# 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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*Keywords:* flapping flight, insect, bumblebee, wing, fluid-structure interaction.

# 1 1. Introduction

Many of insect species are skilful hovering fliers that can generate positive 2 lift during both upstroke and downstroke. This ability is achieved by large 3 pitching (feathering angle) rotations of the wings necessary for maintaining 4 a positive kinematic angle of attack. Earlier research (e.g., Ishihara et al. 5 (2009); Whitney and Wood (2010); Ishihara et al. (2014); Chen et al. (2016); 6 Ishihara and Horie (2017); Zeyghami et al. (2018)) has shown that similar 7 kinematic patterns can be produced by a wing with only up- and downstroke 8 motion being prescribed, and elastic hinge attachment permitting passive 9 pitching rotation. This technique has become widespread in insect-inspired 10 micro-robots because it eliminates the need to directly actuate the pitching 11 rotation (Li et al., 2018; Zhang and Deng, 2017; Liu et al., 2017), and it has 12 led to many successful designs (Farrell Helbling and Wood, 2018). 13

By construction, the passive rotation model mimics dipteran wings, and 14 serves as a mechanism for regulating the high-frequency flapping motion only 15 using low-frequency control input (Bergou et al., 2010; Beatus and Cohen, 16 2015). It is logical to inquire whether this control strategy can be broadly 17 used by all flying insects. In particular, it may be suitable for hymenopterans 18 since their hindwings are connected to the forewings by hooks. To assess the 19 accuracy of this hypothesis, we consider the hovering flight of a bumblebee 20 *Bombus ignitus.* Our work consists of morphological measurements in order 21 to quantify the geometrical and the inertial properties of the wings, con-22 struction of a kinematic model of the insect, free-flight measurement of the 23 body posture and of the wing kinematics, and computational fluid dynamics 24 (CFD) simulations. 25

In Section 2, we reconstruct the wing kinematics of hovering bumblebees, 26 and measure morphological parameters of the wings, including mass distri-27 bution. To the best of our knowledge, this is the first study where moments 28 of inertia based on realistic mass distribution of an insect wing are subse-29 quently used in CFD simulations. Thus, we introduce a torsion-spring hinge 30 element in our CFD model of the bumblebee in Section 3. By varying the 31 spring stiffness coefficient, we find the optimal value that ensures the best 32 agreement between the simulated and measured wing kinematics. Statisti-33

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 36 suggest that the hinged plate model provides a reasonably accurate approxi-37 mation of real bumblebee wing motion. Considering the hinge stiffness factor 38 as a material parameter, we conjecture that the value that we have deter-39 mined in the present study may be adequate for all flight regimes. This opens 40 a new perspective of numerical simulation of complex flight maneuvers using 41 only the wing-tip kinematics as input data, which is much easier to measure 42 in experiments than the full three-dimensional wing kinematics. 43

# 44 2. Morphological measurement and kinematic reconstruction

## 45 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.

# 52 2.2. Wing shape

The input data required for the numerical simulation of passive rotation 53 includes wing shape and moments of inertia. In our model, we approxi-54 mate the wings as flat plates and only take the planar shape into account. 55 Deviation from the planar shape may have important consequences for the 56 aerodynamic force generation but, to account for it properly, wing deforma-57 tion should be taken into consideration, which is beyond the scope of this 58 work. To obtain the outlines, 20 forewings and 18 hindwings were glued on 59 a sheet of millimeter paper and photographic images were taken. All wings 60 were aligned along their major axes, outlines were rescaled by their maxi-61 mum chord length, then aligned to obtain the best match in the leading edge. 62 Average forewing and hindwing contours were obtained in polar coordinates, 63 then transformed into the original Cartesian coordinates, see Kolomenskiy 64 et al. (2019) for more explanation. The red dotted lines in Fig. 1 show the 65 mean forewing and hindwing contours. The dark grey and the light grey color bands show, respectively, the intervals of  $\pm 1$  and  $\pm 2$  standard deviation from 67 the mean. 68



Figure 1: Bumblebee wing morphology. The wing outline shape, including the mean contours,  $\pm 1$  and  $\pm 2$  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. 69 This factor contributed to the wing shape variability. The elastic hinge model 70 discussed in this paper may help to better understand the effect of wing wear 71 on flight performance and behavior of bumblebees, which is an intriguing 72 topic in its own right (Haas and Cartar, 2008; Mountcastle et al., 2016). At 73 this stage, however, we are mainly interested by the performance of nominally 74 intact wings. Therefore, in addition to the statistical analysis, one image of 75 an intact wing was digitized for the purpose of extracting the wing contours 76 for the CFD model and vein coordinates for the mass distribution model 77 described in the next section. This wing contour is shown in Fig. 1 with a 78 black dash-dot line. Most of its part lies within the  $\pm 1$  standard deviation 79 band, and it lies entirely in the  $\pm 2$  standard deviation band. The veins are 80 shown as continuous red, green and blue lines. In the CFD simulations, the 81 wing is represented as a closed contour using Fourier series (Engels et al., 82 2016b). The latter is shown with a black solid line. 83

## <sup>84</sup> 2.3. Wing mass and moments of inertia

Since wing length varies between individuals, it is important to measure 85 the concomitant variation of the wing mass. For this purpose, 13 individ-86 ual bees were cold-anaesthetised, their wings were clipped and immediately 87 weighed using a precision balance (AUW220D, Shimadzu, Japan) with dis-88 play resolution 0.01 mg in the fine mode. We defined  $m_w$  as the total mass 89 of one forewing and one hindwing. The wing length R from the shoulder to 90 the forewing tip was measured using a digital caliper. We found that the 91 linear regression slope of  $\log m_w$  as a function of  $\log R$  is equal to 3.04, which 92 means that the scaling is close to isometric, see Fig. 2(a) and Kolomenskiy 93 et al. (2019). Thus, isometric scaling 94

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

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  $(0.76 \pm 0.10)$ 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



Figure 2: (a) Wing mass  $m_w$  defined as the total mass of one forewing plus one hindwing and (b) body mass m defined as the full mass of the animal, displayed as functions of the wing length R. Crosses show the measured data points. The large cross in figure (b) corresponds to the individual #4. Red dashed lines are the log-log linear regression lines. Solid black lines show the isometric fits (1) for the wings and (8) for the body, respectively. The gray shaded regions visualize the  $\pm 1$  standard deviation intervals of (1) and (8).

each segment was weighed. Then, the veins and the membrane were treated 103 separately. The vein thickness, necessary for estimating the vein mass dis-104 tribution, was measured using a micro-CT scanner (inspeXio SMX-100CT, 105 Shimadzu, Japan), at the vein midpoints. The veins were approximated as 106 circular cylinders having uniform material density equal to that of cuticle, 107  $1300 \text{ kg m}^{-3}$  (Vincent and Wegst, 2004). Hence, the vein moments of inertia 108 were calculated as line integrals along the paths shown in Fig. 1. Contribution 109 of the membrane to the moments of inertia was estimated by surface integra-110 tion using a bilinear surface density distribution  $\rho_f(x,y) = \rho_{f0} + x\rho_{fx} + y\rho_{fy}$ 111 for the forewing, and a uniform distribution  $\rho_h(x,y) = \rho_{h0}$  for the hind-112 wing. The latter simplification is justified by the hindwing being much lighter 113 than the forewing (19% of the full wing mass), and the membrane's weight 114 being of about 10% of the hindwing mass. The fitting parameters were 115 evaluated by minimizing the r.m.s. difference between the calculated and 116 the measured mass of the wing segments, to obtain  $\rho_{f0}/R = 0.826 \,\mathrm{kg}\,\mathrm{m}^{-3}$ , 117  $\rho_{fx} = -0.798 \text{ kg m}^{-3}, \ \rho_{fy} = 0.672 \text{ kg m}^{-3}, \ \rho_{h0}/R = 0.045 \text{ kg m}^{-3}.$  Finally, by 118 summing up the vein and the membrane contributions, we obtained the fol-119 lowing isometric scaling relationships for the moments of inertia: 120

$$J_{xx} = 0.0014R^5, \quad J_{yy} = 0.0426R^5, \quad J_{xy} = -0.0010R^5,$$
 (2)

where R is in meters and  $J_{xx}$ ,  $J_{yy}$ ,  $J_{xy}$  are in kg m<sup>2</sup>. 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 (Kolomenskiv 123 et al., 2019), and our calculation assumes circular piece-wise constant cross-124 section, the approximation error may be significant. One can notice in 125 the micro-CT images in Supplementary figure SF1 that some of the veins 126 have non-circular cross-section and variable thickness. In addition, stigma is 127 treated as belonging to vein number 2. Spatial resolution of the micro-CT 128 data precludes accurate modelling of these features. We only measure the 120 maximum and the minimum thickness of each vein. The vein thickness de-130 viates by less than 26% from the nominal mid-point diameter. To estimate 131 the resulting error, we repeat the inertia calculations 33 times with the vein 132 diameters taken randomly within the measured interval. Thus, we obtain 133 the standard deviation of the moments of inertia, 134

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

# 135 2.4. Three-dimensional kinematic reconstruction

Free-flight measurements were acquired using a setup that consisted of a 136 tunnel with transparent ceiling that was connected with the hive on one end 137 and with a feeding area on the other end, see Fig. 3. A feeder filled with sugar 138 water solution was installed in the feeding area. The bees were trained to fly 139 through the tunnel. Hovering behaviour was observed when a bee was either 140 distracted by lights, or approached an obstacle in the middle of the tunnel, 141 or preparing to exit from the tunnel. In the duration of the experiment, 142 the humidity was near 80% and the temperature was maintained at about 143 22 °C. The test section in the flight tunnel was illuminated using lights. 144 Video recordings were acquired using three synchronized high-speed cameras 145 (FASTCAM SA3, Photron, Japan), equipped with CCTV lens (B2514D or 146 B5014A, Pentax, Japan) at 2000 fps. The image resolution was set to  $1024 \times$ 147 1024 pixels. The shutter speed varied between 1/10000 s and 1/5000 s, since 148 we changed the position of the cameras and the lights several times during 140 the experiment. All three views were used to track the body, but only two 150 were used to track the wings. Sample frames from two cameras, with a zoom 151 on the insect, are shown in Fig. 4. An extended description of the experiment 152 and data acquisition setup can be found in Jakobi et al. (2018). 153

<sup>154</sup> 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 163 study. During hovering, the body orientation is determined by the inclination 164 angle  $\beta$  between the horizontal plane and the longitudinal axis of the body, 165 since the body roll is negligibly small and the azimuthal orientation has no 166 practical importance. The anatomical stroke plane is inclined by an angle 167  $\eta$  with respect to body such as to best-fit the trajectories of both wing tips 168 while respecting the bilateral symmetry. The positional angle  $\phi$  is defined as 160 the angle between the lateral direction in the body reference frame and the 170 projection of the wing longitudinal axis on the stroke plane, then  $\theta$  defines 171 the angular elevation with respect to the stroke plane, and the feathering 172 angle  $\alpha$  measures the wing rotation about its longitudinal axis. Note that, 173 when  $\alpha = 0$ , the wing is perpendicular to the stroke plane. 174

For each video, we first select a hovering sub-sequence such that minimal 175 velocity and constant orientation are maintained for at least 5 wing beats. To 176 determine the body position and orientation, we either use a triangular tag 177 affixed on the dorsal side of the thorax (Jakobi et al., 2018) or morphological 178 features as described in Appendix A. Subsequently, we track the wing tips, 179 calculate their trajectories in the reference frame moving with the body, find 180 the stroke plane angle and the wing kinematic angles with respect to the 181 stroke plane. Finally, we use Fourier analysis to derive the closest periodic 182 and symmetric representation of the measured wing kinematics. An extended 183 explanation of this procedure is provided in Appendix A. 184

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  $\eta$ .  $O_{sp}$  is one of the two shoulder points,  $O_b$  is the body center of mass.

<sup>192</sup> of four derived parameters: the mean chord length

$$c = R/AR,\tag{4}$$

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,

$$r_2 = \sqrt{\frac{1}{S} \int_{wing} x^2 \mathrm{d}x \mathrm{d}y} = 0.57R,\tag{5}$$

<sup>196</sup> the reference average wing speed

$$U_2 = 2\Phi f r_2, \tag{6}$$

<sup>197</sup> and the Reynolds number

$$Re_2 = U_2 c / \nu. \tag{7}$$

<sup>198</sup> The average wing-tip speed is equal to  $U_t = 1.75U_2$  and the wing-tip Reynolds <sup>199</sup> number is equal to  $Re_t = 1.75Re_2$ . The air density and kinematic viscosity at <sup>200</sup> 22 °C are taken as, respectively,  $\rho = 1.197$  kg m<sup>-3</sup> and  $\nu = 1.53 \times 10^{-5}$  m<sup>2</sup> s<sup>-1</sup>.

# 201 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.

Individual	$R, \mathrm{mm}$	f, Hz	$\Phi,^\circ$	$\beta,^{\circ}$	$\eta,^{\circ}$	$c,  \mathrm{mm}$	$r_2, \mathrm{mm}$	$U_2,  {\rm m  s^{-1}}$	$Re_2$	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	_

Table 1: Hovering flight parameters.

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

$$m = (100.4 \pm 19.2)R^3 \tag{8}$$

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.

# 218 3. Dynamical simulation and analysis

# 219 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<sup>1</sup>, a Fourier pseudo-spectral solver with volume penalization (Engels et al., 2016b). In the simulation, the bumblebee is approximated by three

<sup>&</sup>lt;sup>1</sup>Open source code available at https://github.com/pseudospectators/FLUSI

rigid elements: the body and two wings, which move with respect to each 224 other. The wings are flat plates such that the forewing and the hindwing are 225 treated as one piece, with the planform shown in Fig. 1 constructed using 226 Fourier series representation (Engels et al., 2016b). The wing thickness is 227 equal to 0.0125R. An idealized body shape is used, similar to our earlier 228 work Engels et al. (2016a). It is composed of analytically described surfaces 229 of the head, thorax, abdomen, antennae, proboscis and legs. The distance 230 between the shoulder hinge points is equal to 0.351R, which differs slightly 231 from the value used by Engels et al. (2016a). The body and the wings are 232 isometrically scaled such as to match the wing length R as given in Table 1. 233

In all numerical simulations in the present study, the body is fixed in the laboratory reference frame. Prescribed time-periodic functions  $\phi(t)$  and  $\theta(t)$ , as shown in Fig. 6, determine the position of the wing tip. Rotation of the wing about its longitudinal axis is described by  $\alpha(t)$  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  $\alpha(t)$ , as we explain later in Section 3.3. In the numerical simulation, the feathering angle  $\alpha(t)$  is determined from the equation of passive feathering motion,

$$J_{xx}\ddot{\alpha} = M_{aero} - K(\alpha - \alpha_0) - C\dot{\alpha} + J_{xx} \left[ \frac{1}{2} (\dot{\phi}^2 \cos^2 \theta - \dot{\theta}^2) \sin 2\alpha - \ddot{\phi} \sin \theta - \dot{\phi} \dot{\theta} \cos \theta (1 + \cos 2\alpha) \right] + J_{xy} \left[ \ddot{\phi} \cos \theta \cos \alpha + \ddot{\theta} \sin \alpha + \frac{1}{2} \dot{\phi}^2 \sin 2\theta \sin \alpha - 2\dot{\phi} \dot{\theta} \sin \theta \cos \alpha \right], \quad (9)$$

where  $M_{aero}$  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  $M_{aero}$  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 momen-243 tum equation, where the penalization constant is set to  $C_{\eta} = 1.15 \times 10^{-4}/f$ . 244 The air is treated as a viscous incompressible fluid. The penalized Navier-245 Stokes equations are solved on an equidistant uniform Cartesian grid using 246 a Fourier pseudo-spectral discretization. The computational domain is a pe-247 riodic cube with side length 3.2R, discretized using  $1024^3$  grid points (over 1) 248 billion grid points). This yields the resolution of 320 points per wing length 249 and 87 points per mean chord length. Impermeable floor and vorticity sponge 250 layers on the side walls are applied using volume penalization in order to pre-251 vent spurious recirculation of the flow. The bumblebee body centre of mass 252 is offset by a distance of 0.1R above the centre of the domain. This leaves 253 enough space (about 1.4R) between the wings and the floor to ensure that 254 the aerodynamic ground effect is negligible (Kolomenskiy et al., 2016). 255

Strong fluid-structure coupling is used. Equation (9) is transformed 256 in a system of two first-order differential equations and discretized using 257 the second-order Adams–Bashforth scheme. Since the same time marching 258 scheme is also used in the Navier–Stokes solver, it is straightforward to eval-259 uate the right-hand side of the evolution equations, for both the fluid and the 260 solid, at the same time level. Knowing the right-hand side at the previous 261 and at the current time levels, as well as the values of the state variables 262 at the current level, the Adams–Bashforth formula yields the values of the 263 state variables at the next time level that ensure globally second-order accu-264 racy with respect to time. The numerical discretization grid step, time step 265 and domain size independence checks are presented in the Supplementary 266 material S2. 267

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.

#### 275 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 280 m. Two numerical simulations are compared. In the first,  $\alpha(t)$  is prescribed 281 as shown in Fig. 6(b). In the second,  $\alpha(t)$  is passive, i.e., it is modelled using 282 equation (9) as explained in Section 3.1, with  $K = 2.61 \ \mu \text{Nm}, C = 0$  and 283  $\alpha_0 = -1.38^\circ$ . These two time profiles are compared in Fig. 7(a). They 284 agree qualitatively well in terms of the overall shape, the amplitude and the 285 phase, which means that the passive feathering model with only three free 286 parameters can fit  $\alpha(t)$  adequately. The main difference is in the shape of 287 the peaks: they are sharper for the passive (modelled) profile than for the 288 prescribed one, especially on upstroke. 289

Besides that, there is a small phase lag between the passive and the 290 prescribed profiles of  $\alpha(t)$ . As we show later in this section, although it is 291 possible to control the phase by varying K and C, no fine-tuning of the hinge 292 model parameters can reduce this phase lag below a certain threshold, which 293 appears to be small positive in the case of individual #4 shown here and 294 for the individual #2, but almost zero for #1 and small negative for #3. 295 Therefore, this small residual phase lag seems to be a measurement error 296 rather than a modelling artifact. 297

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 303 the middle of each translation phase. They are larger but narrower in the case 304 of passive rotation, which is consistent with the differences in  $\alpha(t)$  discussed 305 above. The pointwise difference in  $F_{az}(t)$  is particularly large on upstroke, 306 when  $\alpha$  differs by as much as 20°. However, this overestimate cancels out 307 with the underestimates before and after the peak, such that the wingbeat 308 time-average force, as shown with the dashed lines, is almost identical in the 309 two cases and it is 8% less than the body weight (the last column in Table 1). 310 The horizontal force, see Fig. 7(c), shows similar trends with the difference 311 that the peak associated with the upstroke is negative, such that the time-312 average horizontal force is close to zero. The body-mass specific aerodynamic 313 power, Fig. 7(d), averages to 59 W kg<sup>-1</sup> and 63 W kg<sup>-1</sup>, respectively, in the 314 cases of prescribed and passive wing rotation. Note that both values are sig-315 nificantly smaller than previously reported  $84 \,\mathrm{W \, kg^{-1}}$  (Engels et al., 2016a), 316 obtained using a similar numerical bumblebee model with simplified wing 317



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.



Figure 8: Three-dimensional visualization of passive feathering motion.

318 kinematics.

In summary, the passive wing rotation model (9) is successful in repro-319 ducing the main dynamical features. Furthermore, it accurately predicts the 320 time-average quantities. With regard to the instantaneous values, discrep-321 ancy can be large. It may be explained by the fact that the model does 322 not account for deformation of the wing. In particular, rotation of the hind-323 wing relative to the forewing should be taken into account. This could help 324 to improve the fidelity of the three-dimensional tracking and the numerical 325 simulations alike. However, it is likely that the simple solid-plate model will 326 be sufficient for flight dynamics simulations that mainly depend on wingbeat-327 average forces. 328

Let us now discuss sensitivity of the results to the elastic hinge parameters 329 K, C and  $\alpha_0$ . Since these parameters cannot be measured directly, they will 330 be evaluated by fitting the model to the experiment data. It will be insightful 331 to see the influence of each parameter separately before solving the full opti-332 mization problem. Figure 9 displays such variation of  $\alpha(t)$ . The parameters 333 are varied around the conditions of the previous simulation. While the most 334 noticeable effect of increasing K is to reduce the amplitude of  $\alpha$ , there is sig-335 nificant asymmetry between stiffening and loosening the hinge with respect 336 to the average value  $K = 2.42 \,\mu\text{Nm}$ . In addition, hinge loosening entails 337 some significant phase delay with respect to the experiment data. The effect 338 of increasing C is also to reduce the amplitude of  $\alpha$ , however, it is accompa-339

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  $d\overline{\alpha}/d\alpha_0 = 0.41$ , 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  $M_{aero}$  is small during the reversals near t/T = 0 and 0.5, when the translation velocity of the wing is small.  $M_{aero}$  is large positive in the middle of downstroke, it is large negative in the middle of upstroke. The inertial pitching moment

$$M_{inertial} = -J_{xx}\ddot{\alpha} + J_{xx} \left[ \frac{1}{2} (\dot{\phi}^2 \cos^2 \theta - \dot{\theta}^2) \sin 2\alpha - \ddot{\phi} \sin \theta - \dot{\phi} \dot{\theta} \cos \theta (1 + \cos 2\alpha) \right] + J_{xy} \left[ \ddot{\phi} \cos \theta \cos \alpha + \ddot{\theta} \sin \alpha + \frac{1}{2} \dot{\phi}^2 \sin 2\theta \sin \alpha - 2\dot{\phi} \dot{\theta} \sin \theta \cos \alpha \right]$$
(10)

peaks during rapid angular deceleration of the wing after reversal (t/T = 0.1)346 and 0.6). Interestingly, acceleration that precedes the reversal is much more 347 gradual. The time profile of the restoring torque  $K(\alpha - \alpha_0)$  repeats that of 348  $\alpha$ , and the structural damping torque  $C\dot{\alpha}$  is identically equal to zero because 349 C = 0. By comparing the three non-trivial contributions, it can be concluded 350 that the restoring torque of the hinge balances the inertia (mainly  $J_{xx}\ddot{\alpha}$ ) in 351 the beginning of each half-stroke (upstroke or downstroke), and it balances 352 the aerodynamic torque in the end of half-stroke. 353

#### 354 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

$$e = \frac{1}{T} \int_0^T \left( \alpha(t) - \alpha_{exp}(t) \right)^2 \mathrm{d}t, \qquad (11)$$

where  $\alpha(t)$  is the time evolution of the feathering angle obtained from the numerical simulation using (9), and  $\alpha_{exp}(t)$  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  $K = 2.42 \ \mu\text{N} \text{ m}$  and  $\alpha_0 = -1.38^\circ$ ; (c) varying  $\alpha_0$  with  $K = 2.42 \ \mu\text{N} \text{ m}$  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* 362 *iqnitus* in general. The full set of 7 individual hovering flights have been 363 divided in the training set (#1 to #4) and the test set (#5 to #7). For 364 each individual in the training set, a parameter sweep is performed to find 365 the optimal stiffness  $K_{opt}$  that minimizes the r.m.s. distance between  $\alpha(t)$ 366 in the simulation and the experiment,  $e_{opt}$ . Prior to the parameter sweep, 367  $\alpha_{0opt}$  that ensures equal time-average  $\overline{\alpha}$  in the simulation and in the exper-368 iment, is determined using linear extrapolation of an auxiliary simulation 369 with  $\alpha_0 = 0$  and the slope  $d\overline{\alpha}/d\alpha_0$  known from previous simulations. Zero 370 structural damping, C = 0, is assumed in all cases. Additional simulations 371 with  $K = K_{opt}$ ,  $\alpha_0 = \alpha_{0opt}$  and C = 0.66 nNms confirm that e becomes 372 larger than  $e_{opt}$  obtained with C = 0. The multivariate optimization in 373 Supplementary material S3 also supports this assumption. 374

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,

$$K = R^3 K^*, \tag{12}$$

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, ..., 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

$$K_{mod}^* = \frac{1}{4} \sum_{i=1}^{4} K_{opt,i}^* = (0.81 \pm 0.089) \text{ N m}^{-2}.$$
 (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 386 all individuals, including those in the test set. For that purpose, numerical 387 simulations are performed with the hinge stiffness calculated using (12) with 388 the stiffness factor  $K_{mod}^* = 0.81 \text{ Nm}^{-2}$ , zero structural damping (C = 0), 389 and rest angle  $\alpha_{0mod} = -0.75^{\circ}$ . The results shown in the last two columns 390 of Table 2 suggest that these values are indeed representative of all indi-391 viduals since, typically,  $e_{mod}$  is close to  $e_{mod}$ . Further, a two-sample t-test 392 for equal means without assuming equal variances has been applied. Mean 393  $e_{mod}$  is equal to 8.178° and 9.76°, for the training and the verification sets, 394 respectively. It has shown no significant difference in the mean  $e_{mod}$  of the 395 two datasets (p = 0.23). 396

Individual	Dataset	$K_{opt}^*,$	$K_{opt},$	$Ch_{opt}$	$\alpha_{0opt},^{\circ}$	$e_{opt},^{\circ}$	$K_{mod},$	$e_{mod},^{\circ}$
		$ m Nm^{-2}$	$\mu Nm$				$\mu Nm$	
#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

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

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

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

using data from multiple sources, and found that Ch 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 (×) show the computed points, circles ( $\circ$ ) show the minima in each case. The dash-dot vertical line corresponds to  $K^*_{mod}$ .

<sup>401</sup> as  $Ch_{opt}$ . They correspond to the optimal stiffness  $K_{opt}$ . Overall, the Cauchy <sup>402</sup> number in the present study is significantly larger than reported previously <sup>403</sup> by Ishihara et al. (2014) for diptera.

## 404 3.4. Aerodynamic analysis

<sup>405</sup> The aerodynamic force generation capacity is conventionally measured by <sup>406</sup> the lift coefficient \_\_\_\_\_

$$c_L = \frac{\overline{L}}{\frac{1}{2}\rho U_2^2 S_{ref}},\tag{15}$$

where  $\overline{L} = \frac{1}{T} \int_0^T F_{az}(t) dt$  is the mean vertical aerodynamic force (i.e., lift),  $U_2 = 2\Phi f r_2$  is the reference velocity and  $S_{ref} = 2S$  is the reference area, 407 408 with the wing area  $S = 0.273R^2$  and the radius of the second moment of 409 area  $r_2 = 0.57R$  calculated for the intact wing in Fig. 1. The evolution of  $c_L$ 410 with  $K^*$  is shown in Fig. 12, for all individuals in the test set. In all cases,  $c_L$ 411 is an increasing function of  $K^*$  in the range considered here. I.e.,  $c_L$  is small 412 when the hinge is very compliant, and  $c_L$  reaches 2 when the hinge is stiffer 413 than normal. It may be expected, by analogy with a flexible wing, that  $c_L$ 414 decreases to zero in the limit of very large  $K^*$ . However, in our numerical 415



Figure 12: Lift coefficient as a function of the hinge stiffness factor  $K^*$ . The dash-dot vertical line corresponds to  $K^*_{mod}$ , dashed lines correspond to  $K^*_{opt,i}$ .

simulations, we do not observe this trend even when  $K^*$  is twice as large as  $K^*_{opt,i}$ . The values of  $c_L$  at  $K^*_{opt,i}$  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  $FM = P_{ideal}/\overline{P}$ , where  $P_{ideal}$  is the ideal power determined by the Rankine–Froude momentum theory as  $P_{ideal} = 2\rho w_0^3 A_0$ , 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

$$FM = \frac{\overline{L}^{3/2}}{\overline{P}} \frac{1}{2R\sqrt{\rho\Phi}}.$$
(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  $K^*_{opt,i}$ , 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 FMis only slightly less than the maximum. Thus,  $FM(K^*_{opt,i})$  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  $K^*_{mod}$ , dashed lines correspond to  $K^*_{opt,i}$ .

## 432 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, orig-439 inally designed for diptera, also provides a reasonably accurate approxima-440 tion of bumblebee wings composed of forewings and hindwings connected 441 by hooks (humuli). Specifically, it produces realistic feathering motion and 442 accurate time-average estimates of the aerodynamic performance in hover, 443 despite that the instantaneous values of aerodynamic forces may differ sig-444 nificantly between the passive feathering and fully prescribed models. These 445 conclusions have been reached on the basis of morphological measurements, 446 kinematic analysis of live bumblebees, and high-fidelity numerical simulation. 447 Using statistical analysis, typical values of the model parameters have 448 been determined. The hinge stiffness can be approximated as  $K = 0.81 R^3$ . 449 where R is the wing length in m and the result is in Nm. The structural 450

damping coefficient is negligible compared with the fluid damping, i.e., C = 0is 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 454 provides the required lift-generation capacity for a realistic energetic cost. It 455 is interesting that the hinge parameters are not exactly tuned to maximum 456 efficiency during hovering, but the stiffness is slightly larger than the optimal 457 value. We conjecture that the difference may be interpreted as a safety factor 458 that helps to avoid abrupt decrease in the efficiency when flight conditions 450 change, but a dedicated study is needed on this point. In addition, it may 460 be necessary to re-examine it using a fully flexible wing model, since even a 461 slight variation of FM near its flat peak may entail a qualitative change in 462 the shape and position of the peak. 463

Regarding the hinge stiffness factor  $K/R^3$  as a fictitious material pa-464 rameter, one may conjecture that the value determined in hover may be 465 adequate for all flight regimes. This opens new perspectives for numerical 466 simulation of complex flight maneuvers using only the wing-tip kinematics 467 as input data, which is much easier to measure in the experiments than the 468 full three-dimensional wing motion. However, elastic element only being a 469 mathematical abstraction of the real hinge, its stiffness may depend on flight 470 conditions. 471

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.

# 477 Acknowledgements

The authors thank Dr. Hiroto Tanaka for his advice on the morphological 478 measurement and Shimadzu corp. for granting access to a micro-CT scanner 479 inspeXio SMX-100CT. This work was granted access to the HPC resources of 480 IDRIS (Institut du Développement et des Ressources en Informatique Scien-481 tifique) under the allocation made by GENCI (Grand Equipment National 482 de Calcul Intensif), project number A0022A01664. DK gratefully acknowl-483 edges financial support from the JSPS KAKENHI Grants Number 15F15061 484 and JP18K13693. HL was partly supported by the JSPS KAKENHI Grant 485 Number 24120007 for Scientific Research on Innovative Areas. TE, JS and 486

KS gratefully acknowledge financial support from the Agence nationale de la recherche (ANR Grant 15-CE40-0019) and Deutsche Forschungsgemeinschaft (DFG Grant SE 824/26-1), project AIFIT, and financial support granted by the Ministère de l'Europe et des affaires étrangères (MEAE), Ministère de l'enseignement supérieur, de la recherche et de l'innovation (MESRI), and the Deutscher Akademischer Austauschdienst (DAAD) within the French-German Procope project FIFIT.

# <sup>494</sup> 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 498 time span of the video. Nevertheless, this small motion should be taken into 499 account when calculating the wing angles, because the latter are sensitive to 500 movement of the shoulder hinges. Therefore, we first reconstructed the three-501 dimensional motion of the body. Since this individual bee was not tagged, 502 we selected three points that can easily be distinguished by morphological 503 features. As shown in Fig. 4, point 1 is on the head between the antennae 504 (red marker), point 2 is an abdominal pigmentation feature (green marker), 505 and point 3 is the rear point of the abdomen (blue marker). Every 10th frame 506 of total 1167 frames in each camera view were analyzed. The points were 507 manually tracked and their coordinates in the laboratory reference frame 508 reconstructed using DLTv5, the result being displayed in figure A.14(a). 509 Figure A.14(b) shows the velocity magnitude of each point, calculated using 510 central finite-difference approximation. The velocity is no greater than  $V_q =$ 511 0.023 m/s, and the corresponding advance ratio is equal to  $\mu = V_g/U_2 =$ 512 0.0042. This small advance ratio is indicative of hovering. 513

The time sequence of almost 6 s is longer than required for digitization 514 of the wing motion. We therefore only select a sub-sequence of 40 ms for the 515 further analysis, which is shaded in figure A.14(b). The velocity in it is less 516 than  $0.015 \,\mathrm{m\,s^{-1}}$ . During this short time interval, time-varying position of 517 the three feature points in the laboratory reference frame is fitted with cubic 518 polynomials in order to filter out the digitization noise. In the body reference 519 frame, relative position of different points (i.e., the shoulder hinges, the center 520 of mass and the three selected morphological features) does not vary in time, 521 therefore, it can be determined from prior morphological measurement or 522



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 535 to the stroke plane, see Fig. 5 for the definitions. The values of the positional 536 angle  $\phi$ , the elevation angle  $\theta$  and the feathering angle  $\alpha$  are determined for 537 the left and for the right wing separately, for every time frame of the selected 538 40-millisecond video sub-sequence. It covers slightly less than 6 wingbeat 530 periods. A first approximation to  $\phi$  and  $\theta$  is calculated using the approximate 540 wing-tip coordinates relative to the hinge point, but this is complicated by 541 the fact that the wing tips hold no point markers. Therefore, to refine  $\phi$  and 542



Figure A.15: Time evolution of the wing kinematic angles. Markers show the raw data points obtained after digitizing each frame. Lines show the result of low-pass filtering and interpolation.

 $\theta$  as well as to determine  $\alpha$ , the wing contour projection is superposed on 543 the video image. It is drawn interactively as the values of  $\phi$ ,  $\alpha$  and  $\theta$  are 544 manually adjusted for the best visual fit by varying the angles with small 545 steps of  $0.36^{\circ}$ . For this purpose, as for the subsequent CFD simulation, we 546 use the archetypal intact wing shown in Fig. 1, scaled with the wing length 547 R = 14.6 mm determined from the video as the average distance between the 548 shoulder and the wing tip. Example visualizations of this fit are shown in 540 Fig. 4. The digitized left (resp., right) wing contour outline is shown with a 550 cyan (resp., magenta) closed curve. Generally, the approximation is visually 551 better during the downstroke (first two frames in a row) than during upstroke 552 (last frame in a row), as the wing deformation is greater during upstroke. 553

The complete measured time sequences of the wing angles are displayed 554 as markers in Fig. A.15. The resolution of 13 points is sufficiently high 555 to describe the important repetitive features of the time profiles, such as 556 the double negative peak of  $\alpha$  during upstroke. The motion is nominally 557 periodic, with small deviations that may be due to actuation, wing-wake 558 interaction and measurement errors. The next processing step consists in 559 low-pass filtering the data at 450 Hz using the 4th order Butterworth filter 560 and upsampling the result on a 100-times finer grid using spline interpolation. 561 Thus we discard those points that produce unrealistically large accelerations. 562 The resulting time profiles are shown with dotted and dashed lines that 563 correspond to the left and the right wing, respectively. 564



Figure A.16: (a) Time evolution of the wing angles reduced to the time scale of one wingbeat (thin lines) and their average (thick lines). (b) Average time profiles of the left and the right wing kinematics (thin lines) and the average of the two wings (thick lines), where the time is normalized by the wingbeat period T. Dotted lines correspond to the left wing, dashed lines correspond to the right wing, and solid lines show the average between left and right.

From frequency analysis of  $\phi(t)$  we find that the flapping frequency is 565 equal to f = 144.6 Hz. We use this value to divide the sequences shown in 566 figure A.15 in cycles of length T = 1/f = 6.92 ms. In figure A.16(a), we plot 567 the time evolution of  $\phi$ ,  $\alpha$  and  $\theta$  during each cycle, with t = 0 corresponding 568 to the beginning of downstroke. The original profiles are shown with thin 569 faded lines. For every time instant t during the cycle, we calculate the average 570 of 4 subsequent wingbeats. The average time profiles are shown with thick 571 bright lines in figure A.16(a), and thin bright lines in figure A.16(b). These 572 time sequences are very close to periodic. There remains less than 10 degree 573 difference between the angles of the left wing and those of the right wing, 574 and we calculate their average. The result is plotted in figure A.16(b) using 575 thick lines. Finally, Fourier analysis of these time sequences is performed. 576 The time evolution of  $\phi$ ,  $\alpha$  and  $\theta$  is described with less than 1 degree error 577 using, respectively, 4, 5 and 4 harmonics. These coefficients are used as input 578 data for the CFD simulation. 579

#### 580 Appendix B. Numerical validation

Whitney and Wood (2010) conducted experiments with an insect-scale mechanically driven artificial wing that, by construction, satisfied the condi-



Figure B.17: Wing shape used in the numerical validation study.

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 sim-588 ulations of the 'short hinge' model of Whitney and Wood (2010) with the 589 hinge stiffness equal to  $K = 2.35 \cdot 10^{-6}$  Nm. The structural damping is 590 negligible small, i.e., C = 0, and the static orientation of the wing is vertical, 591 i.e.,  $\alpha_0 = 0$ . Figure B.17 displays the wing shape used in these numerical 592 simulations. It is derived from the photographic image shown in Whitney 593 and Wood (2010) and closely repeats the outline of the wing membrane, 594 except for some simplification near the root. The wing length is equal to 595 R = 15.14 mm. Its mass is equal to  $m_w = 0.91$  mg. The moments of inertia 596 are  $J_{xx} = 1.7 \cdot 10^{-12} \text{ kg m}^2$  and  $J_{xy} = -3.5 \cdot 10^{-12} \text{ kg m}^2$ . 597

The time evolution of the positional angle  $\phi$  and the elevation angle  $\theta$  used 598 for the numerical similation is obtained by Fourier analysis, Gaussian filter-590 ing and periodization of the experiment data. Since the observed motion is 600 nominally periodic, this process does not introduce any significant error. Two 601 different experiment runs are considered: the 'baseline' case with approxi-602 mately symmetric upstroke and downstroke, and the 'split-cycle' with fast 603 upstroke and slow downstroke. The flapping frequency equals, respectively, 604 f = 99.59 Hz and 100.5 Hz, as evaluated from the measured time profiles 605 of  $\phi(t)$ . In each case, we have performed two numerical simulations: one 606

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  $\nu = 1.53 \cdot 10^{-5} \text{ m}^2 \text{ s}^{-1}$ and  $\rho = 1.2 \text{ kg m}^{-3}$ .

Let us discuss the 'baseline' case first. Time evolution of the kinematic 611 angles is shown in Fig. B.18(a). To compare directly with the data presented 612 in Whitney and Wood (2010), since we use different sign conventions,  $-\theta$  and 613  $-\alpha$  are shown. The result of our numerical simulation of passive feathering 614 rotation,  $-\alpha$ , is plotted using a solid blue line. It is in a good agreement 615 with the experiment shown with black circles, in terms of the phase and 616 the minimum angle. The maximum angle is slightly overestimated which 617 may be related to the asymmetry of the vein-membrane assembly or non-618 linear elasticity of the hinge, which are not accounted for in the numerical 619 simulation. 620

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 numerical simulation is evaluated as

$$F_i = -m_w \frac{\mathrm{d}^2}{\mathrm{d}t^2} \left( y_{cm} \cos \alpha \cos \theta + x_{cm} \sin \theta \right), \qquad (B.1)$$

where  $m_w = 0.91$  mg is the wing mass,  $x_{cm} = 5.74$  mm and  $y_{cm} = -1.31$  mm 625 are the centre of mass coordinates in the spanwise and in the chordwise direc-626 tions of the wing, respectively. When  $\alpha(t)$  is prescribed as in the experiment, 627 the force F(t) follows a remarkably similar path as in the experiment. In the 628 case of passive feathering rotation, when  $\alpha(t)$  is modelled, the overall agree-629 ment is still good but the plateaus that correspond to the translation phase 630 are noticeably smaller. This is explained by the excess of feathering rotation: 631  $\alpha$  predicted by the model during the translation phase is slightly too large. 632 The difference appears small in the kinematics in Fig. B.18(a), but it entails 633 a significant discrepancy in the forces in Fig. B.18(b). The mean force F is 634 equivalent of 74.8 mg in the case of the prescribed motion and 52.8 mg for 635 the passive feathering model, to be compared with 71.6 mg measured in the 636 experiment. Better agreement can be achieved, presumably, if non-linearity 637 and asymmetry are taken into account, or if the linear spring parameters 638 are fitted to the measured data (as opposed to being estimated from the 639 dimensions and material properties of the elastic hinge). 640

<sup>641</sup> 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.

 $\alpha$  are slightly overestimated, which leads to overall lower lift of the passive 642 feathering model. The time evolution of F shows oscillatory behavior due to 643 inertia, since  $\alpha(t)$  does not plateau, in contrast with the baseline case. These 644 oscillations in the simulations and in the experiment agree in phase and in 645 magnitude for most part of the wing beat cycle, except for the beginning of 646 the cycle. The mean forces are equivalent of 64.9 mg in the prescribed feath-647 ering simulation, 46.6 mg in the modelled passive feathering simulation and 648 71.2 mg in the experiment. These validation test cases allow to conclude that 649 the model describes the time-varying feathering angle and lift adequately. At 650 the same time, relatively small error in the feathering angle, that can be ex-651 plained by difference between theoretical (as used here) and real stiffness of 652 the hinge, can have important consequences for force generation. Stiffness 653 tests of similar elastic hinges can be found in, e.g., Li et al. (2018). In view of 654 this result, it appears important to perform a parameter sweep over a range 655 of possible values of the hinge stiffness, as described in the main text of this 656 paper. 657

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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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