1. INTRODUCTION

Any flying device, whether it is an insect, a bird, a bat or a man-made aircraft, generates lift with a certain efficiency. Lift is generated when wings create a pressure differential, causing air to be accelerated normal to the incident flow, commonly referred to as the induced flow. The power required to generate a given lift force, known as the induced power, depends on the aerodynamic performance of the wing (and body) of the flying device. An ideal planar wing with an elliptical loading distribution produces a constant induced flow across the span, resulting in the minimum possible induced power. Deviation from the ideal loading distribution—inevitable for a real wing—will result in an increase in induced power because while the momentum imparted to the wake is equal to the product of mass and velocity (p = mv, where m is the mass of the air and v the velocity of the air), the kinetic energy required is $E_k = mv^2/2$. For an uneven distribution, slower velocities anywhere across the span need to be compensated for by higher velocities elsewhere and thus the square term in the kinetic energy equation means that the energetic cost for the same momentum is higher (e.g. [1]). There are two ways of determining the effect of an uneven downwash distribution on span efficiency, either from actuator disc theory [2,3] or lifting line theory [4]. The former leads naturally to the induced power factor, $k_{ind}$, and the latter to the inviscid span efficiency, $e_i$, but one is the reciprocal of the other (for a thorough description of these, see [5], and for how they are related, see [6]). To date, several models of animal flight have been based on actuator disc theory (e.g. [6–9]). These models have assumed an even induced flow and elliptical loading distribution and, latterly, to account for the fact that the wings of the flying animal were performing less well than an ideal wing, the induced power factor, $k_{ind}$, has been included to adjust the estimate of the animals’ performance. However, the value of $k_{ind}$ has hitherto been largely unknown and so has instead been chosen somewhat arbitrarily. Other studies have conflated the induced power with wing profile power to create ‘wing aerodynamic power’ based on kinematic parameters of the wing stroke. These are summarized by Lehmann [10]. Most recently, wind tunnel experiments using a bird [11] and two bats [12] have estimated wingbeat-averaged values of span efficiency based on measured downwash distributions. Bomphrey et al. [6] made the first attempt to measure the induced power factor on a live animal (the desert locust Schistocerca gregaria, Forskål) in flapping flight by quantifying the deviation of the measured downwash distribution from that of an ideal wing. To measure the distribution of induced flow behind the flying locust, Bomphrey et al. used particle image velocimetry (PIV), with a repetition rate of 15 Hz, to visualize the flow. In that study, the sampling rate was slower than the wingbeat frequency, necessitating that only a single moment within the wingbeat was measured, mid-downstroke and the induced power factor at that instant was found to be $k_{ind} = 1.12$, corresponding to a span efficiency of $e_i = 0.89$. PIV has been used in several studies of aerodynamics in animal flight over the last decade (e.g. birds, [13]; insects, [14]; bats, [15]), but recently techniques have been improved by developments in high-speed cameras, laser equipment and software. Now, time-resolved wake measurements are possible, so-called because the sampling frequency is several times greater than the wingbeat frequency. For example, this is possible for locusts, a species with a low wingbeat frequency which generates most of its lift via downstroke [16]. The locusts are found to operate at a maximum span efficiency of 79 per cent, typically at a plateau of about 60 per cent for the majority of the downstroke, but at lower values during the upstroke. Moreover, the calculated span efficiencies are highest when the largest lift forces are being generated (90% of the total lift is generated during the plateau of span efficiency) suggesting that the combination of wing kinematics and morphology in locust flight perform most efficiently when doing the most work.
frequency, allowing for the description of aerodynamic events within the wingbeat period (e.g. birds at 200 Hz, [16]; bats at 200 Hz, [17,18]). For this study, a 1 kHz PIV system was used giving approximately 46 image pairs per wingbeat cycle of the desert locust. This allows for a detailed examination of how aerodynamic performance varies over the course of the wingbeat. Flapping flight is energetically costly but desert locusts are well known for flying long distances and are therefore a suitable model species to study since one might expect them to be under significant selective pressure for efficient flight. Locusts are also readily available from bred populations and are known to fly well in a wind tunnel (e.g. [6,19–22]). Knowledge of the performance of desert locusts over the entire course of the wingbeat will give us deeper understanding of the complex flow physics of flapping flight. In turn, that insight will provide design guidelines for wing shape and kinematics of flapping micro-air vehicles that can reduce power requirements and increase range or aerobatic performance. The method is also proposed as a basis for the quantification of a simple biomechanical metric of lift efficiency in flying animals that can later be used for interspecific comparative analyses. Here, the measurements of the induced flow distribution across the span and over the course of the wingbeat are presented for five desert locusts and used to estimate the induced power factor, $k_{\text{ind}}$ and span efficiency, $e_i$.

2. MATERIAL AND METHODS

2.1. Desert locusts

A batch of 25 adult desert locusts were obtained from a breeder (Livefoods Direct, UK) and five of these were chosen for experiments based on their flight ability, wing condition and overall vigour. The locusts were rigidly tethered using cyanoacrylate glue onto a mount which could be positioned in the wind tunnel at a favourable location with respect to the measurement area. All locusts were tethered at a body angle of 8° with respect to the freestream flow, since this angle has been shown previously to be close to the pitch equilibrium angle and appropriate to encourage tethered flight in desert locusts [6,20,22]. All of the chosen locusts performed well in the wind tunnel. The criterion for judging that a locust was flying properly was the same as defined by Weis-Fogh [22]—fore- and middle legs drawn up, antennae stretched obliquely forward and abdomen pointing straight backwards. This posture has been shown in previous studies to be the ‘complete flight posture’ of locusts and suggests that they are in weight supporting flight [20,22]. The wind tunnel speed was set to 3.3 m s$^{-1}$ which is the equilibrium (or preferred) flight speed of locusts [20]. Morphological details of the five locusts are presented in table 1.

2.2. Particle image velocimetry

Flow field areas of approximately 150 × 150 mm were recorded using two high-speed CMOS-sensor cameras (Photron SA3: 1024 × 1024 px; 2000 fps, Photron Ltd, Bucks, UK). The cameras were equipped with 50 mm lenses (AF Nikkor 50 mm, f/1.8) set to aperture 1.8 and mounted on Scheimpflug adapters. The wind tunnel was seeded with a thin mist of olive oil from a compressed air aerosol generator (LaVision UK Ltd) located at the inlet upstream of the fans, settling chamber, contraction cone and the test section. The oil mist was illuminated by a 10 mJ laser (Nd: YLF, 527 nm, Litron LDY-300PIV; Litron Lasers Ltd, UK) producing pulse pairs with a repetition rate of 1000 Hz and a pulse separation interval of $\Delta t = 150 \mu$s. The laser beam was delivered via three 45° mirrors from the exit of the laser head to the sheet optics located above the test section (figure 1). The sheet optics chassis

<table>
<thead>
<tr>
<th>individual</th>
<th>mass (g)</th>
<th>forewings span (mm)</th>
<th>area$^a$ (mm$^2$)</th>
<th>aspect ratio</th>
<th>hindwings span (mm)</th>
<th>area$^a$ (mm$^2$)</th>
<th>aspect ratio</th>
<th>wing loading$^b$ (kg m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.41</td>
<td>93</td>
<td>633</td>
<td>13.7</td>
<td>84</td>
<td>1202</td>
<td>6.1</td>
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<tr>
<td>2</td>
<td>2.13</td>
<td>98</td>
<td>704</td>
<td>13.8</td>
<td>92</td>
<td>1343</td>
<td>6.6</td>
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<tr>
<td>3</td>
<td>2.66</td>
<td>96</td>
<td>672</td>
<td>13.7</td>
<td>90</td>
<td>1290</td>
<td>6.4</td>
<td>2.81</td>
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<tr>
<td>4</td>
<td>2.16</td>
<td>107</td>
<td>777</td>
<td>14.6</td>
<td>98</td>
<td>1322</td>
<td>7.4</td>
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<tr>
<td>5</td>
<td>2.17</td>
<td>109</td>
<td>741</td>
<td>13.7</td>
<td>94</td>
<td>1367</td>
<td>6.7</td>
<td>2.12</td>
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</tbody>
</table>

$^a$Area of both wings including body area in between.

$^b$Body mass divided by sum of both forewing and hindwing areas.
was equipped with a −10 mm cylindrical lens spreading the beam into a 2 mm thick sheet perpendicular to the freestream flow illuminating the oil particles in the measurement area.

The laser and the PIV cameras were controlled by Davis v. 7.2.2 software package and were triggered by a communal high-speed controller signal. The PIV cameras were calibrated with the built-in calibration routine in Davis v. 7.2.2 using a 105 × 105 mm dual plane calibration plate (LaVision, type 11). The calibration was further adjusted by means of the built-in self-calibration routine in Davis v. 7.2.2 which corrects for any remaining small misalignment between the calibration plate and the light sheet at the time of calibration.

Locusts, tethered to the mount, were placed in front of the transverse light sheet with a distance between the trailing edge of the hindwing and the light sheet of 40 mm, approximately twice the hindwing maximum chord length (or 1.5 times the combined fore- and hindwing maximum chord length). This was the closest possible position where the locust did not appear in the background of the PIV images and therefore no masking of the images was necessary.

The recorded PIV data were processed using Davis v. 7.2.2. Raw images were filtered by subtracting a sliding minimum over three frames. Vector fields were computed from the filtered images using multi-pass stereo cross-correlation starting with interrogation windows of 64 × 64 pixels, reducing stepwise to 16 × 16 pixels for the final pass. Vectors were considered erroneous if the magnitude was equal to or more than twice the neighbourhood root mean square (r.m.s.) and reinserted as interpolated vectors if the magnitude was less than three times the neighbourhood r.m.s. (closest neighbour vectors). Empty spaces were filled by interpolation (an average of all non-zero neighbour vectors) and the final vector fields were subject to a 3 × 3 smoothing.

Freestream velocities were sampled at the beginning of each experimental session (n = 4) and the mean out-of-plane flow was calculated over 100 stereo-PIV vector fields. The r.m.s of the freestream measurements was calculated for the 100 vector fields of each sequence and was on average 0.24 m s⁻¹, which can be considered the baseline error in the vector fields as a combination of turbulence level of the air flow, spatial velocity variation and PIV noise.

3. ANALYSIS

3.1. The transect method

Out of the total number of recorded sequences (n = 13), eight were chosen for further analysis. Sequences where both hind legs were down or sequences which later in the analysis showed asymmetry in the downwash profile (indicating that the locust had been attempting to turn) were discarded. This resulted in three of the individuals having two usable sequences and two of the individuals having one. Each sequence corresponded to 1361 vector fields recorded at a frequency of 1000 Hz, resulting in a recording duration of 1361 s. On average 29 wingbeats per sequence were recorded resulting in a total number of 230 wingbeats and 10 888 individual frames in the complete dataset.

For each sequence, the centres of the hindwing trailing wingtip vortices (defined as the centre of rotation of the vectors in the vortex) were manually clicked in each vector field using a custom-written Matlab code (The MathWorks, Inc., Natick, MA, USA). A pair of transsects, forming a v-shape following the trailing edge of the wings as they rotate around a notional common wing hinge, were drawn between the two trailing wingtip vortices (figure 2). The transect lines are generated with 50 points each (in excess of the PIV data resolution), and each point is assigned the closest measured PIV velocity vector. The central point was used as an anchor point between the two wingtip vortex centres when drawing the independent transsects in each successive vector field (figure 2). The transsects are then re-interpolated such that the resolution of the transsects matches the resolution of the original PIV data. To sufficiently sample the decay in induced velocities outboard of the vortex cores, tails of 15 mm

Figure 2. Illustration of a typical flow velocity field behind a desert locust in tethered flight in a wind tunnel and the v-shaped transect method. Colour bar indicates x-vorticity (s⁻¹). The transect is drawn from an anchor point at the common centre of wing rotation to each of the wingtip vortex cores. The transect includes a 15 mm ‘tail’ added outboard of the vortex core centres to capture the decay in flow velocity away from solid body rotation. The vector field represents an area of 114 × 56 mm (width × height).
fixed length were added to the transects—approximately twice the vortex core radius (figure 2). Velocity components perpendicular to the transect were taken as the estimate of the induced flow created by the wings. Within the measurement plane these components are approximately tangential to the wing motion. By compiling the successive frames and plotting them with a spacing based on the tunnel freestream velocity the variation in induced flow profiles throughout a sequence can be visualized (figure 3; \( x = U_1 t \); where \( x \) is the location along the \( x \)-axis, \( U_1 \) the freestream velocity and \( t \) the time step of each recorded vector field).

### 3.2. Lift and efficiency calculations

Calculation of span efficiency follows largely the method from Bomphrey et al. [6], which in turn was based on the method of Stepniewski & Keys [1 pp. 74–78]; the salient features are also detailed below. A wing generates lift by imparting momentum to the fluid around it. If we suppose that lift is equal to the rate of flux of vertical momentum through the Trefftz plane, where the pressures have been equalized it is possible to determine the instantaneous lift by measuring the instantaneous flux of vertical momentum near the wing. This assumes that velocities at the measurement location are negligibly higher than at the wing and that the wake has not contracted or deformed to any significant degree. The optimal lift distribution, generating the lowest induced drag, is achieved when the downwash is constant across the span. For an even downwash distribution, the lift is

\[
L = \rho \frac{\pi b^2}{2} V \omega^*.
\]  

(3.1)

where \( \rho \) is the density of the fluid, \( b \) the span of the wake, \( V \) the freestream velocity and \( \omega^* \) the uniform downwash velocity. Subsequently, the induced power requirement is as low as it can be

\[
P_{i, \text{real}} = P_{i, \text{ideal}} = \rho \frac{\pi b^2}{2} V (\omega^*)^2.
\]  

(3.2)

However, the lift contribution per unit span may not be constant and if we assume that the downwash at any given location is associated with the lift generated at that location only, the elemental contribution to lift can then be written as

\[
dL = 2 \rho V \omega(y) \sqrt{b^2 - 4y^2} dy,
\]  

(3.3)

where \( \omega(y) \) is the measured induced flow along the span and \( y \) the spanwise location. The elemental contribution to induced power can be written accordingly

\[
dP_{i, \text{real}} = 2 \rho V \omega^2(y) \sqrt{b^2 - 4y^2} dy.
\]  

(3.4)

Thus, by knowing the downwash distribution across the wing at a given time, the uniform ideal downwash distribution corresponding to the same total lift force can be calculated by integrating equation (3.3) across...
the induced power factor, defined as $P_{\text{ind}} = P_{\text{real}} / P_{\text{ideal}}$, can then be calculated as

$$k_{\text{ind}} = \pi \frac{b}{C_0} \frac{\int_{-b/2}^{b/2} \omega^2(y) \sqrt{b^2 - 4y^2} \, dy}{\frac{1}{2} \int_{-\pi}^{\pi} \omega(y) \sqrt{\pi^2 - \theta^2} \, d\theta}.$$  

(3.6)

To remove explicit dependency on span ($b$) and to simplify, the transform $\theta = 2y/b\pi$ may be applied to give

$$k_{\text{ind}} = \frac{\pi^2}{2} \frac{\int_{-\pi}^{\pi} \omega^2(y) \sqrt{b^2 - 4y^2} \, dy}{\int_{-\pi}^{\pi} \omega(y) \sqrt{\pi^2 - \theta^2} \, d\theta}.$$  

(3.7)

In order to perform the integrations in equation (3.7), the downwash distribution was approximated as an analytical function consisting of a cosine series with five harmonics which was fitted using the ‘gimfit’ function in Matlab. This function makes a symmetrical fit to the measured data.

In contrast to [6] for the adaptive v-shaped transect used here, the downwash distribution or, more appropriately, the induced flow distribution, across the wings was measured as the velocity component perpendicular to the transect in each frame. Loading distribution and induced power factor, $k_{\text{ind}}$, was then calculated based on this distribution. Weight support was calculated by integrating equation (3.3) over the distance of each of the wings separately and using only the vertical vector components along the transect.

The induced power factor, $k_{\text{ind}}$, calculated in this manner measures the difference from ideal elliptic loading, so the inverse of this number, $1/k_{\text{ind}}$, is the inviscid span efficiency, $\epsilon_i$ (following [5]). From each sequence, a phase-averaged wingbeat both with respect to lift and span efficiency was calculated by locating the turning points of the vertical excursion of the wingtip vortices and re-sampling to create a generic wingbeat with a standardized period from 0 to 1.

4. RESULTS

The average wing beat frequency of the five locusts was 21.5 ± 1.48 Hz (mean ± s.d.) and with the 1 kHz repetition rate of the PIV system, approximately 46 frames were sampled per wingbeat. Figure 3 shows a series of successive transects from five consecutive wingbeats plotted as a surface with spacing calculated using the freestream velocity. The plot starts and ends at the beginning of a downstroke and over the course of this short excerpt there are 242 independent transect measurements. A high degree of consistency between wingbeats is apparent and typical for all the sequences used in the analysis. Since the transects extend outboard of the tips of both wings, the colour changes most noticeably where the transects cut through the trailing wingtip vortices, from downward/blue inboard of the vortex core centre to upward/yellow outboard of the vortex core centre. To add context, the mean wing tip vortex vertical excursion is projected above the transect plot, where lighter grey shading represents the downstroke, and instances of stroke reversal are represented by dashed lines extending across the transect plot.

During the early downstroke very little induced flow is measured across the span but as the downstroke progresses the induced flow rapidly grows in strength behind the wings and the dominating velocities are strongly downward. The region behind the body at this stage exhibits very small induced flows (either weak downward velocities or even weak upward velocities), suggesting that this region plays only a small part in force generation at this time.

During the course of the downstroke the transect width increases due to the increase in span caused by changes in the wing angle and the sweep angle, the maximum span occurring around mid-downstroke [23]. During the upstroke the locusts sweep the hindwings aft which results in a narrower upstroke wake compared to the downstroke. For comparison, Walker et al. [23] showed that the locust hindwings reduce in area by 30 per cent during the upstroke.

As an example, figure 4 shows a single transect of induced velocities in the vertical-transverse plane measured from a flow field created when the hindwing is horizontal (cf. [6])—at this position, the induced flow normal to the wing coincides with the more familiar terms ‘upwash’ and ‘downwash’. Upwash and the corresponding negative loading is apparent at the extremities while the majority of the induced flow is downwash behind the wings, reducing somewhat over the centrelines behind the thorax and abdomen. With a distribution such as this, the locust has to expend 38 per cent more energy to create weight supporting induced flow than if it were supported by an ideally loaded actuator disc.

4.1. Efficiency

For each of the locusts tested, span efficiency is close to zero at the beginning of the downstroke but increases quickly as the downstroke progresses (figure 5a–c; $t/T = 0–0.3$, where $t$ is the current time step within the wingbeat and $T$ the wingbeat period). At approximately mid-downstroke ($t/T = 0.3$), $\epsilon_i$ has in all cases grown to a value around 0.6 and remains relatively constant until approximately three-quarters of the downstroke ($t/T = 0.4–0.5$). At this point $\epsilon_i$ drops momentarily, but substantially, before quickly recovering to a similar plateau as before. This temporary drop in span efficiency coincides with mid-downstroke of the forewings. For the remainder of the downstroke, $\epsilon_i$ continues to be relatively stable, even through wing supination and into the upstroke. Approximately one-quarter into upstroke ($t/T \approx 0.7$) $\epsilon_i$ decreases rapidly and by mid-upstroke and onwards, $\epsilon_i$ returns to a value close to zero in all cases (figure 5). During the downstroke, values of $\epsilon_i$ remain at a stable plateau, illustrated in figure 5 with vertical dashed lines marking the start and end of the high $\epsilon_i$ region defined as the instants where it rises and later falls across 50 per cent of its peak value (figure 5).
4.2. Lift

The period during which all the locusts are producing lift sufficient to support their own weight or more ($L/W \geq 1$) coincides with the period where $e_i$ is consistently high (figure S$f$–$j$, $t/T = 0.2$–$0.6$). As the hindwings accelerate following pronation, the lift they generate increases and its magnitude quickly exceeds the weight of the animal (figure S$f$–$j$, horizontal line shows $L/W = 1$). From here on throughout the downstroke the normalized weight support is well above one, apart from the brief moment when the induced flow momentarily decreases. The peak in lift is approximately 2.5 times body weight and occurs at, or just after, mid-downstroke for all five individuals. The five locusts supported $98 \pm 21\%$ of their weight during these bouts of tethered flight. For a brief moment during the final part of the upstroke ($t/T = 0.9$–$1.0$), a small amount of negative lift is generated by all of the locusts.

4.3. Generic locust wingbeat

The weighted means for span efficiency ($e_i$) and weight support ($L/W$) for all recorded wingbeats for all five locusts show the same general pattern as seen for the individual locusts (figure 6$a,b$) with the exception of the momentary drop in lift and span efficiency since the combination of its short duration and variable timing causes the dip to be lost following averaging.

Lift power economy, defined as the ratio of lift ($L$) to induced power ($P_{ind}$), plateaus at a value around 1 N m$^{-1}$ early in the downstroke until halfway through the upstroke (figure 6$c$). At the final half of the upstroke it drops below zero.

The dotted lines in each of the graphs represent standard error of the mean, and their close proximity to the mean suggest that this may be a fairly robust result for this species.

5. CONCLUSIONS AND DISCUSSION

Flapping flight in animals is a challenge to study because of its time-variant nature. High-speed PIV facilitates a time-resolved analysis of the wake generated by animals, despite their high wingbeat frequencies, and renders possible the measurement of instantaneous flow patterns at numerous time intervals within each wingbeat (e.g. [12,17,18,24,25]). This has not previously been possible for insects, since the high wingbeat frequencies necessitate a very fast repetition rate of the laser and cameras. The current study is the first to quantify how flows induced by a flapping insect fluctuate with time, and to resolve how the span efficiency of a flapping insect wing varies, presumably modulated by the combination of wing morphology and kinematics over the course of each wingbeat cycle. The results show that wing lift production and the efficiency with which that lift is generated vary greatly within a wingbeat. Moreover, span efficiency plateaus close to its peak value for much of the wing stroke cycle and this corresponds to the period during which the lift forces are highest and above the weight of the animal (figure 5). This can be shown by calculating the proportion of the total lift produced within the part of the wing stroke where the plateau occurs. For the five locusts it was $90.4 \pm 2.1\%$ (mean $\pm$ s.d.), while the duration of the plateau is only $56.6 \pm 1.9\%$ of the complete wingbeat period. Thus, high lift forces (up to 2.5 times greater than body weight) are produced during the period of relatively high span efficiency. It remains to be seen whether the plateau reflects a maximum efficiency with which

\[
k_{ind} = 1.38
e_i = 0.72
\]
locusts can generate lift forces above a certain threshold, or whether efficiency increases yet further with more extreme force production, for example, when manoeuvring to avoid a collision or during evasive flight.

Consistency in the measured wake behind tethered desert locusts is very high both within and between individuals. This, together with the fact that they fly well in unnatural conditions, makes them an ideal model species for studies of this type. The locusts used in this experiment produced an average calculated lift very close to the force required to balance their weight, which is another indication that the insects behaved more or less naturally in the wind tunnel environment even under the conditions required for PIV. The effect of the tether on the downwash distribution was assumed to be small since all locusts were tethered from below in order to minimize the disturbance to the flow on the upper side of the body (where the wings attach to the thorax) using a tether which was only 2 mm in diameter (approximately 2.2% of the mean wingspan). The shedding frequency of a smooth cylinder with the same dimensions as the tether would be approximately 300 Hz at the speed used for the experiments (calculated as \( f = StU/d \), where \( St \) is the Strouhal number, \( U \) is the wind speed, and \( d \) is the diameter of the cylinder).

Figure 5. Span efficiency (\( \varepsilon_i \)) and weight support (\( L/W \)) presented as standardized wingbeats for each of the five locusts demonstrating the consistency within and between individuals. The solid lines show the mean values with dashed lines indicating the s.d. The grey area corresponds to the upstroke. Dashed vertical lines in all panels show the defined beginning and end of the \( \varepsilon_i \) plateau. (a – e) Span efficiency varies greatly over the course of the wingbeat, but plateaus in all five cases for a large portion of the downstroke and about one quarter of the way into the upstroke (\( t/T \approx 0.3 - 0.7 \)). (f – j) Weight support is well above \( L/W = 1 \) for a large portion of the downstroke, but is below for most of the upstroke. Peak in lift occurs at around mid-downstroke (\( t/T \approx 0.3 \)).

Figure 6. (a) Span efficiency, and (b) weight support lift power economy (c) for the generic desert locust wingbeat based on all five individuals. Solid lines represent the mean of all sequences weighted by the number of wingbeats for each individual and dotted lines represent the standard error of the mean. (c) Lift power economy is around 1 N W\(^{-1}\) for the majority of the wingstroke.

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where $St$ is the Strouhal number and assumed to be $St = 0.2$ for Reynolds number $Re = 440$ of the cylinder at the speed used in the experiments, and $d$ the diameter of the cylinder. This indicates that the shedding frequency of the tether is more than an order of magnitude higher than the wingbeat frequency of the locusts. Moreover, the wake of the tether will have a reduced effect on vertical velocities since the foremost effect would be horizontal fluid acceleration from vertically oriented shedding vortices.

The locusts were placed at a distance of two maximum chord lengths upstream of the laser sheet, which would give little time (12 ms based on freestream velocity) and distance for the wake to contract and deform between leaving the wing and being recorded by the PIV cameras. Nevertheless, to investigate the extent of wake contraction, the span of the wake at mid downstroke was compared with the wingspan of the five locusts. The mean wake span was $88.9 \pm 1.5\%$ (mean $\pm$ s.d.) of the wingspan, suggesting that a minimal contraction has occurred. Again, the calculated lift was close to the weight of the locusts, which supports the conclusion that the wake deformation prior to measurement was minor, and that this relatively simple measure is sufficient to capture the essential, gross, flow physics of the wake while simultaneously neglecting the three-dimensional complexities of the major and minor vortex core structures.

The droop in lift and $\epsilon_i$ that was exhibited in all individuals coincides with mid downstroke of the forewing. It is possible that transverse vorticity is shed into the wake from the forewings at this point as the wing stops accelerating and starts to decelerate, and that this vorticity interferes with the wake of the hindwing. The droop in force production and span efficiency in some of the locusts is quite notable but is also very brief, so the integrated effect of it on overall lift production and efficiency is minor. Young et al. [26] modelled the near-wing aerodynamics of locust flight using computational fluid dynamics (CFD) and the simulations did not show a similar temporary drop in the calculated lift force. This may indicate either that our locusts are shedding small transverse structures that were not apparent in the previous study, or that the droop measured here reflects the effect of interactions between wake elements (either between the wakes of fore- and hindwing or between wake elements shed from the same wing) immediately behind the trailing edge rather than an actual droop in lift experienced by the locust. During the final part of the upstroke a small amount of upwash is observed.

Beginning of the downstroke shows a period with $e_i$ averaged before by a number of authors and reviewed by Lehmann [10]. Most of these calculations are based upon the method set out by Ellington [7,8] and use the kinematics of hovering flight as their foundation. Here, we record the induced flow field and therefore provide a more direct measurement of the induced power by means of the momentum transferred to the wake. As noted by Spedding & McArthur [5], span efficiency taking into account viscous flow, $e_i$, as is referred to in that paper, may represent a lower value than inviscid span efficiency, $\epsilon_i$, used in this study. Nevertheless, $e_i$ as a measure of efficiency is a useful parameter, especially when allied with ecological data and employed in a comparative analysis. In such an analysis, it would be valuable to use a simple biomechanical measure of efficiency, which can be derived in a consistent way irrespective of species. The method presented here can therefore form the basis for a comparative analysis of span efficiency for animals exhibiting a variety of ecological functions.

The beginning of the downstroke shows a period with very little downwash in all five locusts. At the forward flight speeds and advance ratio of locusts, the Wagner effect may be considered small but not necessarily negligible (cf. [28]). The Wagner effect is primarily a phenomenon of impulsively started wings which is typically not the case for flapping wings that can be more closely approximated by a sinusoidal motion. By examining real insects and a simplified flapping model, Thomas et al. [29] showed that dragonflies did not shed a discrete starting vortex that would be exhibited behind an impulsively started wing and acting as an impediment to the build up of circulation. Nevertheless, the wake of locusts is not yet resolved in such detail and it remains a possibility that the relatively low lift in the early downstroke could be the result of a Wagner effect as opposed to being simply a result of lower wing speed or wing elevation.

The part of the locust wingstroke that generates lift equal to or larger than the weight of the animal ranges

$\epsilon_i,\text{ideal}$ represents the induced power needed to create the corresponding amount of lift using a uniform downwash for each time-step and $P_{\text{ideal}}$ represents the measured power of each time step (cf. [11]). The calculation of average span efficiency for the locusts yields $\epsilon_{i,\text{mean}} = 0.53$. The calculation takes into account periods of the wingstroke where the generated lift is low, but it also decouples the ratios at each instant and does not, therefore, encapsulate information about the changing ratio of real and ideal power requirements as they fluctuate relatively throughout the wingbeat cycle.Muijres et al. [11,12] recently studied the downwash profiles of two bat species and pied flycatchers using a similar method. Their analysis derived wingbeat averages of span efficiency rather than describing its variation over the wingbeat. They found that $\epsilon_i$ averaged 0.79 and 0.81 for the two bat species and between 0.8 and 0.9 for the pied flycatchers. Interestingly, those values are similar to the peak $\epsilon_i$ measured here (and also in the earlier locust study by Bomphrey et al. [6]), but rather higher than the wingbeat average for locusts. Surprisingly, lift production appears to be more continuous at lower speeds than higher speeds in some bats [27, supplementary figures].

The aerodynamic efficiency of insects has been estimated before by a number of authors and reviewed by Lehmann [10]. Most of these calculations are based upon the method set out by Ellington [7,8] and use the kinematics of hovering flight as their foundation. Here, we record the induced flow field and therefore provide a more direct measurement of the induced power by means of the momentum transferred to the wake.

Peak values of $e_i$ for the five locusts were on average $\epsilon_{i,\text{max}} = 0.68$ and values of $e_i$ at the time of maximum lift force were on average $\epsilon_{i,\text{max lift}} = 0.58$. The wingbeat average $\epsilon_i$ can be calculated as

$$\epsilon_{i,\text{mean}} = \frac{\sum_{n=1}^{N} P_{\text{ideal}}}{\sum_{n=1}^{N} P_{\text{real}}}$$

where $P_{\text{ideal}}$ represents the induced power needed to create the corresponding amount of lift using a uniform
roughly from one third into the downstroke until end of downstroke (supination). A comparison of the span efficiency graphs in the left-hand side panel of figure 5, with the weight support graphs on the right-hand side panel, shows that this period of high lift production coincides reasonably well with a plateau in the values of $c_i$. The regions of low span efficiency, especially by the end of the upstroke and at the transition to downstroke (pronation), could be argued to be of less significance for the overall performance of the animal—efficiency becomes immaterial when absolute energy expenditure is so low. Apart from the wings actually producing an uneven flow when loading is low, estimating the efficiency using the current method when the net force is close to zero introduces uncertainty since the induced power due to thrust production. The thrust forces are assumed to be small compared with lift. It is important, therefore, to make the distinction between the flight efficiency of the entire flying animal and the span efficiency which is a measure of the efficiency of lift production alone. Nevertheless, span efficiency at the animal’s preferred flight speed is an excellent metric for interspecific comparison, or if the aim is to discover how induced power varies, and can be minimized, over the periodic wing stroke cycle of flapping flight.

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