Elastic wing deformations mitigate flapping asymmetry during manoeuvres in rose chafer beetles (Protaetia cuprea)

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ABSTRACT
To manoeuvre in air, flying animals produce asymmetric flapping between contralateral wings. Unlike the adjustable vertebrate wings, insect wings lack intrinsic musculature, preventing active control over wing shape during flight. However, the wings elastically deform as a result of aerodynamic and inertial forces generated by the flapping motions. How these elastic deformations vary with flapping kinematics and flight performance in free-flying insects is poorly understood. Using high-speed videography, we measured how contralateral wings elastically deform during free-flight manoeuvring in rose chafer beetles (Protaetia cuprea). We found that asymmetric flapping during aerial turns was associated with contralateral differences in chord-wise wing deformations. The highest instantaneous difference in deformation occurred during stroke reversals, resulting from differences in wing rotation timing. Elastic deformation asymmetry was also evident during mid-strokes, where wing compliance increased the angle of attack of both wings, but reduced the asymmetry in the angle of attack between contralateral wings. A biomechanical model revealed that wing compliance can increase the torques generated by each wing, providing higher potential for manoeuvrability, while concomitantly contributing to flight stability by attenuating steering asymmetry. Such stability may be adaptive for insects such as flower chafer species that need to perform delicate low-speed landing manoeuvres among vegetation.

KEY WORDS: Flexible wings, Flapping flight, Free flight, Insect, Manoeuvring flight

INTRODUCTION
Locomotion has direct consequences for the evolutionary success of animals. It affects the ability to exploit resources (e.g. food, shelter), find mates, elude predators, migrate and disperse. Consequently, the locomotion of extant species has been shaped by a very long process of natural, and often sexual, selection (Dickinson et al., 2000). The approximately 400 million years of insect flight evolution (Grimaldi and Engel, 2005) has resulted in insects varying not only in the size and shape of their wings but also in the number of wings used for flight and the internal structure of the wing veins that give the wing its shape and rigidity (Wootton, 1981).

Because of their smaller size and different flapping kinematics, insects engage with the surrounding air in a different manner to that of vertebrates (Chin and Lentink, 2016). At Reynolds numbers of ~10^3 – 10^4, typical of most insects, the relative contribution of air viscosity to flow patterns increases, affecting the attachment of airflow to the wings and, consequently, the aerodynamic forces generated by these wings (Dudley, 2000). In addition, vertebrate wings can be actively shaped, using muscles and skeletal joints, to modulate the aerodynamic and inertial forces required for aerial manoeuvres and perturbation recovery (Hedenström and Johansson, 2015; Lentink et al., 2007). Insect wings, in contrast, lack intrinsic musculature, thereby restricting their active control over wing shape during flight. However, insect wings elastically deform during flapping, resulting in wing twist and camber – two important features that can affect the wing’s efficiency in producing aerodynamic forces (Ennos, 1988; Wootton, 1992; Young et al., 2009).

Wing twist can compensate for the span-wise increase in the angle of attack (AoA) as a result of flapping during forward flight (Pringle, 1957; Walker et al., 2009; Wootton, 1981; Young et al., 2009). Unlike in most flying vertebrates, insect wings twist in both directions, ensuring lift production during both the upstrokes and downstrokes (Sane, 2003; Wootton, 1981). Wing camber improves flow attachment to the wing, increases the lift and delays flow separation during dynamic stall and stroke reversals, whereas the AoA reaches ±90 deg (Shyy et al., 2016; Wang et al., 2003). Therefore, it is generally accepted that some degree of wing flexibility is required in insects. However, there is controversy as to whether wing deformations have an advantage over rigid wings in aerodynamic force production. Whereas studies have shown that wing flexibility enhances load-lifting capacity (Mountcastle and Combes, 2013), down-wash and lift production (Du and Sun, 2010; Nakata and Liu, 2012; Shoele and Zhu, 2013), delays stall during the translational phase (Lehmann, 2004; Marden, 1987), improves wake capture (Vanella et al., 2009) and flight efficiency (Jankeauski et al., 2018; Young et al., 2009), but see Lehmann et al. 2011, for energy losses associated with flexible wings) and increases tolerance to aerial perturbations (Mistick et al., 2016), other studies have suggested that rigid wings would produce greater lift (Tanaka et al., 2011; Tobing et al., 2017; Zhao et al., 2010). These different, sometimes conflicting, findings may arise from the use of simplified model wings and numerical simulations, whereas empirical measurements of real insect wing deformation during flight are scarce. Consequently, measuring wing deformation during free flight is crucial for a deeper understanding of the intricate fluid–structure interaction that underlies the benefits and disadvantages of flexible wings.

Although most manoeuvres originate from asymmetric force production by contralateral wings, the flapping kinematics by which insects produce the asymmetric force are not restricted to a single, uniform mechanism. Different steering kinematics have been shown in Odonata (Li and Dong, 2017), Hymenoptera (Vance et al., 2013), Lepidoptera (Greer and Hedrick, 2016) and Diptera (Bergou et al., 2017).
flapping flight. Rose chafers are pollen feeders, frequently manoeuvring to land in complex 3D environments. During low-speed flight, their wings undergo extensive elastic chord-wise deformations, particularly in the proximal section of the trailing edge, resulting in the formation of considerable twist and positive camber (Meresman and Ribak, 2017). We asked how these extensive wing deformations relate to this beetle’s ability to produce low-speed manoeuvring flight. Wing deformation may have a damping effect on the asymmetric flapping of contralateral wings, helping to restore stability; or it may promote aerial instability and consequently allow sharper manoeuvring. To determine which of these possibilities is correct, we measured wing deformation in free-flying rose chafers performing low-speed aerial manoeuvres. Using high-speed video cameras, we measured wing kinematics and deformation of the left and right wings and compared these deformations between the contralateral wings. To complement the measurement of wing kinematics, we performed a blade-element analysis to estimate the effect of wing compliance on the turning torque produced by the wings.

MATERIALS AND METHODS

Insects

Adult rose chafers, Protaetia cuprea (Fabricius 1775), were obtained from a laboratory population, established in 2014 from insects collected in the field. Wild adults are added annually to prevent a founder bottleneck effect. The beetles were fed apples and provided with compost based on oak leaves for burrowing, oviposition and development of larvae. Males and females have no apparent inter-sex difference in morphology or behaviour (Meresman and Ribak, 2017). Therefore, we pooled sexes in the experiments.

Filming procedure

The beetles were marked with three dots on the pronotum (Fig. 1A), using acrylic paint or adhesive paper, and their body mass was measured to the nearest 0.1 mg using an analytical balance (BAS 32 plus, Boeco, Hamburg, Germany). Both marking methods resulted in negligible added mass (<1 mg) and did not seem to affect the beetles’ behaviour or flight performance. The marked beetles were placed individually on top of a vertical 4 cm rod in the centre of an open flight arena. Three synchronized high-speed cameras (Fastcam SA3_120K, Photron Inc., San Diego, CA, USA) were fitted with 50 mm lenses and set to film at 3000 frames s⁻¹ (shutter speed 66.7 μs, resolution: 768×768 pixels). We placed three LED infrared projectors pointing at each camera to provide background illumination and two 500 W visible light projectors were mounted from above (Fig. 1B). To calibrate the cameras spatially, either a 10 cm³ calibration cube or an 8 cm long wand were used with the software DLTcal5 and easywand5, respectively (Hedrick, 2008; Theriault et al., 2014).

In the flight arena, we allowed the beetles to take off undisturbed in stagnant air multiple times. Each beetle was filmed until it either was reluctant to continue flying or had completed 10 flights. Of the 46 beetles that flew, only 23 performed manoeuvres within the spatially calibrated area. From each of these 23, we selected the film in which it had performed the largest rotation (in degrees) about its longitudinal body axis within three flapping cycles (approximately 30 ms; Movie 1).

Data analysis

High-speed film analysis

From each frame in each film, we digitalized 17 landmarks: the three pronotum points described above and seven natural landmarks on
Each analysed film section comprised three flapping cycles. To control for variance in cycle duration, we divided the serial numbers of each film frame by the number of frames within a flapping cycle, to give a non-dimensional time scale of flapping cycles in the range 0–3.

**Instantaneous body orientation and body frame of reference**

We used the three marked points on the thorax (Fig. 1A) to define a body-fixed Cartesian coordinate system, in each frame, in which the longitudinal body axis \( x \) is represented by a vector connecting the scutellum with a point half-way between the other two points on the pronotum. The lateral body axis \( y \) was defined as the vector connecting the right and left points on the pronotum. The dorso-ventral body axis \( z \) was found from the cross-product:

\[
z = x \times y.
\]

The origin was defined between the wing bases, and all body axes vectors were converted to a unit vector. We used the body axes as a rotation matrix to: (1) transform all instantaneous landmark positions on the wing to a body frame of reference; and (2) define the turning of each beetle using the Euler axis–angle convention.

For the former, the origin was shifted to the relevant wing base and the vector cosines of the three body axes were used as a rotation matrix to convert each wing position to the body frame of reference \((x,y,z)\). Thus, any position on the wing in the camera frame of reference \(P(X,Y,Z)\) is rotated to \(P'(x,y,z)\) in the body frame of
turn into the beetle’s frame of reference before the turn:

$$\mathbf{M} = \mathbf{B}_i \mathbf{B}_f,$$

where $\mathbf{B}_i$ and $\mathbf{B}_f$ are $3 \times 3$ matrices representing the direction cosines of the three body axes in the camera frame of reference, i.e.

$$\begin{bmatrix} x_X & y_X & z_X \\ y_X & y_Y & y_Z \\ z_X & z_Y & z_Z \end{bmatrix},$$

at the beginning and end of the turn, respectively. The Euler axis and angle can be extracted directly from the components of the $3 \times 3$ rotation matrix $\mathbf{M}$ as angle $\theta$:

$$\cos \theta = \frac{M_{1,1} + M_{2,2} + M_{3,3} - 1}{2},$$

**Fig. 2. Body rotation of the free-flying beetles.** (A) 3D visualization of the Euler axis rotations. Here, all rotations are displayed together as rotations towards the left of the beetle by inverting (mirror image) all the rotations to the right. The black arrow marks the longitudinal axis of the beetles, with the head pointing towards the pole of the sphere marked by a black dot. Blue lines represent the rotation axes of the 23 beetles. The green line and arrow represent the mean rotation axis and the direction of the rotation, respectively. (B–D) Same as in A, but illustrating the rotation axes relative to the different body axes. (E) Angular histogram showing the distribution of rotation magnitudes about the rotation axes. (F) Histogram of mean angular velocity for the same data. Arrows in A–D were produced using the Matlab-compatible function mArrow3 (© 2009, Georg Stillfried; all rights reserved).
axis $e$:

$$e_x = \frac{M_{3,2} + M_{2,3}}{2 \sin \theta}, \quad (5a)$$

$$e_y = \frac{M_{1,3} + M_{3,1}}{2 \sin \theta}, \quad (5b)$$

$$e_z = \frac{M_{2,1} + M_{1,2}}{2 \sin \theta}, \quad (5c)$$

where $e_x$, $e_y$, and $e_z$ are the $x$, $y$ and $z$ components of the rotation axis, respectively, in the body frame of reference.

### Wing Flapping Kinematics

Wing flapping kinematics was extracted as three time-varying angles (flapping, deviation and incidence) as in Meresman and Ribak (2017), but with the incidence angle being calculated twice:

1. As the wing pitch relative to the stroke plane for the flexible wing area ($\alpha_f$) near the trailing edge (Fig. 1C,D). The instantaneous wing tip data in the body frame of reference and in the sagittal plane $w(x,z)$ were used to find the stroke plane of each wing from the linear least square error line of these positions throughout the three flapping cycles. The stroke-plane angle (SPA) is defined as the slope of the line as in Ellington (1984a), but in the body frame of reference.

2. Next, we rotated wing data by SPA about the $y$-axis. The instantaneous flapping and deviation angles are defined as the azimuth and elevation of the wing length relative to the stroke plane. Wing incidence was defined as the rotation of the wing about its length (see Fig. 3B). To find this angle in each film frame, for the flexible and rigid wing parts, we rotated the wing about the $z$- and $x$-axes so that the span aligned with the $y$-axis. We then found the vectors connecting MP (Fig. 1A) with point $P_1$, and $P_1$ with $P_2$, where all three points are located on the wing chord at 0.725 wing length.

### Fig. 3. Wing Kinematics

Mean (±s.e.m., $n=23$) (A) flapping, (B) incidence, (C) deviation, (D) stroke-plane angle (see insets with schematic illustrations for definitions) and (E) time-varying Euler angles during three flapping cycles of free-flying P. cuprea, performing hovering aerial manoeuvres. The inner wing (e.g. left wing in a left turn) is marked in red and the outer wing in blue. Grey areas denote the downstrokes. The standard error is denoted by the lighter colours in A–C and E–F and by the error bars in D. Black dots on the horizontal axes mark significant statistical differences between the inner and outer wings in the instantaneous angles (two-tailed, paired t-tests, $P<0.05$). (F) Change in the non-dimensional angular speed during the three flapping cycles comprising the manoeuvre. Non-dimensional angular speed is the instantaneous angular speed divided by the maximal instantaneous angular speed for each manoeuvre. Red, blue and green colours in E and F denote roll pitch and yaw of the beetles’ body, respectively, as illustrated in the inset on the right.
length (Fig. 1C). The angle between each of these vectors and the stroke plane in the \(xz\) plane was the instantaneous incidence angle for the flexible (\(\alpha_f\)) and the rigid (\(\alpha_r\)) wing area, respectively. We chose to measure the incidence angle using MP at 0.725 wing length because of the expected proximity of this spanwise position to the centre of pressure of a flapping wing (~0.7 in fruit flies; Fry et al., 2005).

**Chord-wise wing deformations**

Wing deformation was measured relative to the leading edge. Using the three leading edge landmarks (\(wb, mj\) and \(wt\); Fig. 1A), we defined an instantaneous plane in 3D space that represents the (relatively) rigid surface of the wing. Next, for the four landmarks on the trailing edge (\(RP, MP, CuA\) and \(AA\); Fig. 1A) we calculated their perpendicular distance from this plane. These perpendicular distances represent the chord-wise deflections at these positions along the wing. Deflections of the trailing edge points defined the local wing camber whereas the pattern of these deflections along the wing length gave the wing twist.

To measure the rigid wing plane and deflection of trailing edge landmarks from the digitized data, we first shifted the origin of the wing length gave the wing twist.

Deflections of the trailing edge points defined the local wing camber whereas the pattern of these deflections along the wing length gave the wing twist. To measure the rigid wing plane and deflection of trailing edge landmarks from the digitized data, we first shifted the origin of the body fixed coordinate system to the wing base (point \(wb\) in Fig. 1A). We then defined two vectors connecting \(wb\) with two non-collinear points on the leading edge (\(mj\) and \(wt\) in Fig. 1A). The cross-product of the two vectors defines a vector (\(Z_w\) normal to the plane formed by the three points (yellow triangle in Fig. 1A):

\[
Z_w = mj \times wt
\]

and

\[
Z_w = wt \times mj
\]

for the left and right wings, respectively.

The direction of the wing chord (\(Y_w\)) is defined as the cross-product of \(Z_w\) and \(wt\):

\[
Y_w = Z_w \times wt
\]

and

\[
Y_w = wt \times Z_w
\]

for the left and right wings, respectively, where all vectors are converted to unit vectors.

Using the vector cosines of the three wing axes (\(wt, Y_w, Z_w\)) as a rotation matrix, we transformed all data points on the wing to the wing frame of reference defined by the leading edge. The transformation of a given point \(P\) from the frame of reference of the camera to the frame of reference of the leading edge (\(P'\)) is:

\[
P' = \begin{bmatrix}
w_{tx} & w_{ty} & w_{tz} \\
y_{wx} & y_{wy} & y_{wz} \\
z_{wx} & z_{wy} & z_{wz}
\end{bmatrix}
\begin{bmatrix}
PX \\
PY \\
PZ
\end{bmatrix}.
\]

The procedure was repeated for each film frame. By definition, the \(Z_w\) component of the transformed data points is the deflection of this point out of the plane of the rigid leading edge.

**Net turning moment estimation**

We estimated the instantaneous forces that emerge from flapping the contralateral wings based on the wingtip velocity and the AoA of the wings. We then used the forces of the left and right wings to estimate the net turning torque generated by the asymmetric flapping. The calculations were performed once for flexible wings using the AoA of the flexible wing area (\(\alpha_f\)) and a second time for ‘rigid’ wings using the AoA for the rigid wing area (\(\alpha_r\)).

**Calculation of the AoA**

To find the AoA for the left wing we defined \(\vec{n}_1\) and \(\vec{n}_2\) (Fig. 1C) as the cross-products:

\[
\vec{n}_1 = \hat{s} \times \hat{v},
\]

\[
\vec{n}_2 = \hat{c} \times \hat{s},
\]

where \(\hat{s}\), \(\hat{c}\) and \(\hat{v}\) are unit vector in the direction of \(P1\)–\(wb\), \(P1\)–\(MP\) and the velocity of the wing relative to air at \(P1\), respectively, as shown in Fig. 1C. The instantaneous velocity was found numerically from the position of \(P1\) as in Rayner and Aldridge (1985). The geometric AoA was taken as the angle between \(\vec{n}_1\) and \(\vec{n}_2\) using the dot product:

\[
\text{AoA} = \cos^{-1}(\vec{n}_1 \cdot \vec{n}_2),
\]

where \(\vec{n}_1\) and \(\vec{n}_2\) are the unit vectors of \(\vec{n}_1\) and \(\vec{n}_2\), respectively. For the right wing, the procedure is the same, but with Eqs 11 and 12 adjusted according to the ‘right-hand rule’. Next, we repeated the procedure to calculate the AoA for the rigid (leading edge) part of the wing using the vector connecting \(P2\) with \(P1\) instead of \(P1\) and \(MP\) (Fig. 1C).

**Estimation of the aerodynamic force**

The instantaneous quasi-steady aerodynamic translational force (\(F_{\text{trans}}\)) is (Sane and Dickinson, 2002):

\[
F_{\text{trans}} = \frac{\rho SU^2}{2}(S)[C_L^2(\alpha) + C_D^2(\alpha)]^{1/2},
\]

where \(\rho\) is the air density (taken as 1.225 kg m\(^{-3}\)), \(S\) is wing area, \(U_t\) is the wingtip speed, \(\alpha\) is the non-dimensional second moment of area, and \(C_L\) and \(C_D\) are the lift and drag coefficients, respectively. The instantaneous lift and drag coefficients were estimated as a function of the wing’s instantaneous AoA as in Meresman and Ribak (2017) assuming:

\[
C_L = 3 \sin \alpha \cos \alpha,
\]

\[
C_D = 3.35 \sin^2 \alpha + 0.1,
\]

where \(\alpha\) is the AoA.

The rotational force (\(F_{\text{rot}}\)) is defined as (Sane and Dickinson, 2002):

\[
F_{\text{rot}} = C_{\text{rot}} \rho U_t \alpha^2 R \int_0^1 \hat{c} \hat{r}^2(\hat{r}) d\hat{r},
\]

where \(C_{\text{rot}}\) is the theoretical rotational force coefficient. For lack of a better estimate, we assumed a rotation axis at 0.25 the wing chord from the leading edge. The position of this axis on insect wings is typically at 0.25–0.5 of the wing chord (Ellington, 1984b). Thus, our choice giving \(C_{\text{rot}}=1.57\) (Sane and Dickinson, 2002) uses the upper value of this coefficient. \(\alpha\) is the angular velocity for rotation about the wing length, \(\hat{c}\) is the mean chord length, \(\hat{r}\) is the non-dimensional radial position along the wing length and \(\hat{c}(\hat{r})\) is the non-dimensional chord length.

The aerodynamic inertial force (\(F_a\)) is (Sane and Dickinson, 2002):

\[
F_a = \frac{\pi}{4} R \hat{c}^2(\hat{b} \sin \theta + \hat{b} \hat{\theta} \cos \theta) \\
\times \int_0^1 \hat{c} \hat{r}^2(\hat{r}) d\hat{r} - \hat{b} \frac{\pi}{16} R \hat{c}^3 \int_0^1 \hat{c}^2(\hat{r}) d\hat{r},
\]

where \(\hat{b}\) is the body axis of rotation.
where $\phi$ is the flapping angle and $\theta$ is the incidence angle. The incidence angle is calculated relative to the stroke plane; thus, we used this angle as the AoA for the estimation of $F_a$. To find the time derivative of these angles, we first smoothed the data with a low-pass Butterworth filter with a cut-off frequency of 300 Hz (~3 times the flapping frequency), then calculated the derivatives numerically as in Rayner and Aldridge (1985).

Because the deviation angle was negligible (Fig. 3) the instantaneous directions of the lift and drag vectors were found in the body frame of reference using the stroke plane angles, assuming drag is always parallel to the stroke plane and lift is perpendicular to it. We calculated separately the magnitudes of lift and the drag in Eqn 14 and determined their direction according to the SPA (stroke plane angle $\phi$, see Fig. S1) as:

$$
\begin{align*}
\vec{F}_\text{lift}^{\upstroke} &= [\sin \beta, 0, \cos \beta], \\
\vec{F}_\text{drag}^{\downstroke} &= [\cos \beta, 0, \sin \beta],
\end{align*}
$$

(19)

(20a)

(20b)

where $\vec{F}_\text{lift}$ and $\vec{F}_\text{drag}$ are the directions of the forces (unit vectors).

Vector summation of the lift and drag for each wing gave our estimate of the instantaneous translational force:

$$\vec{F}_\text{trans} = F_{\text{trans}}(\vec{F}_\text{lift} + \vec{F}_\text{drag}).$$

(21)

To calculate the direction of $\vec{F}_\text{rot}$ and $F_a$, we summed their magnitudes and multiplied them by a unit vector normal to the wing area (Sane and Dickinson, 2002). Finally, vector summation gave the total instantaneous aerodynamic force as:

$$\vec{F}_\text{aero} = \vec{F}_\text{trans} + \vec{F}_\text{rot} + \vec{F}_a,$$

(22)

where $\vec{F}_\text{rot}$ and $\vec{F}_a$ are instantaneous rotational and inertial force, respectively.

**Estimation of wing inertia**

To the aerodynamic forces we added the instantaneous inertial force ($\vec{F}_\text{inertial}$) due to the accelerating mass of the wing. We estimated the wings’ centre of mass (CoM) to be at 0.29 the distance between the wing base and the wing tip based on total wing mass and mass distribution of five P. cuprea wings reported elsewhere (Meresman and Ribak, 2017). The position of the CoM was used to find the instantaneous acceleration of the wing from its second time derivative of the position data ($\ddot{\vec{r}}_{\text{CoM}}$). The instantaneous inertial force of the wing mass is represented as:

$$\vec{F}_\text{inertial} = -\ddot{\vec{r}}_{\text{CoM}} \cdot m_w,$$

(23)

where $m_w$ is the total wing mass.

**Calculation of the quasi-steady torque**

Using the instantaneous moment arm between the hinge and $P1$ ($\vec{r}$), the instantaneous aerodynamic force moment of each wing is:

$$\vec{M}_\text{aero} = \vec{r} \times \vec{F}_\text{aero}.$$  

(24)

For the force moment due to inertia of the wing mass we rotated $\vec{F}_\text{inertial}$ and the moment arm from the wing hinge to the wing CoM ($\vec{r}_{\text{CoM}}$) to the beetle’s body frame of reference and calculated the instantaneous inertial torque as:

$$\vec{M}_\text{inertial} = \vec{r}_{\text{CoM}} \times \vec{F}_\text{inertial}.$$  

(25)

The total instantaneous torque per wing is the summation:

$$\vec{M}_\text{total} = \vec{M}_\text{aero} + \vec{M}_\text{inertial}.$$  

(26)

The torques from the inner wing and the outer wing (see inset in Fig. 4 for definition of ‘inner’ and ‘outer’ wings) were summed, to give the net instantaneous torque acting on the beetles’ body:

$$\vec{M}_\text{net} = \vec{M}_\text{total (inner)} + \vec{M}_\text{total (outer)}.$$  

(27)

The vector representation of the net torque was broken into its $x$, $y$ and $z$ components to give the torques about these body axes.

**Torque estimation from body rotation**

We compared the obtained magnitude and direction of net torque with an estimate of the torque ($M_{\text{actual}}$) required to achieve the body rotations observed in the films. The three Euler angles of the body were extracted from the direction cosine matrix of the body axes in the camera frame of reference using the Matlab function dcm2angle.

The second derivative of the Euler angles (i.e. the angular acceleration) was calculated, rotated to the beetle’s body orientation and multiplied by the mass moment of inertia tensor of a prolate spheroid according to the following equation:

$$
\begin{bmatrix}
M_x \\
M_y \\
M_z
\end{bmatrix} =
\begin{bmatrix}
I_z & 0 & 0 \\
0 & I_z & 0 \\
0 & 0 & I_z
\end{bmatrix}
\begin{bmatrix}
\dot{\varphi}_x \\
\dot{\varphi}_y \\
\dot{\varphi}_z
\end{bmatrix},
$$

(28)

where $I_x$, $I_y$ and $I_z$ are the moment of inertia about the primary axes and $\dot{\varphi}_x$, $\dot{\varphi}_y$ and $\dot{\varphi}_z$ are the angular acceleration about these axes (roll, pitch, yaw).

**Fig. 4. Wing deformation.** Examples of trailing-edge deflections taken from two individual rose chafers during aerial manoeuvres where the beetle is turning towards its right (A) and its left (B). The top and central panels show the deflection from the left and right wings, respectively. The bottom panel shows the difference in the deflections (left minus right wing). Colours correspond to colour coded landmarks in Fig. 1A. The ‘inner wing’ (i.e. left wing in a turn to the left of the beetle and right wing in a turn to the right) is highlighted in red in the insets representing the turning beetles (top).
The moment of inertia of the prolate spheroid about the primary x-, y- and z-axes is:

\[ I_x = \frac{2}{5} M \times \left( \frac{b}{2} \right)^2, \]

\[ I_y = I_z = \frac{1}{5} M \times \left( \frac{b}{2} \right)^2 + \left( \frac{a}{2} \right)^2. \]  

Statistical analyses

Wing kinematics and deformation during the three flapping cycles of the 23 beetles were averaged every 5% of the flapping cycle duration by interpolating the data into 60 non-dimensional time steps using cubic-spline. The turns analysed were to the left or right of the beetle. We therefore use the term ‘inner’ and ‘outer’ wings (Fig. 4) where the inner wing is the left wing in a turn towards the left of the beetle and the right wing when the beetle is turning to the right. Paired t-tests were performed to test for differences in instantaneous wing kinematics between the inner wing and the outer wing throughout the flapping cycles. Data are reported as means±s.e.m.

RESULTS

Manoeuvring dynamics and wing kinematics

The beetles in the films (n=23) demonstrated a mean flight speed of 0.41±0.18 m s⁻¹ and a mean wingbeat frequency of 110±2 Hz. The average wing length was 2.08±0.05 cm. The mean wingtip velocity was 2.08±0.05 cm. The mean wingtip velocity for flapping (0.13±0.19 m s⁻¹) was much higher than the beetle’s (3D) flight speed, giving an advance ratio (flight speed/ wingtip speed=0.045±0.003). This advance ratio is low enough to assume hovering conditions (Ellington, 1984a). Similarly, the vertical component of flight speed was only 0.1±0.04 m s⁻¹; therefore, we ignored any vertical inflow. The beetles rotated about the rotation axis by 39±3 deg on average and at a mean turn rate of 1429±124 deg s⁻¹ (Fig. 2). Fig. 3E,F illustrates the change in the beetles’ Euler angles and their time derivatives (angular speeds) during the three flapping cycles comprising the manoeuvre.

During turning, the wingbeat amplitude of the inner wing was higher than that of the contralateral wing (Fig. 3A). It also slightly preceded the outer wing in stroke reversals (Fig. 3A,B). Differences in flapping kinematics were pronounced during the first flapping cycle but began to subside in the second flapping cycle, and by the beginning of the third flapping cycle there was no apparent difference in wing flapping angle. Moreover, after the third wing supination (ventral stroke reversal), the flapping asymmetry seemed to reverse direction, with the outer wing leading and having higher amplitude (Fig. 3). The incidence angle (α<sub>t</sub>) demonstrated a similar waning pattern (between flapping cycles 1–3) to that of the flapping angle. At mid-downstroke, the incidence angles were slightly larger in the inner wing (Fig. 3; Table S1). At mid-upstroke, the inner wing performed smaller wing pitch relative to the direction of wing movement (Fig. 3B). The maximal contralateral difference in incidence angle was higher at the upstroke (19.1 deg at 0.85 of the flapping cycle) than at the downstroke (8.22 deg at 0.2 of the flapping cycle). The deviation angle slightly differed between the wings, with the inner wing deviation angle being higher (Fig. 3C; Table S1). The stroke plane angle remained similar between the wings (paired t-test, t<sub>22</sub>=0.528, P=0.603; Fig. 3).

Wing deformation

The wings of P. cuprea elastically deformed during flapping. During the downstroke, the trailing edge deflected towards the ventral side of the wing, forming wing twist and camber (Fig. 4). During the upstroke, the trailing edge deflected towards the dorsal side of the wing, restoring wing twist and camber in the inverted wing. While the entire trailing edge elastically deformed throughout the flapping cycle, the magnitude of deflection decreased gradually from wing base to wing tip (Table 1, Fig. 4). Turning resulted in consistent contralateral asymmetry in elastic wing deformation (Fig. 4).

The highest instantaneous differences in wing deformation between the contralateral wings occurred at stroke reversals, during which differences in the flapping angles were also highest. Smaller but obvious asymmetries also occurred during midstroke (Fig. 5). The contralateral asymmetry in wing deformation was coupled with the manoeuvre direction, i.e. when turning to the right, the trailing edge of the right wing experienced greater deformation than the trailing edge of the left wing, and vice versa. The angle of incidence for the compliant wing (α<sub>i</sub>), shown in Fig. 3B, was larger than the angle of incidence that the wings would have achieved had they been rigid (α<sub>r</sub>). The trailing edge deformations increased the incidence angle on both the downstrokes and upstrokes and had an attenuating and even reversing (in the upstroke) effect on the bilateral asymmetry in the incidence angle of the rigid leading edge. Moreover, the elastic deformation appears to have had an attenuating effect on the rate of incidence angle change during stroke reversals (Fig. 6).

Estimated forces and torques

In 20 of the beetles, for which we had body mass data, the average vertical force calculated from the quasi-steady model succeeded in explaining 75±7% of body weight support in air (after accounting for any vertical acceleration of the beetle). The beetle’s aerial rotation involved mostly roll and yaw (Figs 2A and 3E). Concordantly, the roll torque estimated from the wing kinematics peaked at mid-upstroke and generated rotation towards the inner wing in the first two flapping cycles (Fig. 7B; see Fig. S3 for the contribution of each wing). Yaw torques also peaked at mid-stroke...
and on average generated rotation towards the outer wing. Applying the incidence angle of the rigid leading edge in the model gave a net roll torque which would not explain the observed body rotation (Fig. 7B; Fig. S3). The estimation of the torque required to rotate the beetles about their body axes was in general agreement with the net aerodynamic torque due to flapping the flexible wings (Fig. 7E,G). The agreement was most pronounced in the first flapping cycle and decreased in the consequent cycles. A breakdown of the model to show the contribution of each of the forces to the net torque can be found in Figs S4 and S5, and Table S2.

DISCUSSION
The empirical measurements reported here demonstrate that temporal asymmetry in wing deformation between contralateral wings is a significant component of the flapping asymmetry during rose chafer turns. Namely, we show that, in rose chafer, the asymmetry in flapping kinematics of the rigid section of the wing (leading edge) is mitigated by chord-wise wing compliance, resulting in smaller asymmetry in the incidence angle of contralateral wings.

Steering wing kinematics
To rotate their body about the vertical axis, rose chafer increased the flapping amplitude of the inner wing and increased and decreased the incidence of this wing, compared with the contralateral (outer) wing, at the downstroke and upstroke, respectively (Fig. 3). The attenuation in contralateral differences in flapping kinematics during the three flapping cycles observed in the means of all beetles (Fig. 3) probably reflects higher torques applied at the beginning of the turn. However, it may also have been affected by our combining data from beetles performing slower or larger turns, which require asymmetric flapping during three flapping cycles, with data from beetles performing fast or smaller turns, which require asymmetric flapping during two or one flapping cycles. There seems to be some evidence for a change in directionality of the flapping asymmetry towards the last upstroke (flapping cycle 3 in Fig. 3), supporting the idea that counteracting torques at the end of the manoeuvre actively stop the rotation of the body (Cheng et al., 2011; Hedrick et al., 2009).

Studies on fruit flies described their steering kinematics for yaw and roll during free flight (Beatus and Cohen, 2015; Bergou et al., 2010). To yaw, fruit flies modulate their wing pitch. They increase the pitch angle of the downstroke compared with the upstroke in the inner wing (Bergou et al., 2010). Our beetle did the same, as seen in the first two flapping cycles of Fig. 6B. To roll, fruit flies increased the amplitude of the outer wing (Beatus et al., 2015), which contradicts our observations on the beetles. However, the fruit flies also supinated the outer wing at an angle that was smaller relative to that for the inner wing. As a result, the AoA of the outer wing should be higher than that of the inner wing, at least during part of the upstroke. This was the case in our beetles as well (Fig. 6B). The steering kinematics of our beetles seem to reflect the fact that the manoeuvres were not about one primary body axis but rather involved a combination of roll, pitch and yaw.

Wing deformation
The extensive wing deformations during both the downstroke and upstroke followed the general trend previously reported for these beetles during straight slow flight (Meresman and Ribak, 2017). However, while turning, the flapping asymmetry resulted in
differences in the chord-wise deformation of contralateral wings that peaked at stroke reversals and mid-strokes (mostly upstrokes) (Fig. 5). The high asymmetry in elastic deformation during stroke reversal was primarily due to slight changes in timing of the left and right wing rotation (see below). In contrast, the asymmetry observed in the angle of incidence ($\alpha$) at midstroke was not a temporal effect of one wing lagging behind the other. Rather, it seemed to be a genuine change in wing deformation due to asymmetry in force production.

During stroke reversals, the rapid wing rotation (pitch) typically generates suction above the wings, eliciting aerodynamic forces when the wings are at their slowest translation speed (Dickinson et al., 1999). The wing rotation generates a wave-like motion running from the wing tip towards the wing base through the flexible trailing edge (Movie 1). In addition to the flexibility of the wing veins and membrane themselves, flower chafer wings have resilin (a rubber-like protein) in the connection between some of the wing veins, further contributing to elastic wing deformation during flight (Haas et al., 2000). The resulting twist causes the proximal area to become highly cambered. Flexibility of the proximal trailing edge, as well as the different timing of wing rotation between contralateral wings, can affect steering by creating instantaneous asymmetry in force production during stroke reversal. Dickinson et al. (1993) showed that tethered fruit flies actively adjust the wing rotation delay between contralateral wings during visually evoked attempted yaw turns. As a result, the outer wing of the tethered fruit flies rotates in advance of the inner wing and the advanced timing is correlated with increased flapping amplitude of the same wing. We found the opposite in our free-flying beetles. The inner wing had a larger flapping amplitude and it consistently started rotating in advance of the outer wing during stroke reversals (Fig. 6). The discrepancy may reflect tethering effects and/or the fact that our manoeuvres were not pure yaw rotations. Regardless of the discrepancy, a closer examination of the rotation of the rigid leading edge of both wings in our beetles (Fig. 6A) reveals that they rotated at the same time but that the rotation amplitude (total angular displacement about the wing length) of the outer wing was 26% higher, meaning that it was moving at a higher mean angular velocity. The compliant area of the trailing edge lagged behind the leading edge, thus delaying the rotation of both wings (compare the
slopes adjacent to the stroke reversal points in Fig. 6), but less so for the inner wing. Thus, the difference in stroke reversal timing between contralateral wings might simply be a consequence of contralateral force asymmetry acting on chord-wise flexible wings. Chord-wise flexibility also attenuated the differences in wing rotation amplitude, allowing a smoother transition between the two half-strokes and starting each half-stroke with a larger AoA in both wings.

During wing translation, the chord-wise wing deformation resulted in twist and camber, thus increasing the effective AoA beyond the incidence angle of the rigid leading edge in both the inner and outer wings, and decreasing the contralateral asymmetry in incidence angle of the compliant wings compared with the rigid leading edges (Figs 3B and 6A). Nevertheless, the incidence angle in the inner wing remained larger during the downstroke and lower during the upstroke compared with that for the outer wing. During upstroke, the incidence angle on the compliant inner wing was up to 12±2% smaller than on the outer wing. As explained above, lowering the pitch angle of the inner wing should affect both drag and lift of this wing, prompting an unbalanced force couple that rotates the beetle in the turning direction (Bergou et al., 2010; Ribak et al., 2012).

Indeed, the flexible wings generated torques that rotated the beetles in the direction towards the inner wing (Fig. 7). Our model underestimated forces, as evident by the mean vertical force explaining only 75% of the body weight of the beetles. Such underestimation could have emerged from a combination of several simplifying assumptions made by the model. However, we were interested in the asymmetry in force production between the inner and outer wings rather than the magnitude of these forces. In that respect, it is important to note that the same assumptions regarding force production were applied in the calculation of force and torques from both wings. With respect to torques, the moment arm in our simplified aerodynamic torque model was always based on point P2 on the wing. However, we note that during flapping the span-wise position of the resultant aerodynamic force may shift, giving flying animals another way to control asymmetry in torque production between contralateral wings.

The increased incidence angle of the flexible wing (αf) compared with the rigid wing (αr), resulting in the former producing larger torques, implies that chord-wise wing flexibility contributes to increasing the torque generated by each wing, so that a small difference in the incidence angle between contralateral wings provides sufficient net torque to rotate the body with higher angular accelerations (Fig. 7). In contrast, the rigid wing kinematics results in odd torques simply because the flapping kinematics of the leading edge is intended to actuate the flexible wing so that, upon deforming, it will assume the desired incidence angle.

Two important aspects of flight performance are the ability to hover and to manoeuvre. While the former requires the ability to hold position steadily in the air, the latter requires rapid deviation from the steady-state flight. Consequently, flight stability and manoeuvrability tend to result in a trade-off, as a design for high flight stability resists manoeuvring, whereas high manoeuvrability requires constant corrections to maintain stable flight (Dickinson et al., 1998; Ellington, 1991). Zeyghami et al.
The results of these studies suggest that wing compliance increases the robustness of hovering insects against flight perturbations, providing a mechanism for adaptation to environmental challenges. The findings also highlight the importance of understanding the mechanical properties of insect wings, which can influence flight performance and maneuverability.

In conclusion, the study of compliant wings in insects offers insights into the design principles of biological systems and the potential for biomimetic applications in robotics and engineering. Further research is needed to fully elucidate the mechanisms underlying the adaptation of insect wings to different flight conditions and to explore the implications for the development of advanced flapping-wing robots.
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