Supplementary Materials for

Flies trade off stability and performance via adaptive compensation to wing damage

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- Movies S1 to S3
Supplementary Text

Wing frequency model

To determine how the natural frequency of the wing-thorax system might scale with wing damage, we assumed the flapping motion of the wing can be modeled as a second order physical pendulum (Figure S7A). The corresponding equation of motion of the pendulum can be written as

\[ I \ddot{\theta} = -C \dot{\theta} - K \theta + \tau \]

where \( \tau \) is the overall torque experienced by the wing due to actuation, \( C \) is the damping ratio at the wing hinge joint, \( K \) is the stiffness of the wing hinge joint, \( I \) is the moment of inertia of the wing, and \( \theta \) is the stroke angle of the wing. This model assumes flies flap at resonant frequency, the wing can be modeled as a rectangular plate, the wing hinge acts as a torsional spring with a constant stiffness, and the wing has uniform density and thickness. The natural frequency \( \omega_n \) is then estimated through the following

\[ \omega_n = \sqrt{\frac{K}{I}} \]

For simplicity, we assumed that the wing has a rectangular shape (Figure S7B). The moment of inertia of a rectangular prism about its x-axis is:

\[ I_{xx} = \frac{m}{3} (l^2 + h^2) \]

By assuming the wing’s thickness is much smaller than the length of the wing \((l \gg h)\) Equation 3 simplifies to:

\[ I_{xx} = \frac{m}{3} l^2 \]

Expanding the mass term yields

\[ I_{xx} = \frac{\rho_w h A}{3} l^2 \]

where \( \rho_w \) and \( A \) are the wing density and area, respectively. Substituting Equation 5 into Equation 2 yields

\[ \omega_n = \sqrt{\frac{3K}{Ah \rho_w l^2}} = \frac{k_1}{l \sqrt{A}} \]

where \( k \) is a constant that accounts for the spring stiffness, wing thickness, and the wing density. By introducing the area of the intact wing \( A_0 \), Equation 6 can be rewritten as

\[ \omega_n = \frac{k_1}{l \sqrt{\frac{A}{A_0}}} = \frac{k_2}{l \sqrt{A_r}} \]

where \( A_r \) is the area ratio. We fit the model to experimental data using a nonlinear least squares minimization method. We constrained the fit through the intact wing data (wing area ratio = 1) due to the certainty in the mean from \( n = 10 \) flies (Figure 3E).

Robophysical model.

To test our hypotheses regarding the contribution of the passive aerodynamics for the control of wing kinematics, we developed an insect-inspired miniature (~10 mm wingspan) robophysical model. We used this setup to experimentally quantify the effect of wing damage on wing kinematics. Further, we developed a passive aerodynamics flapping model that supported our experimental observations. The design of the robophysical model is derived from the wing transmission of the Harvard Robobee, a biologically inspired, insect-scale flapping robot (56). Specifically, we designed a single active degree of freedom wing driver (Fig. S8) inspired by previous work that was used for high-throughput study of flapping wing aerodynamics (57). A solitary wing is attached to the driver through a slot that holds them in place during experiments but allows for easy removal and replacement. The wing motion is actuated by a piezoelectric
bimorph actuator which is coupled to the wing through a four-bar transmission. This enables us to simplify the observed biological wing motions to a reciprocating flapping motion in the robophysical model. In our model, the wing stroke amplitude is actively modulated using the sinusoidal actuation of the piezoelectric bimorph, while the wings’ pitch rotation is regulated with passive compliant flexures (58). The effects of specific design parameter choices and fabrication methods for such a wing driver are addressed in detail in previous work (59). The parameters of our robophysical model are identical to those of the wing driver described previously (60). Of particular interest to our current study are the physical dimensions of the intact wing (Table S4) and the piezoelectric actuator (Table S5) and the inertial properties of the intact wing. We manufactured the robophysical model (including all its sub-components) in-house using the multi-layered laminate fabrication (61) and pop-up assembly techniques (62).

For our experiments, the robophysical model was operated and controlled using the setup shown in Fig. S4A. The low voltage (0-5V) analog signals to drive the single wing flapping robot were generated using a real-time target (Speedgoat Inc.) computer system running at 4 kHz. These signals were then amplified up to 300V using a custom high-voltage amplifiers setup (constructed using BD300 modules from Piezosystems Inc.). The wing motion was filmed synchronously at 4 kHz using high-speed camera setup (Phantom v710 from Visionsystems Inc.). The recorded high-speed images were tracked using a neural network trained with DeepLabCut (63) and analyzed using custom MATLAB scripts. Five sets of experiment were performed on the wing, each with a different wing area (100%, 90%, 80%, 70% and 60%). For each wing area experiment, we collected data from the wing driver operating at fixed frequencies (at least 10 cycles per frequency) ranging from 10 Hz to 350 Hz with increments of 10 Hz. For the above experiments, we limited the piezoelectric actuator input to a sinusoidal driving signal centered around 50V with an amplitude of 30V (with a constant bias voltage of 100V) in order to prevent the mechanical system from damaging itself due to large increases in wing stroke during resonance.

Comparison of model predictions and experimental result yielded an excellent match (Fig. S9,10). The model predicted an increase in flapping frequency and wing stroke angle with an increase in damage, which was corroborated by experimental results. Theoretically, we expect the wingbeat amplitude to increase with loss of wing area (see linear model in supplementary section). However, the experimental data reveals a saturation of wingbeat amplitude around resonant flapping frequency at the small wing areas. This is because the robot approaches the flexure geometry induced joint angle limits of the wing hinge that connects the wing to the rest of the transmission. This observed positive correlation of the increase in wing pitching amplitude with increase in stroke amplitude and frequency upon increased wing clipping is consistent with experiments in other small scale (60, 64) and dynamically scaled robotic systems (65, 66). As noted in these studies, changes to passive wing pitching are crucial in determining the moment in a flapping cycle where wing zero crossing and stroke reversal occur which consequently influence the lift and drag production. These observations suggest the need for active control of pitching in the robophysical systems (and potentially in flies) especially after wing loss and are exciting avenues for future research.

Unilateral wing damage subtly influences the dynamics of saccades. During the yaw optomotor response, flies generate co-directional ‘catch up’ and anti-directional ‘reset’ saccades (14, 19, 55, 67). We compared the dynamics of these saccades by pooling all saccades of intact and damaged flies since both groups had approximately the same ratio of co- and anti-directional saccades (~0.6). Comparison between the two groups yielded subtle differences in saccade dynamics (Fig. S6A), and were consistent with previous work (68). Complicating this analysis is that sample sizes were quite large due to the high frequency of saccades (>2,500 saccades per group), thus tiny differences in means will yield small p values. Furthermore, small differences in saccade dynamics, while
statistically different, might not be biologically relevant. To address this limitation, we computed Hedges’ g, which presents a metric of effect size independent of sample size (69). By using effect size models, we found that the saccades of intact flies had modestly larger durations and peak velocities compared to damaged flies (Hedges’ g = 0.47 and 0.23, respectively) whereas amplitude had a smaller effect size (Hedges’ g = 0.09). Aligning saccades from both groups at peak velocity yielded overall smaller velocities and accelerations in damaged flies (Fig. S6B). Furthermore, the acceleration and velocity profile of damaged flies were visibly more variable than intact flies. Taken together, unilateral wing damage had subtle effects on saccade dynamics.

Investigating the dynamics of saccades grouped by direction for damaged flies—i.e., towards the damaged or intact wing—revealed small to medium effect sizes in saccade dynamics (Hedges’ g = 0.1, 0.26, 0.31 for duration, amplitude, and peak velocity, respectively) (Fig. S6C). Aligning the velocity and acceleration profiles of both groups revealed subtle differences. Saccades toward the intact wing were presumably propelled by the damaged wing, and were slightly slower overall, suggesting some influence of unilateral wing damage on saccade dynamics (Fig. S6D). Performing the same analysis on intact flies (CW vs. CCW saccades) yielded Hedges’ g value of 0.0028, 0.037, and 0.018 for duration, amplitude, and peak velocity, respectively, thus providing some assurance that effect sizes are notable for damaged flies. Overall, unilateral wing damage had subtle influences on saccade dynamics.

Quasi-steady aeromechanical model
To predict (and validate) the performance of our robophysical model from first principles of physics, we adapt a linear time-invariant (LTI) dynamic model (70) for a similar flapping wing system. Below we present a succinct summary of the model and use it to predict the change in wing kinematics as a function of wing damage. Using this approach, we simplify the system dynamics of our robophysical model to resemble a second-order mass-damper-spring system as shown below,

\[ m_{eq} \ddot{x} + b_{eq} \dot{x} + k_{eq} = F \]  

(8)

Where \( x \) is the actuator-tip displacement and \( m_{eq}, b_{eq} \) and \( k_{eq} \) are the equivalent mass, damping and stiffness respectively. The same may be expanded as below,

\[ m_{eq} = m_a + T^2 J_\phi, \]

\[ b_{eq} = T^2 r_{cp} b, \]

\[ k_{eq} = k_a + T^2 k_t. \]

(9)

where \( m_a \) is the actuator mass, \( T \) is the wing transmission ratio that linearly maps \( x \) to flapping angle \( \phi \), \( k_a \) is the actuator stiffness and \( k_t \) is the wing hinge stiffness. The bold terms: \( J_\phi \), the wing inertia, \( r_{cp} \), the radius to center of pressure and \( b \), the drag force linearization term (71), are directly impacted by changes in wing geometry and loss of mass. The second-order system characteristics, \( \omega_n \), the natural frequency; \( \zeta \), the damping ratio; and \( M(\omega_n) \), the magnitude of resonant peak of the system, as a function of wing parameters can be expressed as below, and can provide hints into effects of wing damage (despite ignoring the effect of change in aerodynamics):

\[ \omega_n = \sqrt{\frac{k_a + T^2 k_t}{m_a + T^2 J_\phi}} \]

\[ \zeta = T^2 r_{cp} b \sqrt{\frac{1}{4(k_a + T^2 k_t)(m_a + T^2 J_\phi)}}, \]

\[ M(\omega_n) = \frac{1}{2\zeta\sqrt{1-\zeta^2}}. \]

(10)

In order to account for the change in aeromechanics due to partial wing-loss, we follow the procedure outlined by Whitney (71) to estimate linearized drag force on the wing about an operating point flapping velocity (\( \phi_0 \)) as:
where, $b$ is the linear damper term further expressed as a function of wing geometric parameters as:

$$b = \rho C_D(\alpha_0) \bar{c} R^3 \tilde{F}_N \phi_0$$  \hspace{1cm} (12)

where, $\bar{c}$ is the mean chord length, $R$ is the wing length along the radial axis, and $\tilde{F}_N$ is non-dimensional normal aerodynamic force on the wing.

Similarly, the location of $r_{cp}$ for a linearized model with constant angle of attack can be computed knowing only the wing shape and linearization parameters (71). Further, we numerically compute the center of mass (COM) and the inertia properties of the wing by discretizing it's 2D planform into 4000 spanwise strips and equally-space chordwise strips (based on the aspect ratio) as a function of wing damage from the distal end. The estimates obtained above were in close agreement with the same evaluated from a 3D model of the wing using Solidworks. Thus, we computed the system properties for our intact wing in Table S6. Using the above procedure, we computed the wing geometry dependent system properties as a function of wing area loss as summarized in Table S7 and can predict the effect of wing damage.

**Derivation of closed-loop response from open-loop system**

For the fly model, we can compute the closed-loop response $H$ from the open-loop system $G$ as

$$\hat{H} = \frac{G}{1 + G}$$  \hspace{1cm} (13)

In our first approximation, we substitute the open-loop model $G_{intact}$ which yields

$$H_{intact} = e^{-0.021s} \frac{12.2}{s + 3.1}$$

which we can simplify as

$$H_{intact} = e^{-0.021s} \frac{12.2}{s + 3.1} \left( \frac{s + 3.1}{s + 3.1} \right) = e^{-0.021s} \frac{12.2}{s + 15.3}$$ \hspace{1cm} (15)

Similarly, substituting the open-loop model $G_{damaged}$ and simplifying yields

$$H_{damaged} = e^{-0.022s} \frac{9.8}{s + 5.6} \left( \frac{s + 5.6}{s + 5.6} \right) = e^{-0.021s} \frac{9.8}{s + 15.4}$$ \hspace{1cm} (16)

As can be seen, the roots of the denominator are nearly identical, suggesting similar closed-loop stability between intact and damaged flies.

Next, we approximate the time delay for the same open-loop transfer function of the form:

$$G(s) = e^{-st} \frac{k_p}{s + b}$$  \hspace{1cm} (17)

The time delay term can be represented by a first order Padé approximant of the form:

$$e^{-st} \approx \frac{1 - \frac{t}{2}s}{1 + \frac{t}{2}s}$$  \hspace{1cm} (18)

where $\tau$ is the system delay (30). The open loop transfer function can then be written as:

$$G(s) = \frac{1 - \frac{\tau}{2}s}{1 + \frac{\tau}{2}s} \left( \frac{k_p}{s + b} \right)$$  \hspace{1cm} (19)

The following system contains two poles and one zero and approximates the open loop function with a time delay. Closing the loop yields a transfer function of the following form
\[ H(s) = \frac{b_0s + b_1}{s^2 + a_1s + a_2} \]  \hspace{1cm} (20)

By estimating the closed-loop equation for each fly, we can compare the denominators of both groups to determine if the presence of a time delay alters our conclusion. By calculating the averaged closed-loop transfer function for both groups of flies, we obtained the following results:

\[ H_{\text{Intact}} = \frac{-12.2s + 1215}{s^2 + 90s + 1523} \]  \hspace{1cm} (21)

and

\[ H_{\text{Damaged}} = \frac{-9.8s + 900}{s^2 + 88 + 1436} \]  \hspace{1cm} (22)

Comparing the coefficients of the denominator yielded no statistical differences therefore suggesting that inclusion of the time-delay term does not affect our conclusions (\(t\)-test, \(a_1\): \(p = 0.41\); \(a_2\): \(p = 0.44\); Figure S11).

**Flapping counter-torque model**

We approximated the 3D wing kinematics—specifically the stroke angle \(\Phi\)—of magnetically tethered flies using free flight data from *Drosophila* following unilateral wing damage (9). Further, we used the rotation angle \(\alpha\) data directly from free flight data (9). From this data, we generated a baseline set of 3D wing kinematics of intact and damaged flies. The stroke angle for all flies was estimated by multiplying the base stroke angle from (9) by a correction factor. The correction factor was calculated for both wings of each fly by dividing the experimentally measured WBA of each wing with the total displacement of the baseline stroke angle. This allowed us to translate the 2D kinematics to 3D by scaling the baseline 3D kinematics to match measured 2D wingbeat amplitudes. The new stroke angle was then divided by the stroke plane angle (\(\cos (\pi/6)\)) to project the 2D WBA onto the stroke plane (72). This corrects the WBA which is measured using a bottom-view camera. For rotation angles, we used the intact and damaged baseline rotation angles reported in free flight (9). We used the averaged wingbeat frequencies reported in Figure 3D for intact and damaged flies in the magnetic tether. Using actual 3D wing kinematics data during hovering from the magnetic tether did not change our conclusions (damaged: 32 wing strokes from \(n = 5\) flies; intact: 23 wing strokes from \(n = 5\) flies).

**Estimation of wing morphological parameters**

Wing morphological parameters were estimated from images of intact and damaged wings taken under a microscope. A custom MATLAB script was used to estimate the wing length \(R\), average wing chord \(c\), and the non-dimensional third moment of wing area \(\hat{r}_3\).

**Formulation of the FCT equation**

Using a quasi-steady, blade-element model, the torque \(T\) generated by a flapping wing can be estimated as follows:

\[ T(\hat{t}) = C\Omega_w^2 \]  \hspace{1cm} (23)

where \(\Omega_w\) and \(C\) are the angular velocity of the wing in the body frame and non-kinematic terms, respectively, and \(\hat{t}\) is the normalized time (31). In the case of asymmetric wing motion and morphology, the torque generated by each wing can be estimated as

\[ T_{\text{left}}(\hat{t}) = C_1\Omega_{w1}^2 \]

\[ T_{\text{right}}(\hat{t}) = C_2\Omega_{w2}^2 \]  \hspace{1cm} (24)

For a constant velocity \(\Omega_b\) of the body about the yaw axis, the FCT is estimated by calculating the difference in flapping torque \(T_f\) of the two wings:

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For a constant velocity \(\Omega_b\) of the body about the yaw axis, the FCT is estimated by calculating the difference in flapping torque \(T_f\) of the two wings:
\[ T_f = T_{left} - T_{right} \]

\[ T_f = C_1(\Omega_{w1} - \Omega_b)^2 - C_2(\Omega_{w2} + \Omega_b)^2 \] (25)

Estimation of the damping coefficient from the FCT

While Equation 25 is a nonlinear function of the body and wing velocities, the relationship between yaw velocity and the resulting FCT can be approximated as a linear relationship for small values of \( \Omega_b \) using the following relationship

\[ T_f = -B\Omega + \tau_0 \] (26)

where \( B \) is the damping coefficient about the yaw axis and \( \tau_0 \) is a torque bias. Fitting the numerical FCT data to Equation 26 yielded a \( R^2 \) value of 1 for intact and damaged flies for yaw velocities less than \( 100^\circ \text{s}^{-1} \). This model predicted an overall decrease in damping coefficient following unilateral wing damage (Figure 5H).
**Figure S1. Fly response and stimulus parameters, related to Figure 1.** Average body response for intact (green, $n = 30$) and damaged flies (red, $n = 24$) to a sine visual stimulus oscillating at 0.2 Hz (black). Note that this stimulus did not elicit smooth movement as the fly moved in response to each step of individual pixels of the LED arena. B) Amplitude and velocity of velocity-normalized, sum-of-sines stimulus.
Figure S2. Influence of area loss ratio, stability of flies in the magnetic tether and head responses, related to Figure 2. A) Bode plot generated from measuring the frequency domain response of three groups of damaged wing flies separated by wing area loss ratio. A statistical analysis yielded no significant association between wing damage and area loss ratio (ANOVA). A sample size of eight, 20, 7 for 0.8–0.9, 0.7–0.8, & 0.6–0.7, respectively. See Table S2 for statistics. B) Proportions of stable and unstable flies in the magnetic tether for intact and damaged flies. The proportions were not statistically significant ($p = 0.5$). C) Wing damage area ratio for stable and unstable flies. D) Gain for the head’s motion in the moving body frame (motion of the head relative to the fly’s body). Wing damage had little influence on head movements and head performance was somewhat lower at higher frequencies (Table S3).
Figure S3. Relationship between microphone and wingbeat analyzer data, related to Figure 3. Raw signals generated from measuring the wingbeat frequency of a rigidly tethered fly using the wingbeat analyzer (blue) and a microphone (red) in the rigid tether. By determining that the peaks in the raw microphone signal were aligned with the peaks generated by the wingbeat analyzer signal, we verified that the microphone can accurately estimate the wingbeat frequency in the magnetic tether.
Figure S4. Comparison of fly and robophysical model responses, related to Figure 3. Mathematical and robophysical models corroborate fly flight scaling of wingbeat amplitude and frequency with wing damage. A) Robophysical model setup. The wing was driven by a piezoactuator (PZT) and video recorded at 4 kHz using a high-speed video camera. B) Relationship between wing damage and wingbeat frequency for rigidly tethered flies and the resonant frequency of the robophysical model. C) Relationship between wing damage and wingbeat amplitude of tethered flies (for the left damaged wing) and the robophysical model. \( n = 28 \) flies with damage and \( n = 10 \) intact flies. For B & C, error bars are shown for intact flies (wing area ratio = 1). For details on the fly and robot models, see the Supplementary Information.
Figure S5. PI model and individual fly variation, related to Figure 5. A) Parametric model (fit data) for a second-order transfer function for a putative PI controller, with one zero and one pole fixed at the origin. The goodness of fit for both groups (93% and 90%) was similar to those obtained from fitting a transfer function with no zeros and one pole to the empirical data. B) Pole-zero map of model from A. C) The open-loop gains were statistically different, whereas the integral gains were not. Integral gains were close to zero in some fits suggesting a first-order model is sufficient to model the yaw dynamics. ***: p < 0.001 D) Gain and phase of the open-loop transfer function for intact and damaged flies used in the analysis to generate Figure 5C. Individual lines represent different flies. Intact: n = 40. Damaged: n = 38.
Figure S6. Unilateral wing damage subtly influences the dynamics of saccades. A) Saccade dynamics (rotation, amplitude and peak speed) for intact (green) and damaged (red) flies during the presentation of a panorama rotating at constant velocity. Intact flies had modestly larger durations and peak velocities compared to damaged flies (Hedges’ g = 0.47 and 0.23, respectively). Intact: N = 2,556 saccades; Damaged: N = 2,836 saccades. B) Same data as A but showing saccade velocity and acceleration traces. Thick line: mean. Shaded area: ±1 STD. C) Same damaged data shown in A classified by direction (toward or away from the damaged wing). Statistical analysis revealed small to medium effect sizes in saccade dynamics s (Hedges’ g = 0.1, 0.26, 0.31 for duration, amplitude, and peak velocity, respectively). N = 932 saccades toward the intact wing. N = 758 saccades. D) Same data as C but showing velocity and acceleration. Thick line: mean. Shaded area: ±1 STD.
Figure S7. Dynamic model of the fly wing. A) We modeled the wing as a rigid pendulum with a torsional spring and damper at the center of rotation. $C$ is the damping ratio at the wing hinge joint, $K$ is the stiffness of the wing hinge joint, $I$ is the moment of inertia of the wing, and $\theta$ is the stroke angle of the wing. B) Geometry of the wing model.
Figure S8. Robophysical model based on the Harvard Robobee (56).
Figure S9. Robophysical model prediction. Bode plot showing the predicted frequency response of the Robobee system model for various levels of wing damage (0–40% loss in wing area).
Figure S10. Robophysical model response. Experimental Bode plot showing the frequency response of the Robobee system for various levels of wing damage (0–40% loss in wing area).
Figure S11. Effect of time delay on closed-loop transfer function denominator coefficients. Comparison of denominator coefficients of intact and damaged closed-loop transfer function with Padé approximation.
Table S1. Related to Figure 2. P-values for the gain, phase difference, and coherence of sum-of-sine data (t-test)

| Freq | 0.35 | 0.55 | 0.9 | 1.45 | 2.25 | 3.45 | 5.45 | 8.55 | 13.7 |
|------|------|------|-----|------|------|------|------|------|------|
| Gain | $6.2\times10^{-8}$ | $3.3\times10^{-7}$ | $5.4\times10^{-8}$ | $9.5\times10^{-5}$ | $5.4\times10^{-5}$ | $3.6\times10^{-5}$ | $8.0\times10^{-5}$ | $1.6\times10^{-4}$ | 0.0027 |
| Phase | 0.9 | 0.098 | 0.56 | 0.039 | 0.65 | 0.17 | 0.013 | 0.24 | 0.073 |
Table S2. Related to Figure S3. P-values for the gain and phase difference for data grouped by percentage wing area loss (ANOVA).

| Freq | 0.35 | 0.55 | 0.9  | 1.45 | 2.25 | 3.45 | 5.45 | 8.55 | 13.7 |
|------|------|------|------|------|------|------|------|------|------|
| Gain | 0.34 | 0.34 | 0.73 | 0.58 | 0.345| 0.033| 0.11 | 0.08 | 0.38 |
| Phase| 0.24 | 0.12 | 0.32 | 0.27 | 0.29 | 0.84 | 0.12 | 0.5  | 0.45 |
**Table S3.** Related to Figure S3. P-values for the gain and phase difference for intact and damaged fly head motion (t-test).

| Freq | 0.35 | 0.55 | 0.9  | 1.45 | 2.25 | 3.45 | 5.45 | 8.55 | 13.7 |
|------|------|------|------|------|------|------|------|------|------|
| Gain | 0.58 | 0.7  | 0.36 | 0.66 | 0.013| 0.0045| 0.057| 0.0014| 0.0005|
Table S4. Robophysical model wing dimensions.

| Property                  | Dimension |
|---------------------------|-----------|
| Length                    | 10 mm     |
| Width                     | 4 mm      |
| Thickness (mylar)         | 3 µm      |
| Thickness (carbon fiber)  | 90 µm     |
| Mass                      | 0.78 mg   |
Table S5. Robophysical model actuator dimensions.

| Property                  | Dimension |
|---------------------------|-----------|
| Length                    | 10 mm     |
| Width (wide section)      | 6.5 mm    |
| Width (narrow section)    | 3 mm      |
| Thickness                 | 520 μm    |
### Table S6. Robot intact wing damping and inertial parameters.

| Parameter                  | Symbol | Value | Units          |
|---------------------------|--------|-------|----------------|
| Actuator Mass             | $m_a$  | 96    | $mg$           |
| Wing Inertia              | $J_{\phi}$ | 51.3 | $mg \cdot mm^2$ |
| Transmission Ratio        | $T$    | 5882  | $rad/m$        |
| Radius to center of pressure | $r_{cp}$ | 7.5  | $mm$           |
| Aerodynamic damping       | $b$    | 1.34  | $\mu N \cdot s/rad$ |
| Actuator stiffness        | $k_a$  | 1315  | $N/m$          |
| Wing hinge stiffness      | $k_t$  | 15.2600 | $\mu N \cdot s/rad$ |
| Equivalent mass           | $m_{eq}$ | 1800 | $mg$           |
| Equivalent damping        | $b_{eq}$ | 0.3499 | $N.s/m$        |
| Equivalent stiffness      | $k_{eq}$ | 1842.4 | $N/m$         |
**Table S7. Change in wing-geometry dependent parameters of the system.**

| Parameter | Intact Wing | 10% loss | 20% loss | 30% loss | 40% loss |
|-----------|-------------|----------|----------|----------|----------|
| $J_\phi$  | 51.3        | 40.9     | 32.0     | 24.5     | 18.3     |
| $r_{cp}$  | 7.5         | 7.1      | 6.7      | 6.2      | 5.8      |
| $b$       | 1.34        | 1.06     | 0.82     | 0.63     | 0.46     |
| $m_{eq}$  | 1800        | 1441     | 1132     | 875      | 660      |
| $b_{eq}$  | 0.3499      | 0.2606   | 0.1897   | 0.1352   | 0.0934   |
**Movie S1.** Yaw optomotor response of intact flies. Related to Figure 2. Top left: Bottom view of a single fly within animated virtual reality arena during a full 20 s trial. Magenta line: heading vector. Top right: Same as left video but in the body frame of reference. Red line: left wingbeat amplitude. Blue line: right wingbeat amplitude. Cyan line: Abdominal angle. Bottom: stimulus (green), fly body heading (magenta), left and right wingbeat amplitudes (red and blue, respectively) and abdominal angle (cyan). For visual clarity, the arena is not drawn to scale. Frame rate = 160 fps but showed at 50 fps.

**Movie S2.** Yaw optomotor response of damaged flies. Related to Figure 2. Same as Movie S1 but for damaged flies. Grey arrow: damaged wing.

**Movie S3.** Robophysical model with intact and damaged wings. Related to Figure S4. Piezoelectrically driven, single wing robophysical model illustrating the change in passive dynamics of the system in response to wing damage. Left: flapping kinematics of the intact wing as a function of frequency ranging from 10 Hz to 350 Hz in 10 Hz increments. Right: Motion of the same wing with 40% wing area loss. The video plays sequentially five times in real-time followed by the same slowed-down 160X.
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