The dynamics of passive feathering rotation in hovering flight of bumblebees

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Abstract

The fluid-structure interaction problem of the flapping wings of bumblebees is considered, with focus on the action of elastic joints between wings and body. Morphological measurements and kinematic reconstruction of the wing motion using synchronized high-speed video recordings are described. They provide the necessary input data for numerical modelling. In particular, for the first time, the moments of inertia of bumblebee’s wing are determined using realistic mass distribution. A computational fluid dynamics solver is combined with a dynamical model that describes the wing motion. The model consists of the wings approximated as flat plates, connected with the body by elastic hinges. The results of high-resolution numerical simulations are presented. The hinged plate model produces realistic feathering motion and accurate time-average estimates of the aerodynamic performance in hover, despite some discrepancy in the instantaneous values of aerodynamic forces compared with the fully prescribed model. A parameter sweep reveals that the hinge is not exactly tuned to maximum efficiency during hovering flight, but slightly offset away from the maximum.

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1. Introduction

Many of insect species are skilful hovering fliers that can generate positive lift during both upstroke and downstroke. This ability is achieved by large pitching (feathering angle) rotations of the wings necessary for maintaining a positive kinematic angle of attack. Earlier research (e.g., Ishihara et al. (2009); Whitney and Wood (2010); Ishihara et al. (2014); Chen et al. (2016); Ishihara and Horie (2017); Zeyghami et al. (2018)) has shown that similar kinematic patterns can be produced by a wing with only up- and downstroke motion being prescribed, and elastic hinge attachment permitting passive pitching rotation. This technique has become widespread in insect-inspired micro-robots because it eliminates the need to directly actuate the pitching rotation (Li et al., 2018; Zhang and Deng, 2017; Liu et al., 2017), and it has led to many successful designs (Farrell Helbling and Wood, 2018).

By construction, the passive rotation model mimics dipteran wings, and serves as a mechanism for regulating the high-frequency flapping motion only using low-frequency control input (Bergou et al., 2010; Beatus and Cohen, 2015). It is logical to inquire whether this control strategy can be broadly used by all flying insects. In particular, it may be suitable for hymenopterans since their hindwings are connected to the forewings by hooks. To assess the accuracy of this hypothesis, we consider the hovering flight of a bumblebee Bombus ignitus. Our work consists of morphological measurements in order to quantify the geometrical and the inertial properties of the wings, construction of a kinematic model of the insect, free-flight measurement of the body posture and of the wing kinematics, and computational fluid dynamics (CFD) simulations.

In Section 2, we reconstruct the wing kinematics of hovering bumblebees, and measure morphological parameters of the wings, including mass distribution. To the best of our knowledge, this is the first study where moments of inertia based on realistic mass distribution of an insect wing are subsequently used in CFD simulations. Thus, we introduce a torsion-spring hinge element in our CFD model of the bumblebee in Section 3. By varying the spring stiffness coefficient, we find the optimal value that ensures the best agreement between the simulated and measured wing kinematics. Statisti-
cal analysis of similar results obtained for multiple individuals is presented, followed by aerodynamic analysis.

Conclusions are drawn in Section 4. In particular, the results of our study suggest that the hinged plate model provides a reasonably accurate approximation of real bumblebee wing motion. Considering the hinge stiffness factor as a material parameter, we conjecture that the value that we have determined in the present study may be adequate for all flight regimes. This opens a new perspective of numerical simulation of complex flight maneuvers using only the wing-tip kinematics as input data, which is much easier to measure in experiments than the full three-dimensional wing kinematics.

2. Morphological measurement and kinematic reconstruction

2.1. Study specimens

Bumblebees (*Bombus ignitus*) from a commercial breeder (Mini Polblack, Koppert, Arysta LifeScience Asia, Japan) were maintained in laboratory conditions at Chiba University from October 2015 through September 2016. The hives were part of the flight experiment facility described in a greater detail by Jakobi et al. (2018). Individual bees were randomly selected for the measurements reported in the following sections.

2.2. Wing shape

The input data required for the numerical simulation of passive rotation includes wing shape and moments of inertia. In our model, we approximate the wings as flat plates and only take the planar shape into account. Deviation from the planar shape may have important consequences for the aerodynamic force generation but, to account for it properly, wing deformation should be taken into consideration, which is beyond the scope of this work. To obtain the outlines, 20 forewings and 18 hindwings were glued on a sheet of millimeter paper and photographic images were taken. All wings were aligned along their major axes, outlines were rescaled by their maximum chord length, then aligned to obtain the best match in the leading edge. Average forewing and hindwing contours were obtained in polar coordinates, then transformed into the original Cartesian coordinates, see Kolomenskiy et al. (2019) for more explanation. The red dotted lines in Fig. 1 show the mean forewing and hindwing contours. The dark grey and the light grey color bands show, respectively, the intervals of ±1 and ±2 standard deviation from the mean.
Figure 1: Bumblebee wing morphology. The wing outline shape, including the mean contours, ±1 and ±2 standard deviation intervals calculated using 20 forewing and 18 hindwing samples, the outline shapes of selected intact samples, and the closed-contour approximation used in the CFD simulations. Red, green and blue lines show the position of the veins on the wing. Three different colors are used for visual distinction between different lines that have different numbers, each having its distinct constant diameter in the model. The corresponding biological classification (Michener, 2007, page 50) is shown in the right, for reference. The black and white marker shows the center of mass situated at $x_c/R = 0.379$ and $y_c/R = -0.019$. 
Some of the wing samples were relatively intact and others were worn. This factor contributed to the wing shape variability. The elastic hinge model discussed in this paper may help to better understand the effect of wing wear on flight performance and behavior of bumblebees, which is an intriguing topic in its own right (Haas and Cartar, 2008; Mountcastle et al., 2016). At this stage, however, we are mainly interested by the performance of nominally intact wings. Therefore, in addition to the statistical analysis, one image of an intact wing was digitized for the purpose of extracting the wing contours for the CFD model and vein coordinates for the mass distribution model described in the next section. This wing contour is shown in Fig. 1 with a black dash-dot line. Most of its part lies within the $\pm 1$ standard deviation band, and it lies entirely in the $\pm 2$ standard deviation band. The veins are shown as continuous red, green and blue lines. In the CFD simulations, the wing is represented as a closed contour using Fourier series (Engels et al., 2016b). The latter is shown with a black solid line.

2.3. Wing mass and moments of inertia

Since wing length varies between individuals, it is important to measure the concomitant variation of the wing mass. For this purpose, 13 individual bees were cold-anaesthetised, their wings were clipped and immediately weighed using a precision balance (AUW220D, Shimadzu, Japan) with display resolution 0.01 mg in the fine mode. We defined $m_w$ as the total mass of one forewing and one hindwing. The wing length $R$ from the shoulder to the forewing tip was measured using a digital caliper. We found that the linear regression slope of log $m_w$ as a function of log $R$ is equal to 3.04, which means that the scaling is close to isometric, see Fig. 2(a) and Kolomenskiy et al. (2019). Thus, isometric scaling

$$m_w = (0.2251 \pm 0.0296)R^3$$  \hspace{1cm} (1)

was applied in the subsequent analysis, where $R$ is in meters and $m_w$ is in kilograms. For example, a 15 mm-long forewing and a matching hindwing in sum would weigh $(0.76 \pm 0.10)\text{mg}$, according to this scaling. The forewing and the hindwing mass relative to the total wing mass was estimated from 4 samples as $m_f = 0.806m_w$ and $m_h = 0.194m_w$, respectively.

The moments of inertia were calculated by integration of the distributed mass, as explained in greater detail in Kolomenskiy et al. (2019). In an additional measurement (3 samples), wings were divided in segments and
each segment was weighed. Then, the veins and the membrane were treated separately. The vein thickness, necessary for estimating the vein mass distribution, was measured using a micro-CT scanner (inspeXio SMX-100CT, Shimadzu, Japan), at the vein midpoints. The veins were approximated as circular cylinders having uniform material density equal to that of cuticle, 1300 kg m$^{-3}$ (Vincent and Wegst, 2004). Hence, the vein moments of inertia were calculated as line integrals along the paths shown in Fig. 1. Contribution of the membrane to the moments of inertia was estimated by surface integration using a bilinear surface density distribution $\rho_f(x,y) = \rho_{f0} + x\rho_{fx} + y\rho_{fy}$ for the forewing, and a uniform distribution $\rho_h(x,y) = \rho_{h0}$ for the hindwing. The latter simplification is justified by the hindwing being much lighter than the forewing (19% of the full wing mass), and the membrane’s weight being of about 10% of the hindwing mass. The fitting parameters were evaluated by minimizing the r.m.s. difference between the calculated and the measured mass of the wing segments, to obtain $\rho_{f0}/R = 0.826\text{kg m}^{-3}$, $\rho_{fx} = -0.798\text{kg m}^{-3}$, $\rho_{fy} = 0.672\text{kg m}^{-3}$, $\rho_{h0}/R = 0.045\text{kg m}^{-3}$. Finally, by summing up the vein and the membrane contributions, we obtained the following isometric scaling relationships for the moments of inertia:

$$J_{xx} = 0.0014R^5, \quad J_{yy} = 0.0426R^5, \quad J_{xy} = -0.0010R^5,$$  \quad (2)
where $R$ is in meters and $J_{xx}$, $J_{yy}$, $J_{xy}$ are in kg m$^2$. Afterwards, the values obtained from (3) are used as input data for CFD simulations.

Since veins account for more than 60% of the wing mass (Kolomenskiy et al., 2019), and our calculation assumes circular piece-wise constant cross-section, the approximation error may be significant. One can notice in the micro-CT images in Supplementary figure SF1 that some of the veins have non-circular cross-section and variable thickness. In addition, stigma is treated as belonging to vein number 2. Spatial resolution of the micro-CT data precludes accurate modelling of these features. We only measure the maximum and the minimum thickness of each vein. The vein thickness deviates by less than 26% from the nominal mid-point diameter. To estimate the resulting error, we repeat the inertia calculations 33 times with the vein diameters taken randomly within the measured interval. Thus, we obtain the standard deviation of the moments of inertia,

$$
\Delta J_{xx} = 0.00006R^5, \quad \Delta J_{yy} = 0.00140R^5, \quad \Delta J_{xy} = 0.00023R^5. \quad (3)
$$

### 2.4. Three-dimensional kinematic reconstruction

Free-flight measurements were acquired using a setup that consisted of a tunnel with transparent ceiling that was connected with the hive on one end and with a feeding area on the other end, see Fig. 3. A feeder filled with sugar water solution was installed in the feeding area. The bees were trained to fly through the tunnel. Hovering behaviour was observed when a bee was either distracted by lights, or approached an obstacle in the middle of the tunnel, or preparing to exit from the tunnel. In the duration of the experiment, the humidity was near 80% and the temperature was maintained at about 22°C. The test section in the flight tunnel was illuminated using lights. Video recordings were acquired using three synchronized high-speed cameras (FASTCAM SA3, Photron, Japan), equipped with CCTV lens (B2514D or B5014A, Pentax, Japan) at 2000 fps. The image resolution was set to 1024 × 1024 pixels. The shutter speed varied between 1/10 000 s and 1/5000 s, since we changed the position of the cameras and the lights several times during the experiment. All three views were used to track the body, but only two were used to track the wings. Sample frames from two cameras, with a zoom on the insect, are shown in Fig. 4. An extended description of the experiment and data acquisition setup can be found in Jakobi et al. (2018).

We modified the direct linear transform open-source software DLTv5 (Hedrick, 2008) by introducing the same kinematic model as used in the
Figure 3: Flight experiment.

Figure 4: Sample frames from two synchronized video recordings: camera 1 (top row) and camera 3 (bottom row). Frames 517 and 520 correspond to downstroke, frames 525 correspond to upstroke. Theoretical rigid wing contour lines, shoulder points (plus signs) and body markers (dots) are superposed on the images.
CFD solver FluSI (Engels et al., 2016b). Each forewing-hindwing pair is approximated as a single solid flat plate that can rotate about the hinge point at the shoulder, therefore its orientation with respect to the body is fully described with three angles. The body is also assumed rigid, therefore, it is straightforward to relate the position of the shoulder points in the laboratory reference frame to the position of the center of mass and the three Euler angles of the body.

Figure 5 explains the definitions of the kinematic angles used in this study. During hovering, the body orientation is determined by the inclination angle $\beta$ between the horizontal plane and the longitudinal axis of the body, since the body roll is negligibly small and the azimuthal orientation has no practical importance. The anatomical stroke plane is inclined by an angle $\eta$ with respect to body such as to best-fit the trajectories of both wing tips while respecting the bilateral symmetry. The positional angle $\phi$ is defined as the angle between the lateral direction in the body reference frame and the projection of the wing longitudinal axis on the stroke plane, then $\theta$ defines the angular elevation with respect to the stroke plane, and the feathering angle $\alpha$ measures the wing rotation about its longitudinal axis. Note that, when $\alpha = 0$, the wing is perpendicular to the stroke plane.

For each video, we first select a hovering sub-sequence such that minimal velocity and constant orientation are maintained for at least 5 wing beats. To determine the body position and orientation, we either use a triangular tag affixed on the dorsal side of the thorax (Jakobi et al., 2018) or morphological features as described in Appendix A. Subsequently, we track the wing tips, calculate their trajectories in the reference frame moving with the body, find the stroke plane angle and the wing kinematic angles with respect to the stroke plane. Finally, we use Fourier analysis to derive the closest periodic and symmetric representation of the measured wing kinematics. An extended explanation of this procedure is provided in Appendix A.

In total, 7 video sequences have been analyzed, that correspond to hovering flight of different individuals. These videos have been published in an online repository (Kolomenskiy et al., 2018). The measured parameters include the wing length $R$, the wing beat frequency $f$, the body inclination angle $\beta$ and the anatomical stroke plane angle $\eta$, see Table 1, as well as the time-periodic wing angles $\phi$, $\alpha$ and $\theta$ as functions of the wing beat time fraction $t/T$, see Fig. 6, where $T = 1/f$. In addition, Table 1 contains the values
Figure 5: Definition of the wing positional angle $\phi$, feathering angle $\alpha$, elevation angle $\theta$, body angle $\beta$ and anatomical stroke plane angle $\eta$. $O_x$ is one of the two shoulder points, $O_b$ is the body center of mass.

of four derived parameters: the mean chord length

$$c = R/AR,$$

where $AR = R^2/S = 3.66$ is the aspect ratio evaluated using the area $S = \int_{wing} dx dy = 0.273R^2$ of the intact wing in Fig. 1, the radius of the second moment of area calculated using the same intact wing contour,

$$r_2 = \sqrt{\frac{1}{S} \int_{wing} x^2 dx dy} = 0.57R,$$

the reference average wing speed

$$U_2 = 2\Phi fr_2,$$

and the Reynolds number

$$Re_2 = U_2c/\nu.$$

The average wing-tip speed is equal to $U_t = 1.75U_2$ and the wing-tip Reynolds number is equal to $Re_t = 1.75Re_2$. The air density and kinematic viscosity at $22^\circ C$ are taken as, respectively, $\rho = 1.197 \text{ kg m}^{-3}$ and $\nu = 1.53 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$.

2.5. Body mass measurement

Body mass is not required as input data by the present analysis, but such information might be helpful for developing better insight into the problem.
Figure 6: (a) Positional angle $\phi$, (b) feathering angle $\alpha$ and (c) elevation angle $\theta$ as periodic functions of time $t$ normalized by the wing beat period $T$, for each individual flight.
Table 1: Hovering flight parameters.

| Individual | $R$, mm | $f$, Hz | $\Phi$, $^\circ$ | $\beta$, $^\circ$ | $\eta$, $^\circ$ | $c$, mm | $r_2$, mm | $U_2$, m s$^{-1}$ | $Re_2$ | $m$, mg |
|------------|---------|---------|-------------------|-------------------|-------------------|--------|-----------|-----------------|--------|--------|
| #1         | 15      | 145.1   | 139.4             | 50                | 44.7              | 4.1    | 8.6       | 6               | 1617   | –      |
| #2         | 15.3    | 132.3   | 121.4             | 45.4              | 47.9              | 4.2    | 8.7       | 4.9             | 1332   | –      |
| #3         | 18.2    | 138.2   | 130.4             | 30                | 64.2              | 5      | 10.4      | 6.5             | 2123   | –      |
| #4         | 15.2    | 136     | 137.4             | 41                | 53                | 4.2    | 8.7       | 5.6             | 1534   | 418    |
| #5         | 15.6    | 152.3   | 139.9             | 44                | 45.3              | 4.3    | 8.9       | 6.6             | 1843   | –      |
| #6         | 14.6    | 144.6   | 129.3             | 47.8              | 41                | 4      | 8.3       | 5.4             | 1415   | –      |
| #7         | 15.5    | 132.7   | 116.2             | 36.6              | 60                | 4.2    | 8.8       | 4.7             | 1309   | –      |

In a separate measurement, we weighed 13 individuals on a precision balance (FZ-300i, A&D, Japan) and measured the wing length using a digital caliper. Figure 2(b) shows the results of these measurements. The mass $m$ varied between 152 mg and 668 mg. The wing length $R$ varied between 12 mm and 18.2 mm. An isometric relation

$$m = (100.4 \pm 19.2)R^3$$

fits the data, where $R$ is in meters and $m$ is in kilograms. It follows from comparison with (1), for instance, that the full set of wings only weigh as little as 0.45% of the bee.

In addition, we weighed individual #4 immediately after recording its flight. The result is included in Table 1. It differs by 18.6% from the isometric fit (8), i.e., falls within one standard deviation interval above the isometric fit. This is shown using a large cross marker in Figure 2(b). Note that large variation of the measured body mass relative to the average trend is expected as some bees might be loaded up with pollen and sugar solution.

3. Dynamical simulation and analysis

3.1. Numerical bumblebee model

The computational approach followed in the present study is in continuity with our previous work (Engels et al., 2016b,a; Ravi et al., 2016). We employ FluSI$^1$, a Fourier pseudo-spectral solver with volume penalization (Engels et al., 2016b). In the simulation, the bumblebee is approximated by three

$^1$Open source code available at https://github.com/pseudospectators/FLUSI
rigid elements: the body and two wings, which move with respect to each other. The wings are flat plates such that the forewing and the hindwing are treated as one piece, with the planform shown in Fig. 1 constructed using Fourier series representation (Engels et al., 2016b). The wing thickness is equal to 0.0125R. An idealized body shape is used, similar to our earlier work Engels et al. (2016a). It is composed of analytically described surfaces of the head, thorax, abdomen, antennae, proboscis and legs. The distance between the shoulder hinge points is equal to 0.351R, which differs slightly from the value used by Engels et al. (2016a). The body and the wings are isometrically scaled such as to match the wing length R as given in Table 1.

In all numerical simulations in the present study, the body is fixed in the laboratory reference frame. Prescribed time-periodic functions φ(t) and θ(t), as shown in Fig. 6, determine the position of the wing tip. Rotation of the wing about its longitudinal axis is described by α(t) which is determined from an elastic hinge model similar to that proposed by Whitney and Wood (2010). The model employs an equivalent linear torsional spring-damper element as an abstraction for the combined effect of the compliance and structural damping of the muscles, shoulder joints and proximal parts of the wings. We infer the model coefficients from minimizing the discrepancy between simulated and measured time series of α(t), as we explain later in Section 3.3. In the numerical simulation, the feathering angle α(t) is determined from the equation of passive feathering motion,

\[
J_{xx} \ddot{\alpha} = M_{\text{aero}} - K(\alpha - \alpha_0) - C\dot{\alpha} \\
+ J_{xx} \left[ \frac{1}{2} \left( \dot{\phi}^2 \cos^2 \theta - \dot{\theta}^2 \right) \sin 2\alpha - \dot{\phi} \sin \theta - \dot{\phi} \dot{\theta} \cos \theta (1 + \cos 2\alpha) \right] \\
+ J_{xy} \left[ \dot{\phi} \cos \theta \cos \alpha + \dot{\theta} \sin \alpha + \frac{1}{2} \dot{\phi}^2 \sin 2\theta \sin \alpha - 2\dot{\phi} \dot{\theta} \sin \theta \cos \alpha \right],
\]

where \( M_{\text{aero}} \) is the aerodynamic pitching moment, \( K \) is the elastic hinge stiffness coefficient and \( C \) is the hinge structural damping coefficient, \( \alpha_0 \) is the rest angle. Positive \( \theta \) is upwards. Typically, \( \alpha \) is positive during downstroke and negative during upstroke. The moments of inertia are calculated using the isometric scaling laws (3).

The aerodynamic pitching moment \( M_{\text{aero}} \) is obtained from numerical solution of the Navier–Stokes equations using a Fourier pseudo-spectral method with volume penalization to handle the no-slip boundary conditions on the time-varying geometry (Engels et al., 2016b). Geometrical representation of
the bumblebee is encoded in a penalization term that enters in the momentum equation, where the penalization constant is set to $C_\eta = 1.15 \times 10^{-4}/f$.

The air is treated as a viscous incompressible fluid. The penalized Navier–Stokes equations are solved on an equidistant uniform Cartesian grid using a Fourier pseudo-spectral discretization. The computational domain is a periodic cube with side length $3.2R$, discretized using $1024^3$ grid points (over 1 billion grid points). This yields the resolution of 320 points per wing length and 87 points per mean chord length. Impermeable floor and vorticity sponge layers on the side walls are applied using volume penalization in order to prevent spurious recirculation of the flow. The bumblebee body centre of mass is offset by a distance of $0.1R$ above the centre of the domain. This leaves enough space (about $1.4R$) between the wings and the floor to ensure that the aerodynamic ground effect is negligible (Kolomenskiy et al., 2016).

Strong fluid-structure coupling is used. Equation (9) is transformed in a system of two first-order differential equations and discretized using the second-order Adams–Bashforth scheme. Since the same time marching scheme is also used in the Navier–Stokes solver, it is straightforward to evaluate the right-hand side of the evolution equations, for both the fluid and the solid, at the same time level. Knowing the right-hand side at the previous and at the current time levels, as well as the values of the state variables at the current level, the Adams–Bashforth formula yields the values of the state variables at the next time level that ensure globally second-order accuracy with respect to time. The numerical discretization grid step, time step and domain size independence checks are presented in the Supplementary material S2.

Quasi-periodic regime is in our case is reached after three wing beat cycles. Therefore, we use the results obtained during the 4th wing beat cycle for analysis in this study, unless otherwise is stated. One simulation requires about 200 hours elapsed time using 320 CPU cores of a scalar type computer at JAMSTEC, Yokohama, which consists of HPE Apollo 6000 and HPE Apollo 2000 nodes, or it takes 35 hours on 8192 CPU cores of the IBM Blue Gene/Q computer at IDRIS, Orsay.

3.2. Example time sequences

Let us begin the discussion of the numerical results with focusing on one selected flight. We choose individual #4 for which the body mass is known, see Table 1. Fig. 7 depicts the time evolution of feathering angle $\alpha$, vertical and horizontal aerodynamic force $F_{az}$ and $F_{ax}$, respectively, normalized by
the body weight $mg$, and the aerodynamic power $P_a$ divided by the body mass $m$. Two numerical simulations are compared. In the first, $\alpha(t)$ is prescribed as shown in Fig. 6(b). In the second, $\alpha(t)$ is passive, i.e., it is modelled using equation (9) as explained in Section 3.1, with $K = 2.61 \mu \text{N.m, } C = 0$ and $\alpha_0 = -1.38^\circ$. These two time profiles are compared in Fig. 7(a). They agree qualitatively well in terms of the overall shape, the amplitude and the phase, which means that the passive feathering model with only three free parameters can fit $\alpha(t)$ adequately. The main difference is in the shape of the peaks: they are sharper for the passive (modelled) profile than for the prescribed one, especially on upstroke.

Besides that, there is a small phase lag between the passive and the prescribed profiles of $\alpha(t)$. As we show later in this section, although it is possible to control the phase by varying $K$ and $C$, no fine-tuning of the hinge model parameters can reduce this phase lag below a certain threshold, which appears to be small positive in the case of individual #4 shown here and for the individual #2, but almost zero for #1 and small negative for #3. Therefore, this small residual phase lag seems to be a measurement error rather than a modelling artifact.

Three-dimensional reconstruction in Fig. 8 provides a visual explanation how orientation of the wing changes in time. This motion is indeed very typical of the flapping wings of insects in hover. Additional three-dimensional visualization of passive feathering rotation and vortical structures in the wake is provided as a Supplementary video.

The vertical aerodynamic force, Fig. 7(b), shows two distinct peaks around the middle of each translation phase. They are larger but narrower in the case of passive rotation, which is consistent with the differences in $\alpha(t)$ discussed above. The pointwise difference in $F_{\alpha z}(t)$ is particularly large on upstroke, when $\alpha$ differs by as much as $20^\circ$. However, this overestimate cancels out with the underestimates before and after the peak, such that the wingbeat time-average force, as shown with the dashed lines, is almost identical in the two cases and it is 8% less than the body weight (the last column in Table 1). The horizontal force, see Fig. 7(c), shows similar trends with the difference that the peak associated with the upstroke is negative, such that the time-average horizontal force is close to zero. The body-mass specific aerodynamic power, Fig. 7(d), averages to $59 \text{ Wkg}^{-1}$ and $63 \text{ Wkg}^{-1}$, respectively, in the cases of prescribed and passive wing rotation. Note that both values are significantly smaller than previously reported $84 \text{ Wkg}^{-1}$ (Engels et al., 2016a), obtained using a similar numerical bumblebee model with simplified wing
Figure 7: Time evolution of (a) the feathering angle, (b) the vertical and (c) the horizontal aerodynamic force components normalized with the body weight, and (d) the body-mass specific aerodynamic power. The time interval shown corresponds to the fourth wing beat cycle.
In summary, the passive wing rotation model (9) is successful in reproducing the main dynamical features. Furthermore, it accurately predicts the time-average quantities. With regard to the instantaneous values, discrepancy can be large. It may be explained by the fact that the model does not account for deformation of the wing. In particular, rotation of the hindwing relative to the forewing should be taken into account. This could help to improve the fidelity of the three-dimensional tracking and the numerical simulations alike. However, it is likely that the simple solid-plate model will be sufficient for flight dynamics simulations that mainly depend on wingbeat-average forces.

Let us now discuss sensitivity of the results to the elastic hinge parameters $K$, $C$ and $\alpha_0$. Since these parameters cannot be measured directly, they will be evaluated by fitting the model to the experiment data. It will be insightful to see the influence of each parameter separately before solving the full optimization problem. Figure 9 displays such variation of $\alpha(t)$. The parameters are varied around the conditions of the previous simulation. While the most noticeable effect of increasing $K$ is to reduce the amplitude of $\alpha$, there is significant asymmetry between stiffening and loosening the hinge with respect to the average value $K = 2.42 \, \mu\text{N.m}$. In addition, hinge loosening entails some significant phase delay with respect to the experiment data. The effect of increasing $C$ is also to reduce the amplitude of $\alpha$, however, it is accompa-
nied with a phase shift in the opposite direction. The limiting case \( C = 0 \) has the least phase shift. Finally, varying \( \alpha_0 \) primarily manifests in the overall shift of \( \alpha(t) \), i.e., the rest angle of the elastic hinge model controls the time average feathering angle with the linear gain being equal to \( \frac{d\bar{\alpha}}{d\alpha_0} = 0.41 \), where the overbar stands for time averaging over the duration of one wing beat cycle.

Contributions of each term in the passive feathering equation (9) are illustrated in Fig. 10. The aerodynamic pitching moment \( M_{\text{aero}} \) is small during the reversals near \( t/T = 0 \) and 0.5, when the translation velocity of the wing is small. \( M_{\text{aero}} \) is large positive in the middle of downstroke, it is large negative in the middle of upstroke. The inertial pitching moment

\[
M_{\text{inertial}} = -J_{xx}\ddot{\alpha}
+ J_{xx}\left[\frac{1}{2}(\ddot{\phi}^2 \cos^2 \theta - \dot{\phi}^2) \sin 2\alpha - \ddot{\phi} \sin \theta - \dot{\phi} \dot{\theta} \cos \theta (1 + \cos 2\alpha)\right]
+ J_{xy}\left[\ddot{\phi} \cos \theta \cos \alpha + \ddot{\theta} \sin \alpha + \frac{1}{2} \ddot{\phi}^2 \sin 2\theta \sin \alpha - 2\dot{\phi} \dot{\theta} \sin \theta \cos \alpha\right]
\]

peaks during rapid angular deceleration of the wing after reversal (\( t/T = 0.1 \) and 0.6). Interestingly, acceleration that precedes the reversal is much more gradual. The time profile of the restoring torque \( K(\alpha - \alpha_0) \) repeats that of \( \alpha \), and the structural damping torque \( C\dot{\alpha} \) is identically equal to zero because \( C = 0 \). By comparing the three non-trivial contributions, it can be concluded that the restoring torque of the hinge balances the inertia (mainly \( J_{xx}\ddot{\alpha} \)) in the beginning of each half-stroke (upstroke or downstroke), and it balances the aerodynamic torque in the end of half-stroke.

3.3. Optimization and statistical analysis

In this section, we look for the optimal values of \( K, C \) and \( \alpha_0 \) that minimize the cost function

\[
e = \frac{1}{T} \int_0^T (\alpha(t) - \alpha_{\text{exp}}(t))^2 \, dt,
\]

where \( \alpha(t) \) is the time evolution of the feathering angle obtained from the numerical simulation using (9), and \( \alpha_{\text{exp}}(t) \) is the feathering angle measured in the experiment.

It may be expected that the hinge parameters vary among different individuals. In this section, we quantify this inter-individual variability and
Figure 9: The effect of (a) varying $K$ with $C = 0$ and $\alpha_0 = -1.38^\circ$; (b) varying $C$ with $K = 2.42$ μN·m and $\alpha_0 = -1.38^\circ$; (c) varying $\alpha_0$ with $K = 2.42$ μN·m and $C = 0$. The time interval shown corresponds to the fourth wing beat cycle.
Figure 10: Time evolution of the left wing pitching moment due to the aerodynamic forces ($M_{aero}$), inertia ($M_{inertial}$), hinge stiffness ($K(\alpha - \alpha_0)$), and hinge damping ($C\dot{\alpha}$). The time interval shown corresponds to the fourth wing beat cycle.

determine the values that can be taken as representative of hovering Bombus ignitus in general. The full set of 7 individual hovering flights have been divided in the training set (#1 to #4) and the test set (#5 to #7). For each individual in the training set, a parameter sweep is performed to find the optimal stiffness $K_{opt}$ that minimizes the r.m.s. distance between $\alpha(t)$ in the simulation and the experiment, $e_{opt}$. Prior to the parameter sweep, $\alpha_{0opt}$ that ensures equal time-average $\overline{\alpha}$ in the simulation and in the experiment, is determined using linear extrapolation of an auxiliary simulation with $\alpha_0 = 0$ and the slope $d\overline{\alpha}/d\alpha_0$ known from previous simulations. Zero structural damping, $C = 0$, is assumed in all cases. Additional simulations with $K = K_{opt}$, $\alpha_0 = \alpha_{0opt}$ and $C = 0.66$ nN m s confirm that $e$ becomes larger than $e_{opt}$ obtained with $C = 0$. The multivariate optimization in Supplementary material S3 also supports this assumption.

In view of the isometric scaling (1) of the wing mass versus length, it is reasonable to introduce a similar isometric scaling for the hinge stiffness,

$$K = R^3K^*, \quad (12)$$

that holds for flexible-plate hinges with thickness, width and length scaled linearly with $R$ (Whitney and Wood, 2010). We refer to $K^*$ as the hinge stiffness factor. It can be regarded as a composite material property. The cost function $e$ for all individuals of the test set is plotted in Fig. 11 with
respect to $K^*$. The optima $K_{opt,i}^*$, where $i = 1, \ldots, 4$ is the individual index, are indicated with circles and included in Table 2. The average stiffness factor plus/minus standard deviation is equal to

$$K_{mod}^* = \frac{1}{4} \sum_{i=1}^{4} K_{opt,i}^* = (0.81 \pm 0.089) \text{ N m}^{-2}. \quad (13)$$

Table 2 also contains the values of $\alpha_{0opt}$ of each individual in the training set. They average to $\alpha_{0mod} = (-0.75 \pm 8.97)^\circ$.

Let us now verify that these values $K_{mod}^*$ and $\alpha_{0mod}$ are representative of all individuals, including those in the test set. For that purpose, numerical simulations are performed with the hinge stiffness calculated using (12) with the stiffness factor $K_{mod}^* = 0.81 \text{ N m}^{-2}$, zero structural damping ($C = 0$), and rest angle $\alpha_{0mod} = -0.75^\circ$. The results shown in the last two columns of Table 2 suggest that these values are indeed representative of all individuals since, typically, $e_{mod}$ is close to $e_{mod}$. Further, a two-sample t-test for equal means without assuming equal variances has been applied. Mean $e_{mod}$ is equal to 8.178$^\circ$ and 9.76$^\circ$, for the training and the verification sets, respectively. It has shown no significant difference in the mean $e_{mod}$ of the two datasets ($p = 0.23$).

Table 2: Inter-individual variability of the elastic hinge.

| Individual | Dataset | $K_{opt}$, N m$^{-2}$ | $K_{opt}$, $\mu$N m | $C h_{opt}$ | $\alpha_{0opt}$, $^\circ$ | $e_{opt}$, $^\circ$ | $K_{mod}$, $\mu$N m | $e_{mod}$, $^\circ$ |
|-----------|---------|------------------------|---------------------|------------|----------------------|-----------------|----------------------|----------------------|
| #1 training | 0.888 | 3.00 | 1 | 11.69 | 7.23 | 2.73 | 7.44 |
| #2 training | 0.722 | 2.57 | 0.81 | -3.8 | 9.57 | 2.89 | 9.95 |
| #3 training | 0.885 | 5.34 | 1.18 | -9.5 | 6.33 | 4.88 | 6.89 |
| #4 training | 0.744 | 2.61 | 1.05 | -1.38 | 7.94 | 2.84 | 8.43 |
| #5 validation | - | - | - | - | - | 3.08 | 7.94 |
| #6 validation | - | - | - | - | - | 2.52 | 10.69 |
| #7 validation | - | - | - | - | - | 2.99 | 10.64 |

To evaluate the relative flexibility of the wing under the aerodynamic load, Ishihara et al. (2014) calculated the Cauchy number of different dipterans,

$$C h = \frac{4\rho \Phi^2 f^2 c^3 r_2^2}{K} \quad (14)$$

using data from multiple sources, and found that $C h$ varied between 0.19 and 0.27. Similar values for the bumblebees are included in Table 2, denoted
Figure 11: Parameter search for the best-fit hinge stiffness. R.m.s. distance $e$ between time profiles of measured and computed feathering angle is plotted as a function of the hinge stiffness factor $K^*$ for 4 different individuals. Crosses ($\times$) show the computed points, circles ($\circ$) show the minima in each case. The dash-dot vertical line corresponds to $K^*_\text{mod}$.

as $C_{\text{h opt}}$. They correspond to the optimal stiffness $K_{\text{opt}}$. Overall, the Cauchy number in the present study is significantly larger than reported previously by Ishihara et al. (2014) for diptera.

3.4. Aerodynamic analysis

The aerodynamic force generation capacity is conventionally measured by the lift coefficient

$$c_L = \frac{\mathcal{T}}{\frac{1}{2}\rho U_2^2 S_{\text{ref}}},$$

where $\mathcal{T} = \frac{1}{T} \int_0^T F_{az}(t) dt$ is the mean vertical aerodynamic force (i.e., lift), $U_2 = 2\Phi fr_2$ is the reference velocity and $S_{\text{ref}} = 2S$ is the reference area, with the wing area $S = 0.273R^2$ and the radius of the second moment of area $r_2 = 0.57R$ calculated for the intact wing in Fig. 1. The evolution of $c_L$ with $K^*$ is shown in Fig. 12, for all individuals in the test set. In all cases, $c_L$ is an increasing function of $K^*$ in the range considered here. I.e., $c_L$ is small when the hinge is very compliant, and $c_L$ reaches 2 when the hinge is stiffer than normal. It may be expected, by analogy with a flexible wing, that $c_L$ decreases to zero in the limit of very large $K^*$. However, in our numerical
Figure 12: Lift coefficient as a function of the hinge stiffness factor $K^*$. The dash-dot vertical line corresponds to $K^*_{\text{mod}}$, dashed lines correspond to $K^*_{\text{opt},i}$.

Simulations, we do not observe this trend even when $K^*$ is twice as large as $K^*_{\text{opt},i}$. The values of $c_L$ at $K^*_{\text{opt},i}$ vary between 1.35 and 1.7, depending on the individual.

The energetic efficiency of hovering flight can be measured using the figure of merit $FM = P_{\text{ideal}}/\overline{P}$, where $P_{\text{ideal}}$ is the ideal power determined by the Rankine–Froude momentum theory as $P_{\text{ideal}} = 2\rho w_0^3 A_0$, where $A_0 = 2\Phi R^2$ is actuator disc area and $w_0 = \sqrt{\overline{L}/2\rho A_0}$ is the induced velocity, and $\overline{P} = \frac{1}{T} \int_0^T P_a(t)dt$ is the mean aerodynamic power from the numerical simulation. After arithmetic simplification, we obtain a short formula

$$FM = \frac{L^{3/2}}{P} \frac{1}{2R\sqrt{\rho \Phi}}. \quad (16)$$

The numerical results are shown in Fig. 13. For all individuals, the plots of $FM(K^*)$ have visually similar shape with a maximum slightly to the left from $K^*_{\text{opt},i}$, steep decrease to the left and gentle decrease to the right. It follows that the elastic hinge is not exactly tuned to maximize the efficiency during hovering, but rather to ensure stable operation in a range of $K^*$ where $FM$ is only slightly less than the maximum. Thus, $FM(K^*_{\text{opt},i})$ varies between 0.17 and 0.19, while the maximum $FM$ is in the range between 0.18 and 0.2.
Figure 13: Figure of merit as a function of the hinge stiffness factor $K^*$. Dash-dot vertical line corresponds to $K^*_{\text{mod}}$, dashed lines correspond to $K^*_{\text{opt,i}}$.

4. Conclusions

The passive feathering model with rigid wings offers an attractive approximate solution to the fluid-structure interaction of flapping insect wings in the sense of pitching rotation. It requires much less input data than flexible-wing models, but still accounts for adaptation of the wing orientation to external forcing by adjustment of the feathering angle $\alpha$, which can be regarded as the lowest, and probably the most efficient, mode of elastic deformation.

In the present study, it is shown that a single hinged plate model, originally designed for diptera, also provides a reasonably accurate approximation of bumblebee wings composed of forewings and hindwings connected by hooks (humuli). Specifically, it produces realistic feathering motion and accurate time-average estimates of the aerodynamic performance in hover, despite that the instantaneous values of aerodynamic forces may differ significantly between the passive feathering and fully prescribed models. These conclusions have been reached on the basis of morphological measurements, kinematic analysis of live bumblebees, and high-fidelity numerical simulation.

Using statistical analysis, typical values of the model parameters have been determined. The hinge stiffness can be approximated as $K = 0.81 R^3$, where $R$ is the wing length in m and the result is in N·m. The structural
damping coefficient is negligible compared with the fluid damping, i.e., $C = 0$ is a fair approximation. The rest angle obtained for different individuals shows no clear trend, but the mean value is close to zero, $\alpha_0 \approx 0$.

From the aerodynamic perspective, it is found that passive feathering provides the required lift-generation capacity for a realistic energetic cost. It is interesting that the hinge parameters are not exactly tuned to maximum efficiency during hovering, but the stiffness is slightly larger than the optimal value. We conjecture that the difference may be interpreted as a safety factor that helps to avoid abrupt decrease in the efficiency when flight conditions change, but a dedicated study is needed on this point. In addition, it may be necessary to re-examine it using a fully flexible wing model, since even a slight variation of $FM$ near its flat peak may entail a qualitative change in the shape and position of the peak.

Regarding the hinge stiffness factor $K/R$ as a fictitious material parameter, one may conjecture that the value determined in hover may be adequate for all flight regimes. This opens new perspectives for numerical simulation of complex flight maneuvers using only the wing-tip kinematics as input data, which is much easier to measure in the experiments than the full three-dimensional wing motion. However, elastic element only being a mathematical abstraction of the real hinge, its stiffness may depend on flight conditions.

Another possible direction of future research is to improve the model for better agreement with the experiments. Potential improvements include treatment of the hindwings as separate plates, varying stiffness between upstroke and downstroke (Ennos, 1988; Tanaka et al., 2011), or considering nonlinear elasticity.

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Appendix A. Example of kinematic analysis

In this Appendix, the three-dimensional kinematic reconstruction process is explained with an example. The video sequence selected for the present analysis corresponds to the hovering flight #6 in Table 1.

At first, we track the body. It only moves very little during the entire time span of the video. Nevertheless, this small motion should be taken into account when calculating the wing angles, because the latter are sensitive to movement of the shoulder hinges. Therefore, we first reconstructed the three-dimensional motion of the body. Since this individual bee was not tagged, we selected three points that can easily be distinguished by morphological features. As shown in Fig. 4, point 1 is on the head between the antennae (red marker), point 2 is an abdominal pigmentation feature (green marker), and point 3 is the rear point of the abdomen (blue marker). Every 10th frame of total 1167 frames in each camera view were analyzed. The points were manually tracked and their coordinates in the laboratory reference frame reconstructed using DLTv5, the result being displayed in figure A.14(a).

Figure A.14(b) shows the velocity magnitude of each point, calculated using central finite-difference approximation. The velocity is no greater than $V_g = 0.023$ m/s, and the corresponding advance ratio is equal to $\mu = V_g/U_2 = 0.0042$. This small advance ratio is indicative of hovering.

The time sequence of almost 6 s is longer than required for digitization of the wing motion. We therefore only select a sub-sequence of 40 ms for the further analysis, which is shaded in figure A.14(b). The velocity in it is less than 0.015 m s$^{-1}$. During this short time interval, time-varying position of the three feature points in the laboratory reference frame is fitted with cubic polynomials in order to filter out the digitization noise. In the body reference frame, relative position of different points (i.e., the shoulder hinges, the center of mass and the three selected morphological features) does not vary in time, therefore, it can be determined from prior morphological measurement or
Figure A.14: (a) Trajectories of three points on the body - one on the head, one on the dorsal surface of the abdomen, and one on the rear end of the abdomen. (b) Time evolution of the velocity magnitude of these points.

time-averaging over the duration of the entire flight sequence. Hence, after reconstructing the three-dimensional motion of the selected morphological feature points, we determine the motion of the entire body including the shoulder hinge points. The latter are shown in Fig. 4 with cyan and magenta plus signs.

As a next step, we track the wing tips, reconstruct the wing tip trajectories, convert them to the body reference frame and best-fit a plane, in the least-mean-square sense. The morphological stroke plane angle is determined as the angle between the normal to that plane and the body longitudinal axis. The stroke plane, in our definition, is inclined by the same angle to the body, but it passes through the shoulder hinge points and respects the bilateral symmetry, as shown in Fig. 5.

Finally, we determine the time evolution of the wing angles with respect to the stroke plane, see Fig. 5 for the definitions. The values of the positional angle $\phi$, the elevation angle $\theta$ and the feathering angle $\alpha$ are determined for the left and for the right wing separately, for every time frame of the selected 40-millisecond video sub-sequence. It covers slightly less than 6 wingbeat periods. A first approximation to $\phi$ and $\theta$ is calculated using the approximate wing-tip coordinates relative to the hinge point, but this is complicated by the fact that the wing tips hold no point markers. Therefore, to refine $\phi$ and
θ as well as to determine α, the wing contour projection is superposed on the video image. It is drawn interactively as the values of φ, α and θ are manually adjusted for the best visual fit by varying the angles with small steps of 0.36°. For this purpose, as for the subsequent CFD simulation, we use the archetypal intact wing shown in Fig. 1, scaled with the wing length $R = 14.6$ mm determined from the video as the average distance between the shoulder and the wing tip. Example visualizations of this fit are shown in Fig. 4. The digitized left (resp., right) wing contour outline is shown with a cyan (resp., magenta) closed curve. Generally, the approximation is visually better during the downstroke (first two frames in a row) than during upstroke (last frame in a row), as the wing deformation is greater during upstroke.

The complete measured time sequences of the wing angles are displayed as markers in Fig. A.15. The resolution of 13 points is sufficiently high to describe the important repetitive features of the time profiles, such as the double negative peak of α during upstroke. The motion is nominally periodic, with small deviations that may be due to actuation, wing-wake interaction and measurement errors. The next processing step consists in low-pass filtering the data at 450 Hz using the 4th order Butterworth filter and upsampling the result on a 100-times finer grid using spline interpolation. Thus we discard those points that produce unrealistically large accelerations. The resulting time profiles are shown with dotted and dashed lines that correspond to the left and the right wing, respectively.
From frequency analysis of $\phi(t)$ we find that the flapping frequency is equal to $f = 144.6$ Hz. We use this value to divide the sequences shown in figure A.15 in cycles of length $T = 1/f = 6.92$ ms. In figure A.16(a), we plot the time evolution of $\phi$, $\alpha$ and $\theta$ during each cycle, with $t = 0$ corresponding to the beginning of downstroke. The original profiles are shown with thin faded lines. For every time instant $t$ during the cycle, we calculate the average of 4 subsequent wingbeats. The average time profiles are shown with thick bright lines in figure A.16(a), and thin bright lines in figure A.16(b). These time sequences are very close to periodic. There remains less than 10 degree difference between the angles of the left wing and those of the right wing, and we calculate their average. The result is plotted in figure A.16(b) using thick lines. Finally, Fourier analysis of these time sequences is performed. The time evolution of $\phi$, $\alpha$ and $\theta$ is described with less than 1 degree error using, respectively, 4, 5 and 4 harmonics. These coefficients are used as input data for the CFD simulation.

Appendix B. Numerical validation

Whitney and Wood (2010) conducted experiments with an insect-scale mechanically driven artificial wing that, by construction, satisfied the condi-
tions of the passive rotation model (9). The flapping motion in the direction of $\phi$ was driven by a piezoelectric actuator, while passive rotation in $\alpha$ was allowed by an elastic hinge. These angles, as well as the small out-of-plane deviation $\theta$ due to compliance, were measured simultaneously with the vertical force produced by the wing.

For numerical validation of our solver, we have performed numerical simulations of the ‘short hinge’ model of Whitney and Wood (2010) with the hinge stiffness equal to $K = 2.35 \cdot 10^{-6}$ N.m. The structural damping is negligible small, i.e., $C = 0$, and the static orientation of the wing is vertical, i.e., $\alpha_0 = 0$. Figure B.17 displays the wing shape used in these numerical simulations. It is derived from the photographic image shown in Whitney and Wood (2010) and closely repeats the outline of the wing membrane, except for some simplification near the root. The wing length is equal to $R = 15.14$ mm. Its mass is equal to $m_w = 0.91$ mg. The moments of inertia are $J_{xx} = 1.7 \cdot 10^{-12}$ kg m$^2$ and $J_{xy} = -3.5 \cdot 10^{-12}$ kg m$^2$.

The time evolution of the positional angle $\phi$ and the elevation angle $\theta$ used for the numerical simulation is obtained by Fourier analysis, Gaussian filtering and periodization of the experiment data. Since the observed motion is nominally periodic, this process does not introduce any significant error. Two different experiment runs are considered: the ‘baseline’ case with approximately symmetric upstroke and downstroke, and the ‘split-cycle’ with fast upstroke and slow downstroke. The flapping frequency equals, respectively, $f = 99.59$ Hz and 100.5 Hz, as evaluated from the measured time profiles of $\phi(t)$. In each case, we have performed two numerical simulations: one
with $\alpha$ determined from the passive feathering equation (9), and one with $\alpha$
prescribed as a periodic function derived from the experiment data. In all
numerical simulations, the properties of the air are set as $\nu = 1.53 \cdot 10^{-5}$ m$^2$ s$^{-1}$
and $\rho = 1.2$ kg m$^{-3}$.

Let us discuss the ‘baseline’ case first. Time evolution of the kinematic
angles is shown in Fig. B.18(a). To compare directly with the data presented
in Whitney and Wood (2010), since we use different sign conventions, $-\theta$ and
$-\alpha$ are shown. The result of our numerical simulation of passive feathering
rotation, $-\alpha$, is plotted using a solid blue line. It is in a good agreement
with the experiment shown with black circles, in terms of the phase and
the minimum angle. The maximum angle is slightly overestimated which
may be related to the asymmetry of the vein-membrane assembly or non-
linear elasticity of the hinge, which are not accounted for in the numerical
simulation.

A comparison of the total vertical force $F$ in this case is presented in
Fig. B.18(b). It is the sum of the aerodynamic and the inertial forces, as
directly measured in the experiment. The inertial vertical force in the nu-
merical simulation is evaluated as

$$F_i = -m_w \frac{d^2}{dt^2} (y_{cm} \cos \alpha \cos \theta + x_{cm} \sin \theta), \quad (B.1)$$

where $m_w = 0.91$ mg is the wing mass, $x_{cm} = 5.74$ mm and $y_{cm} = -1.31$ mm
are the centre of mass coordinates in the spanwise and in the chordwise direc-
tions of the wing, respectively. When $\alpha(t)$ is prescribed as in the experiment,
the force $F(t)$ follows a remarkably similar path as in the experiment. In the
case of passive feathering rotation, when $\alpha(t)$ is modelled, the overall agree-
ment is still good but the plateaus that correspond to the translation phase
are noticeably smaller. This is explained by the excess of feathering rotation:
$\alpha$ predicted by the model during the translation phase is slightly too large.
The difference appears small in the kinematics in Fig. B.18(a), but it entails
a significant discrepancy in the forces in Fig. B.18(b). The mean force $\overline{F}$ is
equivalent of 74.8 mg in the case of the prescribed motion and 52.8 mg for
the passive feathering model, to be compared with 71.6 mg measured in the
experiment. Better agreement can be achieved, presumably, if non-linearity
and asymmetry are taken into account, or if the linear spring parameters
are fitted to the measured data (as opposed to being estimated from the
dimensions and material properties of the elastic hinge).

The ‘split-cycle’ case is presented in Fig. B.19. Similarly, the peaks of
Figure B.18: Baseline validation case. (a) Measured and computed wing kinematics. (b) Time evolution of the lift.
α are slightly overestimated, which leads to overall lower lift of the passive
feathering model. The time evolution of $F$ shows oscillatory behavior due to
inertia, since $\alpha(t)$ does not plateau, in contrast with the baseline case. These
oscillations in the simulations and in the experiment agree in phase and in
magnitude for most part of the wing beat cycle, except for the beginning of
the cycle. The mean forces are equivalent of 64.9 mg in the prescribed feather-
ing simulation, 46.6 mg in the modelled passive feathering simulation and
71.2 mg in the experiment. These validation test cases allow to conclude that
the model describes the time-varying feathering angle and lift adequately. At
the same time, relatively small error in the feathering angle, that can be ex-
plained by difference between theoretical (as used here) and real stiffness of
the hinge, can have important consequences for force generation. Stiffness
tests of similar elastic hinges can be found in, e.g., Li et al. (2018). In view of
this result, it appears important to perform a parameter sweep over a range
of possible values of the hinge stiffness, as described in the main text of this
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Figure B.19: Split-cycle validation case.  
(a) Measured and computed wing kinematics.  
(b) Time evolution of the lift.
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