarsely treat the hindwing downstroke loop as an isolated structure by way of example, the angle of its axis tilts by up to 12° during the wake deformation that operates over the short period of the downstroke. This highlights the need for time-resolved measurements, and for those measurements to be recorded in close proximity to the trailing edge of the animal so that the wake has had little time in which to deform. By way of an example, if the hindwing downstroke vortex loop—the most significant wake structure for the locust in terms of force generation—was captured one wavelength downstream (fewer than 10 hindwing mean chord lengths) and subsequently used in a simple vortex model to calculate lift to drag ratios or propulsive forces, then the results would be rather misleading. Indeed, because the hindwing downstroke loop becomes more horizontal (and the jet oriented more vertically downwards), lift would be overestimated at 111 per cent and thrust underestimated at just 65 per cent of the real value. The issue is further complicated by considering wake elements other than the largest observed vortex structure (for example, the negatively loaded upstrokes generate vortex loops that will convect upwards rather than downwards—akin to the inner and outer portions of the bat wake described in Johansson et al. [26]), and by taking into account deformations in other axes resulting from spanwise and streamwise convection. On the basis of the hypothetical example in figure 7, these substantial errors are likely to be less than the true effect.

5. CONCLUDING REMARKS

In summary, we used the new technique of tomo-PIV to measure flow fields in the wake behind six desert locust individuals and captured the complexity of the three-dimensional wake structure in unparalleled detail. With the enhanced resolution we were able to achieve, previously unseen sections of the vortex wake were discovered.
methods. In 9th Int. Symp. on Particle Image Velocimetry—PIV’11, Tsukuba, Japan, July 21–23.


