Distinct forms of resonant optimality within insect indirect flight motors

Arion Pons\textsuperscript{1,2} and Tsevi Beatus\textsuperscript{1,2}

\textsuperscript{1}The Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Israel
\textsuperscript{2}The Benin School of Computer Science and Engineering, The Hebrew University of Jerusalem, Israel

Insect flight motors are extraordinary natural structures that operate efficiently at high frequencies. Structural resonance is thought to play a role in ensuring efficient motor operation, but the details of this role are elusive. While the efficiency benefits associated with resonance may be significant, a range of counterintuitive behaviours are observed. In particular, the relationship between insect wingbeat frequencies and thoracic natural frequencies is uncertain, with insects showing wingbeat frequency modulation over both short and long time scales. Here, we offer new explanations for this modulation. We show how, in linear and nonlinear models of an indirect flight motor, resonance is not a unitary state at a single frequency, but a complex cluster of distinct and mutually exclusive states, each representing a different form of resonant optimality. Additionally, by characterizing the relationship between resonance and the state of negative work absorption within the motor, we demonstrate how near-perfect resonant energetic optimality can be maintained over significant wingbeat frequency ranges. Our analysis leads to a new conceptual model of flight motor operation: one in which insects are not energetically restricted to a precise wingbeat frequency, but instead are robust to changes in thoracic and environmental properties—an illustration of the extraordinary robustness of these natural motors.

1. Introduction

Insect flight motors are extraordinary: insects show the highest recorded relative locomotion velocities for any animal, reaching up to one thousand body lengths per second [1], and can exhibit wingbeat frequencies in the hundreds of hertz [2]. This level of flight motor performance has not been surpassed by any of the wide range of biomimetic analogues under development [3,4]. Insect flight motors take a range of different forms: one form which has seen detailed study is the indirect flight motor, as found in orders Diptera (flies) and Lepidoptera (butterflies, moths), as well as in a range of species across other orders [2,5,6]. In the indirect flight motor, the contraction of the primary flight muscles—the dorsoventral (DVM) and dorsolongitudinal (DLM) muscles—is transmitted to wingbeat motion via the elastic thorax. This process is thought to involve wing–thorax resonance [7–10]—the absorption of wing inertial loads via thoracic elasticity—but details are elusive. While there is evidence for the significance of resonant effects [11,12], including consistent wingbeat frequency changes in response to wing mass changes [13], several counterintuitive behaviours are observed. For instance, species that are thought to use resonant effects are observed to undergo additional notable, but seemingly random, wingbeat frequency variation—for instance, variation of up to 15% in fruit flies [14]. A range of these species are also observed to alter wingbeat frequency in a controlled manner: in honeybees, fruit flies and hawkmoths, as a mechanism of aerodynamic force control [9,15–17], and in mosquitoes, for acoustic courtship interactions [18,19]. More complex relationships are also observed: both positive and negative [20,21] correlations between wingbeat frequency and ambient temperature in species of bee and fly, with population-averaged frequency alterations of up to 30% [21]. These relationships are also observed: both positive and negative [20,21] correlations between wingbeat frequency and ambient temperature in species of bee and fly, with population-averaged frequency alterations of up to 30% [21]. These
behaviours are counterintuitive in the sense that they defy classical conceptions of resonance as a unitary state, existing at a specific frequency. Either insects often deviate from resonance, or more complex effects are at work (table 1).

In this vein, several explanations for these behaviours have been proposed. The operation of sets of pleurosternal and tergopleural muscles has been proposed as a mechanism for time-varying control of the thoracic resonant frequency [9,22–26], potentially allowing wingbeat frequencies to vary while maintaining a state of continued resonance. Alternatively, behaviour involving intentional frequency control has been motivated in terms of the trade-off between deviating from resonance and achieving other goals: for instance, performing a manoeuvre [9], or engaging in courtship [18]. One of the impediments to understanding these effects, and candidate explanations, is the lack of any clear information on what resonance actually represents in an insect indirect flight motor—and what costs, exactly, would be associated with deviating from resonance. It is currently unclear exactly what forms of optimality (e.g. in displacement, velocity, energy, etc.) flight motor resonance can represent; at which frequencies these optimal states occur; and how structural properties (e.g. elasticity distribution within the thorax and aero-structural damping) affect these frequencies.

In this work, we study these aspects of indirect flight motor resonance in more detail and obtain some surprising results. We illustrate how there may be up to eight distinct and mutually exclusive resonant frequencies in the flight motor system, including classical forms of resonance, and the novel form of global resonance [27–30], defining energetic optimality. Using published data from a range of insect species, we demonstrate how the flight motor elasticity distribution and damping alter these resonant states. These fundamental theoretical results shed light on discrepancies between wingbeat frequencies and measured thoracic resonant frequencies [11]. They also offer explanations for counterintuitive insect behaviours: how insects can apparently afford to undergo moderate variations in wingbeat frequency [9,14–16], without any form of time-varying control of the thoracic resonant frequency. The existence of these distinct flight motor resonant frequencies has significant implications both for the interpretation of insect flight and the design of flapping-wing micro-air-vehicles.

2. Transfer functions of hybrid parallel-elastic actuation–series-elastic actuation systems

2.1. Dynamics of parallel-elastic actuation, series-elastic actuation and hybrid systems

Insect indirect flight motors are complex dynamical structures [10,31]. Following Lynch et al. [10], we will develop a new hybrid model for these motors, but consider first its two key
Figure 1. Hybrid single-degree-of-freedom system model of the insect indirect flight motor. Examples of pure PEA (a) and SEA (b) systems are illustrated, as well as the resulting hybrid model that arises when both a series \((k_s)\) and parallel \((k_p)\) elasticity is present. This resulting hybrid model (c) can be used as a simple general model of the elasticity distribution within an insect indirect flight motor (d).

Figure 2. (a) Parallel-elastic actuation (PEA) \(F = \frac{d}{k_p} \ddot{x} + k_p x = F(t)\), actuator \(u(t) = x(t)\).

(b) Series-elastic actuation (SEA) \(F = k_s \ddot{u} + k_s u = F(t)\), where \(u(t) = 0\).

(c) Hybrid actuation \(k_p \ddot{x} + k_s \ddot{u} = F(t)\), with \(x(t)\) and \(u(t)\) proportional to actuator force.

(d) Insect indirect flight motor with pleural hinge and sternum, scutum, pleural wall and sternum, and indirect flight muscles.

\[ F = \frac{d}{k_p} \ddot{x} + k_p x = F(t) \quad \text{or} \quad \ddot{x} + 2\zeta_p \omega_n \ddot{x} + \omega_n^2 x = F(t) \]

PEA: \(m \ddot{x} + d \dot{x} + k_p x = F(t)\), \(u(t) = x(t)\).

SEA: \(m \ddot{x} + d \dot{x} + k_s \ddot{u} = F(t)\), \(u(t) = 0\).

\[ F = \frac{k_p (u(t) - x(t))}{m} \]

with natural frequencies \(\omega_n = \sqrt{k_p/m}\) and damping ratios \(\zeta_p = \frac{d}{2\sqrt{mk_p}}\).

Several properties of these systems can be observed. The PEA system behaves as a classical second-order oscillator under prescribed load, \(F(t)\), and the SEA system behaves as such under prescribed displacement, \(u(t)\). However, consider the reverse: the PEA system under prescribed \(u(t)\) behaves as a kinematic link \((u(t) = x(t))\), and the SEA system under prescribed \(F(t)\) is governed by an inelastic second-order system \((m \ddot{x} + d \dot{x} = F(t))\) or \(\ddot{x} + 2\zeta_p \omega_n \ddot{x} = \omega_n^2 x\).

These two systems are simplified models of an insect indirect flight motor (figure 1) [10]. They are simplified in three senses. (i) The model is linear: inertia and elasticity are linear, and damping is linear and viscous. Nonlinear or viscoelastic flight motor properties are not modelled [6,10,11,33]. (ii) We have assumed that the flight motor damping is dominated by damping forces that arise at the wing (from \(x(t)\), rather than from \(u(t)\)). These damping forces could be comprised of aerodynamic drag (modelled linearly or nonlinearly) and wing hinge structural damping. (iii) We have assumed the distribution of elasticity within the motor: either pure SEA or pure PEA. Consider this last simplification: which distribution of elasticity accurately represents an indirect flight motor? Indirect flight motors are commonly considered to undergo PEA [34–36]. The behaviour of these motors points to dominant parallel-elastic behaviour: to a large degree, insect wings and muscles largely behave as if kinematically connected, as per PEA (\(u(t) = x(t)\), equation (2.1)). Under quasi-static conditions, insect flight muscle deformation is directly coupled to wing motion [7,11,37] and induces an elastic response [11]. During tethered flight experiments, the phase difference between muscular deformation and wingbeat motion is often small [5,31,38,39]. However, recent studies [10] have contemplated an additional series-elastic element in indirect flight motors, to account for inexactness in this kinematic connection: the possibility of a phase difference between \(u(t)\) and \(x(t)\). In some species, e.g. fruit flies [8,39] and hawkmoths [5], a phase difference between muscular contraction and wingbeat motion is observed, pointing to the possible existence of this series-elastic effect. There is physiological rationale for considering this series-elastic effect: the transmission of motion from musculature to wing occurs through elastic thoracic structures [7,10,31], which have their own local modal frequencies; in principle, introducing series-elastic effects. In physiological terms, a parallel-elasticity corresponds approximately to elasticity within the pleural wall and a series-elasticity to elasticity within the scutum and pleural mechanism (figure 1, also see [40]). More precisely, the addition of this series-elastic element can be seen as providing one linear spring’s worth (i.e. one linear mode’s worth) of dynamic variation between the muscles \((u)\) and wing \((x)\).
Introducing additional series-elastic elements, and series masses, could be used to simulate more complex dynamic variation effects, but as the simplest possible dynamic variation model, we will study as single series-elastic element.

Consider, therefore, a new hybrid PEA–SEA model of an insect flight motor (figure 1). We have a choice in how to represent the system equation of motion: with actuation under $u(t)$ or under $F(t)$, that is

$$
\begin{align*}
\dot{x} + \frac{\dot{d}}{C_0} \dot{x} + k x = F(t), & \quad \text{or,} \\
\dot{x} + (k_0 + k_1) x = u(t), & \quad \text{with} \\
F(t) = k_0 u(t) - x(t).
\end{align*}
$$

With these two representations are equivalent, the distinction is more than one of notation. Fundamentally, the system’s dynamic response to prescribed displacement, $u(t)$, differs from its response to prescribed load, $F(t)$—just as this response differs in pure PEA and SEA systems. This effect is further elucidated by the canonical form of the hybrid system:

$$
\begin{align*}
\dot{x} + 2 \zeta_0 \omega_0 \dot{x} + \omega_0^2 x = f(t), \\
\dot{x} + 2 \zeta_0 \omega_0 \dot{x} + (\omega_0^2 + \alpha_0^2) x = \alpha_0^2 u(t), \\
\text{with} \\
f(t) = \alpha_0^2 (u(t) - x(t)),
\end{align*}
$$

and with parameters identical to those of the pure PEA and SEA systems (equation (2.2)). As can be seen from equation (2.4), depending on the actuator behaviour (prescribed $f(t)$, or prescribed $u(t)$), the system response is governed by either the purely parallel natural frequency, $\omega_0$, or a hybrid natural frequency, dependent on both $\alpha_0$ and $\omega_0$. In physical terms: in the limit of low damping, $\omega_0$, represents the system’s natural frequency for oscillations in which $u$ is free, and the hybrid natural frequency, the natural frequency for oscillations in which $u$ is held fixed. To study the system behaviour under stronger damping, we now characterize these natural frequencies in more detail.

### 2.2. Distinct transfer functions and resonant frequencies

The linearity of this hybrid system permits a frequency domain analysis. We represent the system’s time-varying parameters as complex exponentials, or phasors:

$$
\begin{align*}
x(t) &= \text{Re}(\xi \exp(i\Omega t)), \\
u(t) &= \text{Re}(\dot{\xi} \exp(i\Omega t)), \\
f(t) &= \text{Re}(\dot{\xi} \exp(i\Omega t)),
\end{align*}
$$

where $\dot{x}$, $\dot{u}$ and $\dot{f}$ are complex-valued amplitudes, $\Omega$ is the input/output frequency and $\text{Re}(\cdot)$ is the real part. These complex-valued amplitudes are equivalent to a real-valued amplitude and phase angle:

$$
\begin{align*}
x(t) = |x| \text{Re}(\exp(i\Omega t + \psi_x)), \\
\psi_x = \tan^{-1} \left( \frac{\text{Im}[x]}{\text{Re}[x]} \right),
\end{align*}
$$

where $|x| \in \mathbb{R}$ is the real amplitude, and $\psi_x \in \mathbb{R}$ is the phase angle. The complex components in equation (2.5) allow us to define two key complex-valued transfer functions; between input and output displacements ($\dot{x}/\dot{u}$) and between input load and output displacement ($\dot{x}/f$):

$$
\begin{align*}
\frac{\dot{x}}{\dot{u}} &= \frac{i \omega_0 \Omega}{\omega_0^2 + \alpha_0^2 - \Omega^2 + 2i \zeta_0 \omega_0 \Omega}, \\
\frac{\dot{x}}{f} &= \frac{1}{\omega_0^2 - \Omega^2 + 2i \zeta_0 \omega_0 \Omega}.
\end{align*}
$$

These complex-valued transfer functions can be separated into components of magnitude:

$$
\begin{align*}
|\dot{x}| &= \frac{\omega_0^2}{\sqrt{(\omega_0^2 + \alpha_0^2 - \Omega^2)^2 + 4 \zeta_0^2 \omega_0^2 \Omega^2}} \frac{\omega_0}{\omega_0^2 + \alpha_0^2 - \Omega^2}, \\
|\dot{u}| &= \frac{1}{\sqrt{(\omega_0^2 + \alpha_0^2 - \Omega^2)^2 + 4 \zeta_0^2 \omega_0^2 \Omega^2}}.
\end{align*}
$$

and phase:

$$
\psi_x - \psi_u = - \tan^{-1} \left( \frac{2 \zeta_0 \omega_0 \Omega}{\omega_0^2 + \alpha_0^2 - \Omega^2} \right), \\
\psi_x - \psi_f = - \tan^{-1} \left( \frac{2 \zeta_0 \omega_0 \Omega}{\omega_0^2 - \Omega^2} \right).
$$

We can then probe two key properties of the system: at what frequencies are the response magnitudes, $|\dot{x}|/|\dot{u}|$ and $|\dot{x}|/|f|$, maximized? Via the first derivative test, we compute these two distinct frequencies as

$$
\begin{align*}
\arg\max_n \left( \frac{|\dot{x}|}{|\dot{u}|} \right) &= \sqrt{\omega_0^2 + \alpha_0^2 - 2 \omega_0^2 c_n - 2 \alpha_0^2 c_n^2 + \omega_0^2 \sqrt{1 + \alpha^2 - 2 \beta}}, \\
\arg\max_n \left( \frac{|\dot{x}|}{|f|} \right) &= \omega_0 \sqrt{1 - \frac{2 \zeta_0^2}{\beta}},
\end{align*}
$$

where $\alpha = \frac{\omega_0}{\omega_0}$, $\beta = \frac{\omega_0}{\omega_0}$

and $\arg\max_n (H(\Omega)) = \{ \Omega : H(\Omega) \text{ max} (H(\Omega)) \}$.

In equation (2.10), we have introduced the parameter $\alpha$, which conveniently represents systems that are neither pure SEA ($\omega_0 = 0$ and $\alpha_0 > 0$), so $\alpha \to \infty$ nor pure PEA ($\omega_0 = 0$ and $\alpha_0 > 0$), so $\alpha \to 0$: both pure cases alias onto the same $\alpha$.

The two frequencies in equation (2.10) are not the only system resonant frequencies. Following the definition of resonance as a state of peak response in some state variable [41], we can define transfer functions in velocity (phasor amplitude $i\dot{\xi} \Omega$) and acceleration (phasor amplitude $\dot{x} f$):
The peaks of these transfer functions are the velocity and acceleration resonant frequencies, which are distinct from the displacement resonant frequencies [41]. These four resonant frequencies are as follows:

\[
\begin{align*}
\arg \max_{\alpha} \left( \frac{|s\Omega|}{|a|} \right) &= \omega_p \sqrt{1 + \alpha^2}, \\
\arg \max_{\alpha} \left( \frac{|s\Omega|^2}{|a|} \right) &= \omega_p \sqrt{1 + \alpha^2 - 1}, \\
\arg \max_{\alpha} \left( \frac{|s\omega|}{|f|} \right) &= \omega_p, \\
\text{and } \arg \max_{\alpha} \left( \frac{|s\omega|^2}{|f|} \right) &= \frac{\omega_p}{\sqrt{1 - 1}}.
\end{align*}
\]

(2.12)

There is now a total of six resonant frequencies in the system. In general, these six frequencies are distinct, as each depends on damping (via $\zeta_p$) and the strength of series-elastic effects (via $\alpha$) in different ways. Figure 2 illustrates these dependencies. Several points can be noted.

(i) The existence of these distinct frequencies raises a point not previously recognized in the study of insect flight. Even in our simple single-degree-of-freedom linear model, there are multiple distinct resonant frequencies: multiple mutually exclusive states of optimal actuation. This has implications for the study of indirect flight motor resonance: for instance, existing estimates of honeybee thoracic resonant frequency [11] are based on actuation point acceleration (ii) with respect to load ($f$). The distinction between this frequency and other resonant frequencies may contribute to observed wingbeat frequency differences [11].

(ii) In terms of the input function variable: broadly, the force-based transfer functions ($s\omega/f$, etc.) would appear to be more relevant to insect flight, as the flight motor metabolic cost is related to its force output [42]. The displacement-based transfer functions ($s\omega/a$, etc.) are only likely to be relevant in cases of extreme performance: where metabolic cost is irrelevant, and the insect’s only objective is to extract maximum response from the limited range of muscular motion. It is possible that this situation could be realized in certain extreme evasive or corrective manoeuvres [43–45].

(iii) In terms of the output function variable: broadly, the displacement-output ($s\omega/f$, $s\omega/a$, etc.) and velocity-output ($s\omega/f$, $s\omega/a$, etc.) transfer functions would appear to be the more relevant to insect flight, as these output variables are directly related to the insect’s aerodynamic performance (via the wingbeat amplitude and peak velocity).

3. Power consumption and the global-resonant frequency

3.1. Power consumption

The six resonant frequencies defined thus far are not a complete characterization of the optimal operating points of our simplified hybrid model of an indirect flight motor. We have not yet characterized the flight motor power consumption, and the frequencies at which the flight motor is most efficient.
The role of thoracic elasticity, and structural resonance, in reducing motor muscular power consumption can be seen through the lens of negative work absorption: the potential for thoracic elasticity to absorb negative work—work done by the wing on the flight motor—and then release this stored energy at other points during the wingbeat cycle [14, 46–48]. To compute the frequency at which this effect is optimal, we require a more sophisticated analysis. Defining a canonical mechanical power requirement, \( p = f u \), we find that, as a product of two phasors, \( p \) is not representable as a pure phasor [49]. Instead, \( p \) is composed of a phasor term, of some amplitude \( |p| \), and a constant term, \( \bar{p}_0 \):

\[
p(t) = \bar{p}_0 + |p| \text{Re} \exp (2i\Omega t + \phi_p).
\]

(3.1)

With some manipulation, we will next obtain explicit forms of these phasor and constant terms. Extending equations (2.5)–(2.6), we represent \( f(t) \) and \( u(t) \) in their analytic forms, \( f(t) \) and \( u(t) \):

\[
f(t) = \text{Re}(f(t)), \quad f(t) = \hat{f} \exp (i\Omega t)
\]

and

\[
u(t) = \text{Re}(u(t)), \quad u(t) = \hat{u} \exp (i\Omega t),
\]

(3.2)

where \( \hat{f} \) and \( \hat{u} \) are complex-valued amplitudes, encoding both magnitude and phase. As a reference, we take \( \hat{f} \) as a phasor with zero phase \( \hat{f} \in \Re \), without loss of generality. To obtain the relation between \( p(t) \) and \( \hat{f} \), we compute \( \dot{u} \) in terms of \( \hat{f} \) via a chain of the transfer functions defined in equation (2.8):

\[
\dot{u} = \left( \frac{\alpha}{\beta} \right)^{-1} \left( \frac{\beta}{\alpha} \right) \hat{f}.
\]

(3.3)

Then, we compute \( p(t) \) using an appropriate product of its analytic forms [50]:

\[
p(t) = \text{Re}(af) = \frac{1}{4} \left( \hat{u} f + \hat{u}^\dagger \right) + \frac{1}{4} \left( \hat{a} \hat{f} + \hat{a}^\dagger \hat{f} \right),
\]

(3.4)

where \( ( \cdot )^\dagger \) denotes the complex conjugate. As noted in equation (3.4), terms in this product can be identified with the constant \( \bar{p}_0 \) and oscillatory \(( |p| ) \) components of the time domain signal, depending on whether the complex exponents, \( \pm i\Omega t \), sum to zero (a constant) or to \( 2\Omega t \). The constant term is given by the associated complex product:

\[
\bar{p}_0 = \frac{\xi_p a_0 \omega_0^2}{\omega_0^2 - \Omega^2} + \frac{4\xi_p^2 a_0 \omega_0^4 \Omega^2}{\omega_0^2 - \Omega^2}.
\]

(3.5)

The magnitude of the time-varying term is given by the coefficients of the complex exponentials \( |p| \) in the complex product:

\[
\frac{1}{4} (\hat{a} \hat{f} + (\hat{a} f)^\dagger) = p^* \exp (2i\Omega t) + p^* \exp (-2i\Omega t)
\]

(3.6)

and

\[
|p| = \sqrt{(p^*)^2 + (p)^2},
\]

(3.6)

with magnitude, \( |p| \), given by

\[
|p| = \frac{\Omega}{2\alpha^2 a_0 \omega_0} \sqrt{((1 + \alpha^2) a_0^2 - \Omega^2)^2 + 4\xi_p^2 a_0^2 \omega_0^2 \Omega^2}.
\]

(3.7)

The parameters \( \bar{p}_0 \) and \( |p| \) define the power consumption of our hybrid model of an indirect flight motor (equation (3.1)).

With them, we can characterize the state of negative work absorption in the motor.

### 3.2. Global resonance and optimal efficiency

The insight that thoracic elasticity can absorb flight motor negative work and thereby decrease motor muscular power consumption [14, 46–48] is connected to a more general phenomenon of linear and nonlinear dynamics: the generalized energy-based conception of resonance sometimes referred to as global resonance [27–30]. In a general system, the core condition of global resonance is the absence of negative work in the system overall power requirement:

\[
p(t) \geq 0, \forall t.
\]

(3.8)

If this condition is satisfied—e.g. at a certain frequency, or state of elasticity—then the system is optimally efficient in a particular sense that we now study. Consider the overall power consumption of our indirect flight motor model measured by the integrals:

\[
p_{\text{abs}} = \frac{1}{T} \int_0^T |p(t)| \, dt, \quad p_{\text{pos}} = \frac{1}{T} \int_0^T p(t)[p(t) \geq 0] \, dt,
\]

(3.9)

where \( T = 2\pi/\Omega \) and \( | \cdot | \) is the Iverson bracket [51]. The metric \( p_{\text{abs}} \) is the absolute power consumption [52, 53]. It describes the behaviour of an actuator without energy regeneration, in which both positive \(( p > 0) \) and negative work requirements \(( p < 0, \text{e.g. for braking wingbeat motion}) \) must be provided at full energetic cost. The metric \( p_{\text{pos}} \) is positive-only power [46, 47]. It describes the behaviour of an actuator with imperfect energy regeneration, in which a specialized dissipative element is available to absorb, but not store, negative work. Note that, in the ideal case of perfect energy regeneration, the actuator power consumption would simply be represented by the net work \( \int_0^T p(t) \, dt \), but this is only realistic in certain tailored electrical actuators [32]. Exactly which of these metrics best describes the flight motor musculature is unclear. However, it is clear at least that this musculature does not show perfect energy regeneration, i.e. the ability to innately convert negative work back to metabolic energy. In fact, muscles often consume energy when doing negative work [54]. In any case, under global resonance, i.e. the absence of negative work (equation (3.8)), \( p_{\text{abs}} \) and \( p_{\text{pos}} \) necessarily take identical values.

In dynamical-systems sense, both \( p_{\text{abs}} \) and \( p_{\text{pos}} \) are metrics of the input (i.e. muscular) cost. Individually, as a function of input/output frequency \( (\Omega) \), both of these metrics (and the net power) have identical global extrema: a global minimum at \( \Omega = 0 \) and a global maximum at \( \Omega \rightarrow \infty \). However, more fundamental behaviour is elucidated when these input cost metrics are considered in ratio against a metric of the output (i.e. wing) response—in the manner of the transfer functions in §2.2. One pair of transfer ratios which are particularly important in the context of global resonance is the mechanical power transfer efficiencies:

\[
\eta_{\text{abs}} = \frac{\int_0^T p(t) \, dt}{\int_0^T |p(t)| \, dt}, \quad \eta_{\text{pos}} = \frac{\int_0^T p(t) \, dt}{\int_0^T |p(t)| p(t) \geq 0] \, dt},
\]

(3.10)

representing the ratio of actual net power output/throughput to actuator power consumption \(( p_{\text{abs}}, p_{\text{pos}}) \). The maximum possible efficiency is \( \eta_{\text{abs}} = \eta_{\text{pos}} = 1 \), which is reached only in the absence of negative work, i.e. at global resonance (equation (3.8)). In this way, these mechanical efficiencies not only represent the effectiveness of energy regeneration...
in the flight motor, but also, equivalently, how much net power throughput the flight motor achieves (as a proxy for its aerodynamic performance), per absolute or positive-only power it consumes (as a proxy for its metabolic cost).

Denoting, therefore, the global-resonant frequency of our hybrid model as \( \omega_g \), we can translate equation (3.8) to a condition on the power offset \( p_0 \) and amplitude \( |p| \):

\[
\omega_k = \Omega : p_0 \geq |p|,
\]

(3.11)

Analysing equation (3.11) in detail, via equations (3.5) and (3.7), we can confirm that there exists no \( \Omega \) such that \( p_0 > |p| \) strictly: the equation \( p_0 = |p| + \epsilon \) has no real solutions in \( \Omega \) for \( \epsilon > 0 \). Therefore, the condition for no negative work is uniquely:

\[
\omega_k = \Omega : p_0 = |p|,
\]

(3.12)

which we can solve explicitly by equating equations (3.5) and (3.7). Note first that, for pure PEA (the limit \( \omega_{0,p} \to \infty \), or equation (2.2) directly) and pure SEA (the limit \( \omega_{0,p} \to 0 \) or equation (2.2) directly), we have simply:

\[
\begin{align*}
\text{PEA:} & \quad \omega_{0,p} \to \infty & \omega_{0,p} = 0, \\
\text{SEA:} & \quad \omega_{0,p} = \omega_{0,p} & \omega_{0,p} = \omega_{0,p} \sqrt{1 - 4 \zeta_p^2}.
\end{align*}
\]

(3.13)

We pause briefly on this result. In a pure PEA system, the global-resonant frequency is precisely the undamped natural frequency of the system: a seemingly fundamental link, but it does not generalize to other actuator configurations. In the pure SEA system, the global-resonant frequency involves the factor \( 4 \zeta_p^2 \), distinct from all other resonant frequencies (equations (2.10) and (2.12)). And in the full hybrid case, the solution to equation (3.12) is the root of a quartic polynomial:

\[
\omega_k^\pm = \omega_{0,p} \sqrt{1 + \delta \pm \sqrt{\delta^2 - 4 \zeta_p^2}}, \quad \delta = \frac{1}{2} \alpha^2 - 2 \zeta_p^2.
\]

(3.14)

These \( \omega_k^\pm \) are resonant frequencies which, to our knowledge, have not previously been studied. Their behaviour is illustrated in figure 3. We note:

(i) The hybrid system has up to two global-resonant frequencies, \( \omega_k^+ \) and \( \omega_k^- \), associated with PEA- and SEA-type behaviour, respectively. These frequencies are distinct from the classical resonant frequencies (equations (2.10) and (2.12)), and, when real-valued, are always \( \geq \omega_{0,p} \).

(ii) There exist some \( a \) and \( \zeta_p \), for which \( \omega_k^\pm \) are complex-valued. In this situation, true global resonance does not exist. The efficiencies (\( \eta_{abs} \) and \( \eta_{pool} \)) may still have maxima, but not at \( \eta_{abs} = \eta_{pool} = 1 \): we term these maxima pseudo-global-resonant states. Further analysis is required to determine the exact frequencies and maxima of these pseudo-global-resonant states, but we propose an approximation for the frequencies: \( \Re(\omega_k^\pm) \). Consider the classical complex-valued transfer functions (equations (2.7) and (2.11)): the natural frequency, \( \omega_{0,p} \), is the real (oscillatory) part of the transfer function poles and thus approximates their resonant peak locations. In the same way, the real part of the transfer function efficiency poles approximates their pseudo-global-resonant peak locations (e.g. as verified numerically in figure 3a).

(iii) Irrespective of whether true global resonance exists or not, a state of near-global resonance, where \( \eta_{abs} \approx 1, \)

may be available over a comparatively wide range of frequencies. As figure 3a illustrates, the efficiency profiles are notably flat-topped, compared to equivalent classical transfer functions (figure 2). For parameters roughly indicative of a fruit fly flight motor (§§4.1–4.2), a state of \( \leq 1\% \) inefficiency (\( \eta_{abs} \geq 99\% \)) is satisfied over a frequency band of width 0.31\( \omega_{0,p} \). In classical transfer functions, a comparable state (magnitudes \( \geq 99\% \) of peak value) is available only over windows of width \( \approx 0.09\omega_{0,p} \). Physically, this is significant: an indirect flight motor only needs to operate in the broad vicinity of the global-resonant state to attain almost all of its energetic benefit. This provides some explanation for insects’ ability to afford variation in wingbeat frequency [9,14–16], as we discuss in §5.

(iv) An interesting feature that arises in the study of global resonance states is a dependency on the input/output waveform. Global resonance is defined in the time domain (equation (3.11)), and thus the hybrid system’s global-resonant frequencies (equation (3.13)) are defined for harmonic waves. Their application to indirect flight motor resonance is thus dependent on the assumption of insect wing stroke motion as simple-harmonic. Insect wing stroke kinematics do sometimes involve higher harmonics [5,17,33,46], and these harmonics could have an effect on the global-resonant properties of the flight motor.

4. Effects of increasing model fidelity

4.1. Viscoelasticity and nonlinearity in insect flight motors

We have thus far considered a linear model of an insect’s indirect flight motor. This linear model allowed us to illustrate, analytically, the distinction between different forms of flight motor resonance, and study the effect of motor elasticity distribution on this distinction. In reality, and as alluded to in §2.1, insect flight motors show more complex behaviours, including viscoelastic structural damping [6,10], nonlinear aerodynamic damping [10,33] and nonlinear structural elasticity [6,11]. Studying the effect of these behaviours on flight motor resonance is a complex process. First, when the system is nonlinear a range of nonlinear resonant phenomena may exist, each may generalize or be approximated by different properties of linear resonance [30,55]. Second, analytical techniques are often insufficient to characterize nonlinear resonant phenomena, making a general treatment of these phenomena more difficult. And third, the exact nature, combination and relative significance of these behaviours is unclear—for instance, currently there is insufficient experimental data regarding the relative strengths of viscoelastic, viscous and aerodynamic damping within the flight motor. Together, these complexities lead to a much richer landscape of resonant properties than in the linear model. To chart a course through this landscape, we perform two initial studies on a pure PEA system: one with viscoelasticity, representing a higher fidelity linear model of thoracic structural damping [6]; and one with quadratic damping, representing a higher fidelity model of the damping arising from wing aerodynamic drag [10]. Our purpose is both to investigate which properties of classical linear resonance propagate to these more complex cases—illustrating which aspects of our linear analysis may be more widely applicable—and to develop and demonstrate a methodology by which our analysis of resonant...
behaviour that is very close to global-resonant (examples illustrate the rich behaviour of the hybrid system under global resonance. In a pure PEA system, the hybrid system, as a function of elastic structural damping [6,10]:

4.2. Dynamics of a system with viscoelasticity

Consider a pure PEA model of a flight motor with viscoelastic structural damping [6,10]:

\[
\begin{align*}
\text{dimensional:} & \quad -mt^2 \dddot{x} + (1 + i\gamma)k_p \ddot{x} = \ddot{f}, \\
\text{canonical:} & \quad -\Omega^2 \ddot{x} + (1 + i\gamma)\omega^2_{0p} \dot{x} = \ddot{f},
\end{align*}
\]

(4.1)

where \(\gamma\) is the viscoelastic loss factor. Equation (4.1) is formulated in the frequency domain, to enable a complex-valued definition of the viscoelastic dynamic modulus, as \((1 + i\gamma)k_p\). This model represents an incremental extension of the classical PEA model: we will test the extent to which conclusions from the classical linear analysis (§3.2) extend to this representative viscoelastic case. The restriction of equation (4.1) to a pure PEA system is to remove the ambiguity over the distribution of viscoelasticity within the thorax: the relative strength of viscoelasticity in the series and parallel-elastic components, which has not been empirically studied.

From equation (4.1), a transfer function formulation of this viscoelastic model is

\[
\begin{align*}
\frac{\ddot{x}}{f} &= \frac{1}{(1 + i\gamma)\omega^2_{0p} - \Omega^2}, \\
\frac{i\ddot{x}}{f} &= \frac{i\Omega}{(1 + i\gamma)\omega^2_{0p} - \Omega^2},
\end{align*}
\]

and

\[
\begin{align*}
\frac{-\dddot{x}\Omega^2}{f} &= \frac{-\Omega^2}{(1 + i\gamma)\omega^2_{0p} - \Omega^2}.
\end{align*}
\]

(4.2)
The resonant frequencies of these transfer functions are as follows:
\[
\begin{align*}
\arg \max_n \left( \frac{i\dot{x}}{\dot{f}} \right) &= \omega_{0,P}, \\
\arg \max_n \left( \frac{i\dot{x}\Omega}{\dot{f}} \right) &= \omega_{0,P} \sqrt{1 + \gamma^2}, \\
\text{and} \quad \arg \max_n \left( \frac{i\dot{x}\Omega^2}{\dot{f}} \right) &= \omega_{0,P} \sqrt{1 + \gamma^2}.
\end{align*}
\]

Following the same process as in §3, we can also derive the global-resonant frequency of this viscoelastic system: it is simply \(\omega_{0} = \omega_{0,P}\), as per the classical PEA system (equation (3.13)). Comparing these results to the viscous-damped system (equations (2.10) and (2.12)) more broadly: a distinction between resonant frequencies still exists, though the ordering is reversed—higher kinematic derivatives (velocity, acceleration, etc.) have higher, rather than lower, resonant frequencies. In practical terms, however, the actual difference in frequency that arises solely from viscoelastic effects is likely to be low. Empirical studies of hawkmoth thoracic dynamics indicate a viscoelastic loss factor of \(\gamma = 0.1\) [6], which would lead to an acceleration frequency only 0.5% greater than \(\omega_{0,P}\). This would lead us to conclude that accurate viscoelastic modelling may not be required to accurately characterize resonant distinct in insect flight motors—instead, a more accurate aerodynamic modelling may be more important.

### 4.3. Dynamics of a system with quadratic nonlinearity

Consider a pure PEA model of an indirect flight motor with quadratic damping:

\[
\begin{align*}
\text{dimensional:} \quad m\ddot{x} + c\dot{x}\ddot{\dot{x}} + k_p \dot{x} = F(t), \\
\text{canonical:} \quad \dddot{x} + \beta \dot{x} \dddot{x} + \omega_{0,P}^2 \dot{x} = f(t), \quad \beta = \frac{c}{m}.
\end{align*}
\]

This nonlinear model could be used to as a higher fidelity model of an insect flight motor which is (i) dominated by wing aerodynamic damping; (ii) behaves as if the wings and muscles are kinematically connected, i.e. shows pure PEA; and (iii) shows linear thoracic elasticity. For our purposes, this model represents a physically relevant incremental extension of the linear PEA model: we will test the extent to which conclusions from the linear analysis (§§2–3) still hold in this nonlinear model. The restriction to a pure PEA system is for reasons of analysis complexity: given that numerical analysis processes are required, we seek to minimize the number of variables needed to parameterize the system.

To analyse the nonlinear resonant behaviour of this system, we assume that the system output response is simple-harmonic: \(x(t) = \dot{x} \cos(\Omega t)\). This alludes to our earlier assumption of simple-harmonic wing stroke kinematics in the context of global resonance. Insect wing stroke kinematics are broadly simple-harmonic, but can involve higher harmonics [5,17,33,46], which may interact with nonlinear properties of the flight motor (such as aerodynamic drag) in nontrivial ways. Normalizing this assumed response in amplitude and time, as \(x(t) = \dot{x} \cos(\Omega t) = \dot{x} \cos(\tau)\), yields the complete dimensional reduction:

\[
\tau = \Omega t, \quad \Lambda = \frac{\Omega}{\omega_{0,P}}, \quad \eta = \frac{x(t)}{\dot{x}}, \quad \nu = \frac{f(t)}{\omega_{0,P} \dot{x}} = \left\{ \begin{array}{l} \end{array} \right.
\]

where \((\cdot)\) denotes d/dt. An important property is observed in equation (4.5): the system dynamics, under this prescribed output response, are not governed by \(\beta\) and \(\dot{x}\) independently, but only by the product \(\beta \dot{x}\). This property significantly simplifies the analysis. Expressing the relationship in equation (4.5) as a functional, \(\nu(\tau) = V[q(\tau)]\), we can define nonlinear transfer ratios relating the peak output response (in non-normalized \(x, \dot{x}, \dddot{x}\)) to the peak load requirement:

\[
\begin{align*}
\max_{\tau} |\dot{x}| &= \frac{1}{\max_{\tau} |V[\cos(\tau)]|}, \\
\max_{\tau} |\dot{x}| &= \frac{\Lambda}{\max_{\tau} |V[\cos(\tau)]|}, \\
\max_{\tau} |\dot{x}| &= \frac{\Lambda^2}{\max_{\tau} |V[\cos(\tau)]|}.
\end{align*}
\]

Note that these transfer ratios capture only a segment of this nonlinear oscillator’s behaviour: its peak load requirement when outputting simple-harmonic waves. A range of other transfer ratio definitions, involving different metrics of amplitude (root-mean-square, etc.), and different input/output waveforms, are also available. The maximization in equation (4.6) can be performed numerically. Three-dimensionally reduced resonant frequencies for this nonlinear system can then be computed, as a function of the damping product parameter (\(\beta \dot{x}\)):

\[
\begin{align*}
A_{\nu}(\beta \dot{x}) &= \arg \max_{\Lambda} \left( \frac{1}{\max_{\tau} |V[\cos(\tau)]|} \right), \\
A_{\nu}(\beta \dot{x}) &= \arg \max_{\Lambda} \left( \frac{\Lambda}{\max_{\tau} |V[\cos(\tau)]|} \right), \\
A_{\nu}(\beta \dot{x}) &= \arg \max_{\Lambda} \left( \frac{\Lambda^2}{\max_{\tau} |V[\cos(\tau)]|} \right).
\end{align*}
\]

Continuing in this harmonic-output framework, we seek to compute the frequency at which this nonlinear system is global-resonant. The system power requirement can be expressed in a functional form analogous to equation (4.5):

\[
p = f \dot{x} = \omega_{0,M}^2 \Omega \nu(\tau) \eta(\tau), \quad \text{and} \quad P[q(\tau)] = \nu(\tau) |q(\tau)| \\
\Rightarrow \quad p = \omega_{0,M}^2 \Omega \cdot P[q(\tau)].
\]

Using \(P[q(\tau)]\), we can compute the power transfer ratios defined in equation (3.10) (via numerical integration), and the frequencies \(\Lambda\), at which these transfer ratios take their maxima (as a function of \(\beta \dot{x}\), via numerical optimization).
For instance, for \( \eta_{\text{abs}} \):

\[
\eta_{\text{abs}}(\beta \dot{X}, A) = \frac{\int_0^T P(\theta) d\theta}{\int_0^T P(\theta) d\theta} = \frac{\int_0^{2\pi} P[\cos(\theta)] d\tau}{\int_0^{2\pi} [P[\cos(\theta)] d\tau}
\]

and

\[
A_r(\beta) = \arg \max_A (\eta_{\text{abs}}(\beta \dot{X}, A)).
\]

(4.9)

In general, these resonant states may be true global-resonant (peak \( \eta_{\text{abs}} = 1 \)) or pseudo-global-resonant (peak \( \eta_{\text{abs}} < 1 \)).

4.4. Distinction between resonant frequencies under quadratic damping

Figure 4 illustrates these resonant frequencies over a representative range of the product parameter \( \beta \dot{X} \), with transfer functions and ratios illustrated for example insect parameter values derived from the analysis in §5.1. Overall, the behaviour of this nonlinear system is strikingly similar to the linear PEA model (figure 2). Several points may be noted:

(i) The distinctness of frequencies (figure 4a). Over the studied range, the acceleration resonant frequency \( (A_{\beta,1}) \) is always equal to the undamped natural frequency (=1). The global-resonant frequency, \( A_{\beta} \), is also always equal to the undamped natural frequency (=1), and it is always true global-resonant (peak \( \eta_{\text{abs}} = 1 \)). Numerically, these equivalences are confirmed to within machine precision. The displacement and velocity resonant frequencies, \( A_{\beta,1} \) and \( A_{\beta,2} \), differ from the undamped natural frequency and from each other. This distinctness parallels the behaviour of linear PEA systems (figure 2), except acceleration resonance, rather than velocity resonance, coincides with the undamped natural frequency. The resonant frequencies are also ordered in the same way \( (A_{\beta,2} \geq A_{\beta,1} \geq A_{\beta,3}) \).

(ii) The variation in frequencies. The velocity and displacement resonant frequencies show a strong decreasing trend with \( \beta \). The effect of decreasing resonant frequency with increasing damping (analogous to the linear PEA system) becomes more pronounced with increasing amplitude, as per the analogy of a variable linear damping coefficient that depends on velocity \( (d = \alpha \dot{X}) \). This would suggest the existence of a damping-driven coupling effect between wingbeat amplitude and resonant frequency in insects; an effect that appears in in vitro experimentation (§5.3).

These results, while specific to the case of quadratic damping, nevertheless help elucidate the wider landscape of flight motor nonlinear dynamics. First, they illustrate how certain properties of the linear model still hold in the nonlinear case. For instance, the distinctness between resonant states—displacement, velocity, etc.—is not a unique property of linear systems, but is found also in nonlinear systems. While the exact nature of the distinctness can differ, the existence of these distinct peaks appears to be a general property which we would expect to extend to a wide range of other nonlinear models. Another property which extends in this way is the flat-topped nature of the power transfer ratio (i.e. global resonance, figure 4b) peaks. In the linear PEA system (§3.2), we observe that, at high damping, the flight motor maintains efficient energy regeneration (less than 1% inefficiency) over a wide frequency range—a range much wider than equivalent windows in classical resonant transfer functions. In the quadratically damped PEA system, we observe a similar effect: at \( \beta \dot{X} = 1 \), representative of a strongly damped insect (§5.1), the less than 1% inefficiency frequency window is 17% of \( \Delta \omega_{0,p} \). The equivalent window in the displacement transfer function is 7% of \( \Delta \omega_{0,p} \). These results suggest that this phenomenon may be present more broadly in nonlinear models of insect flight motors. The second way in which these results elucidate a wider landscape is in demonstrating a methodology for analysing resonant distinctness that is robust to nonlinearity. Altering the functional \( V[\theta(\theta)] \) to include other forms of nonlinearity (e.g. further aerodynamic nonlinearity and elastic nonlinearity) allows these nonlinearities to be analysed in the same context. This methodology should also be extensible to SEA or hybrid system dynamics, with the addition of further transfer ratios (equation (4.6)) with respect to actuator displacement. The generality of this analysis method should allow more complex models of specific insect species to studied in the same framework.

5. Practical application to insect flight

5.1. Identifying damping parameters

To use the results of §§2-4 to characterize flight motor resonance in specific insect species, model parameters must be identified: in particular, the overall motor damping \( (\zeta_p, \omega_p) \) and \( \beta \) and the strength of the series-elastic effect \( (\alpha) \). A range of disparate data sources can be drawn upon for parameter estimation. We begin with a characterization of motor damping. As studied in §4, insect flight motor damping is nonlinear. To best represent the overall energetic effect of nonlinearity in our linear model, we use estimates of the quality factor \( (Q\text{-factor}) \) for insect flight. Using the \( Q \)-factor, we can translate nonlinear system information (energy loss per cycle) to linear model properties (approximate damping ratio, \( \zeta_p \)). Two approaches for empirical \( Q \)-factor estimation have been presented in the literature: estimates based on flight motor energetics [56] or empirical correlations based on the Weis-Fogh number [10]. Reported \( Q \)-factor estimates based on these two approaches show significant inconsistency: estimates, e.g. for bumblebees range from \( Q = 1.6 \) [10] to \( Q = 19 \) [56]. We note that this inconsistency is due to a factor four calculation error in [56]. As a corrected calculation, consider an energetic definition of the \( Q \)-factor of a linear oscillator [56]:

\[
Q = \frac{2\pi K}{\Delta E},
\]

(5.1)

where \( \Delta E \) is the oscillator energy loss per cycle and \( K \) is the peak potential energy (=peak kinetic energy). To compute \( Q \) using energetic parameters, two values are used [56]: \( P_{\text{aero}} \), the mean wing aerodynamic power dissipation, and \( P_{\text{acc}} \), the mean inertial power requirement over a single wingbeat quarter-cycle. To relate these semi-empirical terms to \( \Delta E \) and \( K \), respectively, note that (i) the relationship between \( \Delta E \)
and $\bar{P}_{\text{aero}}$ is simply the definition of the mean \([56]\):

$$\Delta E = TP_{\text{aero}} = \frac{2\pi}{\Omega} \bar{P}_{\text{aero}}, \quad (5.2)$$

and (ii) the relationship between $K$ and $P_{\text{acc}}$ is given by the definition of $P_{\text{acc}}$ \([56]\):

$$P_{\text{acc}} = \frac{K}{(1/4)T} = \frac{2}{\pi} \Omega K, \quad (5.3)$$

that is, $P_{\text{acc}}$ integrated over a quarter-cycle yields the peak system kinetic energy. The consistent estimate of $Q$, based on $P_{\text{acc}}$ and $P_{\text{aero}}$, is thus

$$Q = \frac{\pi \bar{P}_{\text{aero}}}{2 P_{\text{aero}}}. \quad (5.4)$$

This yields a revised estimate of $Q = 1.6$ for fruit flies \([14]\), $Q = 2.5$ for hawkmoths, and $Q = 4.7$ for bumblebees \([35]\).

These values are now consistent with those computed via Weis-Fogh number correlations \([10]\): $Q = 1.2$ for fruit flies, $Q = 1.7$ for hawkmoths and $Q = 1.6$ for bumblebees. To translate these $Q$-factors to estimates of $\zeta_p$, we assume $\Omega \approx \omega_{0,\mu}$ implying that \([57]\) $Q \approx 1/2\zeta_p$. This yields estimates of 0.31 $\leq \zeta_p \leq 0.42$ for fruit flies, 0.20 $\leq \zeta_p \leq 0.29$ for hawkmoths and 0.11 $\leq \zeta_p \leq 0.31$ for bumblebees. Via Weis-Fogh number correlation \([10,36]\), we can extend this analysis to different species, noting, e.g. an estimate of $N = 6.3$, $Q = 2.2$, $\zeta_p = 0.22$ for honeybees. This analysis resolves the discrepancy in the literature regarding insect $Q$-factor estimates. This resolution is significant not only for existing biological applications of $Q$-factor analysis (e.g. understanding insect flight scaling across species and estimating flight performance trends \([10,35]\)), but has renewed importance in the context of our analysis of resonant distinctness. The flight motor damping, estimated via the $Q$-factor, is a key driving factor behind the distinctness of resonant frequencies in our flight motor models. Estimates of insect $Q$-factors are thus of key importance to understanding this resonant distinctness in the context of real insect flight motors: for instance, in identifying which resonant frequency these flight motors operate at, why they do so, and how wingbeat frequency variation affects flight motor resonance. It is fascinating to consider that effects which have often been attributed to flight motor elastic properties, such as the discrepancy between measured thoracic resonant frequencies \([11]\), and wingbeat frequency variation behaviour \([9,22–26]\), may be just as much the effect of flight motor damping—as we discuss further in §§5.3–5.4. There is significant scope for further extension of the current analysis. For instance, we note that existing $Q$-factor estimates can be used to identify nonlinear motor model properties. Seeking to match peak damping loads from the linear model (peak $2\zeta_p\omega_{0,\mu}x$) to the quadratically damped model (peak $\beta b\zeta_p x^2$), we find that, for $\Omega \approx \omega_{0,\mu}$, $\beta \approx 2\zeta_p$, and thus $\beta b \approx 1/Q$. There is considerable leeway in this estimate: for instance, matching mean damping loads instead of peak damping loads, we estimate instead

![Figure 4. Resonant properties of a PEA system with quadratic damping. Resonant frequencies (as per equations (4.7) and (4.9)) for a PEA system with quadratic damping, as a function of the damping product parameter ($\beta b$). These frequencies pertain to the case in which the oscillator generates a simple-harmonic output, and define frequencies of minimum peak load requirement (and, for global resonance, the state of no negative work). Transfer functions and transfer ratios are illustrated for two example product parameter values ($\beta b = 0.5,1$), broadly representative of insect flight (§5.1).](image-url)
\( \beta \xi \approx 8 \zeta_p / \pi, \) and \( \beta \xi \approx 4 / \pi Q \) (i.e. \( \beta \xi \) is 27% larger). Applying both these approximate matching strategies to reported insect Q-factors, we would estimate the range \( 0.2 \leq \beta \xi \leq 1.1 \) to be broadly representative of insect flight—this range is illustrated in figure 4. These estimates could be refined by further non-linear analysis, as well as via energy loss estimates given by recent results in computational fluid dynamics [46]—both allowing a deeper understanding of the role of resonant effects within insect flight motors, and the scaling of these effects across insect species.

5.2. Identifying series-elastic parameters

The second parameter we require an estimate of is the strength of the series-elastic effect (\( \alpha \)). We can identify this parameter using measurements of the phase difference across the motor, e.g., between muscular contraction (DVM/DLM) and wingbeat motion. For instance, the sarcomere deformation peak for each muscle group can be matched against particular wingbeat motion. For instance, the sarcomere deformation peak of each muscle group can be matched against particular wingbeat motion. Using measurements of the phase difference across the motor, we can identify this parameter as a function of different resonant states (equations (2.10), (2.12) and (3.14)).

Displacement resonance: Velocity resonance:

\[
\Omega = \omega_{0,\alpha} \sqrt{1 - 2z^2} \quad \Omega = \omega_{0,\alpha},
\]

\[
\alpha^2 = 2z^2 \left(1 + \epsilon \sqrt{1 - 2z^2} \right), \quad \alpha^2 = 2z^2 \epsilon.
\]

Acceleration resonance: Global resonance:

\[
\Omega = \frac{\omega_{0,\alpha}}{\sqrt{1 - 2z^2}}, \quad \Omega = \omega_{0,\alpha},
\]

\[
\alpha^2 = \frac{2z^2 \left(-z^2 + \epsilon \sqrt{1 - 2z^2} \right)}{1 - 2z^2}, \quad \alpha^2 = \frac{2z^2 (1 + \epsilon^2) \left(\epsilon^2 \pm \sqrt{\epsilon^2 + z^2} \right)}{\epsilon^2}.
\]

These values provide bounds on \( \alpha \), assuming that the flight motor is operating at a frequency bounded by these four frequencies. In practical terms, the velocity resonance/undamped natural frequency (\( \omega_{0,\alpha} \)) estimate serves as a useful simple indicator of whether series-elastic effects are significant.

To estimate motor phase differences, a range of sources, including microCT [31], X-ray diffraction [38,39] and laser profilometry [5] studies, are available. Figure 5 shows two representative analysis processes:

(i) For bumblebees (Bombus spp.) [38]: X-ray diffraction data provide estimates of DVM and DLM sarcomere length variation under tethered flight. This variation is well-described by sinusoidal fits (figure 5a). Referring these fits against approximate wingbeat cycle tracking [38], we estimate a mean phase lag of \( \Delta \phi = -3.2° \) (\( \epsilon = 17.9 \)) averaged across both muscle groups. This implies that series-elastic effects are insignificant (\( Q = 3.2, \zeta_p = 0.16, \) and so \( \alpha = 2.4 \)). With low damping and weak series-elastic effects, resonant frequencies are clustered close together: within 6% of \( \omega_{0,\alpha} \) (equations (2.10), (2.12) and (3.14)). Nevertheless, the frequency variation available under less than 1% inefficiency is broad: a window of 12% of \( \omega_{0,\alpha} \). Hence, even in insects with lightly damped flight motors, near-perfect elastic energy absorption may be available over a significant frequency window.

(ii) For fruit flies (Drosophila mettleri) [39]: X-ray diffraction data provide estimates of DLM sarcomere length variation under tethered flight (figure 5b), which we take as representative. Although the time resolution of these data is relatively coarse, maxima can still be identified, as per [39], and phase lags estimated: a mean of \( \Delta \phi = -22.0° \) (\( \epsilon = 2.47 \)). Using damping estimates from other Drosophila species (\( Q = 1.4, \zeta_p = 0.36 [10,14] \)), we estimate \( \alpha = 1.3 \). Series-elastic effects are significant, and resonant frequencies are widely dispersed: classical force-based frequencies lie within a window of 30% of \( \omega_{0,\alpha} \), and a pseudo-global-resonant frequency exists at approximately 1.28\( \omega_{0,\alpha} \). Based on the computed efficiency profiles, the frequency variation available under less than 1% inefficiency is very broad: a window of 54% of \( \omega_{0,\alpha} \). Even if this system had no series-elastic effects (\( \zeta_p = 0.36, \alpha \to \infty \)), this window would still be 27% of \( \omega_{0,\alpha} \). This is illustrative of how, in insects with more strongly damped indirect flight motors, ensuring high motor efficiencies via elastic energy absorption may not be a practical limit on wingbeat frequency variation. Note that there are other factors, including the tuning of the passive wing hinge [58,59], which may limit the available frequency variation: but the absorption of negative work is unlikely to be one of them. We note also that strong flight motor series-elastic effects do not appear to be a necessary property of dipteran insects: in blowflies [31], microCT visualization shows phase lags of no more than a few degrees between thoracic motion and wingbeat motion, indicating that series-elastic effects are insignificant. As of yet, there appears no simple predictor as to which insect species have strong series-elastic effects, and which do not.

(iii) For hawkmoths (Agrius convolvuli) [5]: laser profilometer data provide estimates of the time and spatial distribution of the thoracic deformation, across the thorax and wing root. Fitting sinusoidal profiles to each measurement point, and then filtering points with a high goodness-of-fit (\( R^2 > 0.95 \)), we can visualize the spatial distribution of oscillatory phase across the thorax and wing root (figure 5c). This allows us to estimate the phase lag between the wings and the centre of the thorax (assumed to be a reference point for the muscles), using four sample points, as \( \Delta \phi = -22.6° \) (\( \epsilon = 2.40 \)). Note that this technique allows the spatial location of series-elastic effects to be identified: for instance, a sizeable proportion of the phase lag is generated at the wing hinge point, indicating the presence of series-elastic structures within the wing hinge. Using damping estimates from a hawkmoth of different species (M. sexta: \( Q = 2.1, \zeta_p = 0.24 [10,14] \)), we estimate \( \alpha = 1.07 \). Series-elastic effects are significant, and this contributes to a significant distinction between the global-resonant frequency, located at 1.21\( \omega_{0,\alpha} \), and the classical PEA-type resonant frequencies, which are located in a band within 7% of \( \omega_{0,\alpha} \). The frequency variation available under less than 1% inefficiency is very broad: a window of 40% of \( \omega_{0,\alpha} \). It is interesting to consider...
the relationship between these resonant state estimates and reported wingbeat frequency modulation for hawkmoths (M. sexta) in the literature. Rapid frequency modulation, involving frequency increases of up to ca 30%, is reported in hawkmoths undergoing perturbation responses [9]. A 30% frequency increase would be consistent, for instance, with a switch from the global-resonant frequency (a state of maximum efficiency) to the SEA-type resonant frequencies (response peaks w.r.t. input displacement)—potentially, an example of a switch between maximally efficient resonant states and maximum-performance resonant states.

5.3. Implications for insect thoracic dynamics

The results of our analysis in §§5.1–5.2 have implications for thoracic functional morphology, and the ways in which this morphology is characterized experimentally. First, our results indicate that in some insect species, thoracic series-elastic effects are significant, whereas in others, they are not. This raises the possibility of, and provides a discerning factor between, two dynamically distinct forms of thoracic and pleural mechanism transmission systems. This distinction could point to differences in insect operating priorities and conditions (e.g. based on insect scale); differences in evolutionary background; and physiological differences in the flight motor mechanism. Second, in the experimental analysis of thoracic resonance, it may be important to distinguish between distinct resonant frequencies within the thorax. For example, consider recent estimates of honeybee thoracic resonant frequency: an average resonant frequency of 368 Hz [11], relative to a species wingbeat frequency of 220–250 Hz [60]. The resonant frequency measured is the peak of the transfer function between actuation acceleration (i) and actuation load (f).

As per §§2–4, several factors could lead to a difference between this frequency and other thoracic resonant frequencies: linear viscous damping (ζp); series-elastic effects (α); viscoelastic damping (γ); and nonlinear damping (βi). Beginning with a linear analysis, the representative transfer function shown in [11] has a full-width at half-maximum of 34 Hz. This corresponds to a Q-factor of 12.2 [10], or ζp = 0.04: significantly lower than in-flight damping estimates (ζp ≈ 22, §5.1). At ζp = 0.04, damping-based distinctions between resonant frequency are small (equations (2.10) and (2.12)). Assuming therefore that ω0 ≈ 368 Hz, we can estimate in-flight motor resonant frequencies: based on equation (2.10), we estimate the displacement resonant frequency to be 5% below ω0, at 350 Hz. Going further, we observe that the discrepancy between damping estimates obtained via vibrational experiments (ζp ≈ 0.04), and those obtained by empirical analysis of in-flight conditions (ζp ≈ 0.22) is qualitatively well-explained by nonlinear aerodynamic damping (§4). The increase in effective linear damping can arise from the larger wingbeat amplitude that is present during flight (βi ≈ 2ζp, §5.1). Additional information, e.g. simultaneous wingbeat tracking, is needed for quantitative predictions, but the existence of this effect supports the prediction of damping-driven nonlinear coupling between wingbeat amplitude and thoracic resonant frequency. Additional information is also required for a characterization of series-elastic effects: in this section, we have assumed these effects are insignificant, in the absence of available data. If series-elastic effects are significant, then interpreting these experimental results is much more complex. In our hybrid linear model, the transfer function

Figure 5. Application of our analysis process to different insect species. (a) Bumblebees, Bombus spp., with DVM and DLM X-ray diffraction data, against wingbeat kinematic cycle [38]. (b) Fruit flies, D. mettleri, with DLM X-ray diffraction data, against wingbeat kinematic cycle [39] (14.5 nm relative spacing, 19.3 nm integrated intensity). (c) Hawkmoths, A. convolvuli, with wing and thorax laser profilometer data [5]. These datasets allow estimates of the phase lag (Δϕ) between muscular and wingbeat oscillation during tethered flight. Alongside damping estimates §5.1, this allows an estimate of the series-elastic effect (α), and the wingbeat frequency variation available while maintaining less than 1% inefficiency (§3.2). Even in the lightly damped bumblebee, this variation is significant: 12% of the natural frequency, ω0p.
between \( \ddot{u} \) \((-\Omega^2 \ddot{u})\) and \( f \) is as follows:

\[
-\frac{\Omega^2 \ddot{u}}{f} = -\Omega^2 \left( \frac{\ddot{x}}{x} \right)^{-1} \left( \frac{\ddot{z}}{z} \right).
\]

(5.6)

Even in this simple linear system, the expression for the resonant frequency of this transfer function is complicated, involving the root of a general quartic polynomial. In species in which series-elastic effects may be significant (e.g. fruit flies and hawkmoths), a reliance on actuation point input/output transfer functions may not be feasible: simultaneous wingbeat tracking may be required to accurately measure thoracic resonant frequencies. We note also that, throughout this analysis, we have assumed linear parallel- and series-elasticity. Certain elasticities in honeybees [11] and hawkmoth [6] thoraces have been shown to be weakly nonlinear (strain-hardening). We would anticipate our results to generalize these weakly nonlinear cases, but potentially not to much stronger nonlinearities—for instance, the bistable elasticities that have sometimes been considered in the context of dipteran insects [40]. There is a need for further experimental characterization, and dynamical analysis, of this topic.

6. Discussion and conclusion

In this work, we have characterized the resonant properties of linear and nonlinear models of insect indirect flight motors. The distinctness between resonant frequencies in these flight motor models provides two possible explanations for observed insect wingbeat frequency variation. First, with reference to flight control: it is possible that insects prioritize particular resonant states (e.g. peak energetic efficiency versus peak performance) under particular conditions. This would represent controlled variation in wingbeat frequency to achieve particular distinct optimal states—a feature which could relate to wingbeat frequency modulation as a mechanism of flight control [9,15,16]. Gau et al. [9] observe frequency variation windows of up to 32% of the mean in hawkmoths; Combes et al. [15], up to 17% in honeybees; Lehmann and Dickinson [16], up to 19% in fruit flies. These frequency changes are broadly consistent with differences between resonant frequencies with respect to force \((f/x)/\Omega \), etc.) and/or a global-resonant frequency. It is possible that, in insects with strong series-elastic effects (e.g. fruit flies, §5.2), the resonant frequencies with respect to displacement \((d/x)/\Omega \), etc.) could also be involved. A meta-analysis of reported wingbeat frequency variation is tabulated in Gau et al. [9]. If these variations represent switches between distinct resonant frequencies, then finely tuned resonant frequency control via pleurosternal and tergopleural muscular actuation [9,22–26] would not be required.

Second, with reference to energetic optimality: if, as is often thought [14,46–48], the purpose of thoracic elasticity is to absorb negative power requirements, then this purpose is fulfilled over frequency ranges, not only at a single frequency. These frequency ranges are sufficient to explain most currently reported wingbeat frequency variations. Again, for this purpose, finely tuned resonant frequency control via pleurosternal and tergopleural muscular actuation [9,22–26] would not be required. Broadly, our characterization leads to a new conceptual model of insect wingbeat frequency behaviour. Instead of a model in which insects are bound to a precise wingbeat frequency, determined by structural and environmental parameters and muscular tuning, we propose that insects can afford, energetically, to operate at a state in which wingbeat frequency and motor/thoracic resonant frequency do not precisely match. This robustness to frequency mismatch provides additional basis for other forms of flight robustness observed in the literature: robustness to wear [61], damage [8,62], and environmental and metabolic conditions [17].

In this work, we have described the distinctness of resonant frequencies within a model of the insect indirect flight motor: a multiplicity of mutually exclusive resonant states, each of which could represent different optimal operating states. The distinctness of these resonant states alters our understanding of indirect flight motors, sheds new light on counterintuitive insect behaviour and leads to methods for identifying motor structural parameters from observable data. We introduce several forms of resonance that have not previously been considered in a flight motor context, including global resonance, and illustrate the dependency of these resonant states on flight motor structural parameters, including damping, and the distribution of structural elasticity. Via the analysis of global resonance, we are able to characterize the effect of wingbeat frequency variation on the level of negative work absorption within the motor and show how near-perfect negative work absorption is maintained over significant frequency windows. These new aspects of flight motor model behaviour potentially explain wingbeat frequency modulation behaviour observed in many insect species and contribute to our increasing understanding of the remarkable robustness of insect flight.

Data accessibility. The paper used data extracted from previously published works. We use only the data (numeric values). We did not take figures from other papers.

Authors’ contributions. A.P.: conceptualization, data curation, formal analysis, investigation, methodology, software, validation, visualization, writing—original draft and writing—review and editing; T.B.: funding acquisition, project administration, resources, supervision, validation and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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Endnote

\[ \{l\} = 1 \text{ for true statement } l, \text{ and } \{l\} = 0 \text{ for false statement } l. \]

References

1. Fartisekov SE, Lapina NA, Petrov PN, Polilov AA. 2020 Extraordinary flight performance of the smallest beetles. Proc. Natl Acad. Sci. USA 117, 24643–24645. (doi:10.1073/pnas.2012404117)
2. Dudley R. 2002 The biomechanics of insect flight. Princeton, NJ: Princeton University Press.
16. Lehmann FO, Dickinson MH. 1997 The changes in power requirements and muscle efficiency during elevated force production in the fruit fly Drosophila melanogaster. *J. Exp. Biol.* **200**, 1133–1142. (doi:10.1242/jeb.200.7.1133)

17. Vance JT, ALTSHULER DL, Dickson WB, Dickinson MH, Roberts SP. 2014 Hovering flight in the honeybee *Apis mellifera*: kinematic mechanisms for varying aerodynamic forces. *Physiol. Biochem. Zool.* **87**, 870–881. (doi:10.1086/678955)

18. Somers J et al. 2022 Hitting the right note at the right time: circadian control of audibility in *Anopheles* mosquito mating swarms is mediated by flight tones. *Sci. Adv.* **8**, eabj4844. (doi:10.1126/sciadv.abj4844)

19. Cator LJ, Arthur BJ, Harrington LC, Hoy RR. 2009 Harmonic convergence in the love songs of the dengue vector mosquito. *Science* **323**, 1077–1079. (doi:10.1126/science.1166541)

20. Spangler HG, Buchmann SL. 1991 Effects of temperature on wingbeat frequency in the solitary bee *Centris caesaripinaea* (Anthophoridae: Hymenoptera). *J. Kansas Entomol. Soc.* **64**, 107–109.

21. Unwin DM, Corbet SA. 1984 Wingbeat frequency, temperature and body size in bees and flies. *Physiol. Entomol.* **9**, 115–121. (doi:10.1111/j.1365-3032.1984.tb00687.x)

22. Lehmann FO, Dickinson MH. 1998 The control of wing kinematics and flight forces in fruit flies (Drosophila spp.). *J. Exp. Biol.* **201**, 385–401. (doi:10.1242/jeb.1.3.385)

23. Harne RL, Wang KW. 2015 Dipteran wing motor-inspired flying flutter versatility and effectiveness enhancement. *J. R. Soc. Interface** **12**, 20141367. (doi:10.1098/rsif.2014.1367)

24. Boettiger EG, Furshpan E. 1952 The mechanics of flight movements in Diptera. *Biol. Bull.* **102**, 200–211. (doi:10.2307/1538368)

25. Nachtigall W, Roth W. 1983 Correlations between stationary measurable parameters of wing movement and aerodynamic force production in the blowfly (Calliphora vicina R. D.). *J. Comp. Physiol. A* **150**, 251–260. (doi:10.1007/BF00606375)

26. Miyan JA, Ewing AW. 1985 How Diptera move their wings: a re-examination of the wing base articulation and muscle systems concerned with wings. *Biol. Bull.* **176**, 302–308. (doi:10.1242/jeb.176.1.302)

27. Harne RL. 2015 Dipteran wing motor-inspired flying flutter versatility and effectiveness enhancement. *J. R. Soc. Interface** **12**, 20141367. (doi:10.1098/rsif.2014.1367)

28. Zhang H, Ma T. 2015 Roles of the excitation in nonlinear energy harvesting with tunable damping transmission mechanisms for bio-inspired flapping-wing vehicles. *Bioinspir. Biomim.* **10**, 046002. (doi:10.1088/1748-3190/10/5/046002)

29. Miyan JA, Ewing AW. 1985 How Diptera move their wings: a re-examination of the wing base articulation and muscle systems concerned with wings. *Biol. Bull.* **176**, 302–308. (doi:10.1242/jeb.176.1.302)

30. Pons A, Beatus T. 2022 Elastic-bound conditions for visually directed banked turns. *J. Exp. Biol.* **225**, 056007. (doi:10.1242/jeb.202507)

31. Walker SM, Schwyn DA, Mokso R, Wicklein M, Lapina NA, Lehmann FO, Onishi R, Liu H, Polillo AA. 2022 Novel flight style and light wings boost flight performance of tiny beetles. *Nature* **602**, 96–100. (doi:10.1038/s41586-021-04303-7)

32. Verstraten T, Beckerle P, Furnemont R, Mathijssen G, Vanderborght B, Lefebvre D. 2016 Series and parallel elastic actuation: impact of natural dynamics on power and energy consumption. *Mech. Mach. Theory* **102**, 232–246. (doi:10.1016/j.mechmachtheory.2016.04.004)

33. Dickinson MH, Lehmann FO, Sane SP. 1999 Wing rotation and the aerodynamic basis of insect flight. *Science* **284**, 154. (doi:10.1126/science.284.5422.154)

34. Ellington CP. 1984 The aerodynamics of hovering insect flight. II. Morphological parameters. *Phil. Trans. R. Soc. Lond. B** **305**, 17–40. (doi:10.1098/rstb.1984.0050)

35. Ellington CP. 1999 The novel aerodynamics of insect flight: applications to micro-air vehicles. *J. Exp. Biol.* **202**, 3439. (doi:10.1242/jeb.202.23.3439)

36. Weis-Fogh T. 1973 Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift production. *J. Exp. Biol.* **59**, 169–230. (doi:10.1242/jeb.59.1.169)

37. Deora T, Singh AK, Sane SP. 2015 Biomechanical basis of wing and halterede coordination in flies. *Natl Acad. Sci. USA* **112**, 1481–1486. (doi:10.1073/pnas.1412791112)

38. Iwamoto H, Yagi N. 2013 The molecular trigger for high-speed wing beats in a bee. *Science* **341**, 1243–1246. (doi:10.1126/science.1237266)

39. Dickinson M, Farman G, Frye M, Bekyarova T, Gore D, Maughan D, Irving T. 2005 Molecular dynamics of cyastically contracting insect flight muscle in vivo. *Nature* **433**, 330–334. (doi:10.1037/0033-2923)

40. Ennos AR. 1987 A comparative study of the flight mechanism of Diptera. *J. Exp. Biol.* **127**, 355–372. (doi:10.1242/jeb.127.1.355)

41. Thomesen L. 2021 Vibrations and stability: advanced theory, analysis, and tools. Berlin, Germany: Springer.

42. Wang Q, Zhao C, Swank DM. 2011 Calcium and stretch activation modulate power generation in drosophila flight muscle. *Biophys. J.* **101**, 2207–2213. (doi:10.1016/j.bpj.2011.09.034)

43. Muirjes FT, Etting E, Melis JM, Dickinson MH. 2014 Flies evade looming targets by executing rapid visually directed banked turns. *Science* **344**, 172–177. (doi:10.1126/science.1248955)

44. Whitehead SE, Beatus T, Canale L, Cohen I. 2015 Pitch perfect: how fruit flies control their body pitch angle. *J. Exp. Biol.* **218**, 3508–3519. (doi:10.1242/jeb.122622)

45. Beatus T, Guckenheimer J, Cohen I. 2015 Controlling roll perturbations in fruit flies. *J. R. Soc. Interface** **12**, 20150077. (doi:10.1098/rsif.2015.0077)

46. Zhu H, Sun M. 2020 Kinematics measurement and power requirements of successful attacks at various flight speeds. *Energies** **13**, 4271. (doi:10.3390/en13114271)

47. Reid HE, Schwab RK, Maxer M, Peteson RD, Johnson EL, Jankauskas M. 2019 Wing flexibility reduces the energetic requirements of insect flight. *Bioinspir. Biomim.* **14**, 056007. (doi:10.1088/1748-3190/ab2bdc)

48. Fatsenkov SE, Kolomenskiy D, Petrov PN, Engels T, Lapina NA, Lehmann FO, Onishi R, Liu H, Polillo AA. 2022 Novel flight style and light wings boost flight performance of tiny beetles. *Nature* **602**, 96–100. (doi:10.1038/s41586-021-04303-7)
49. Findeisen D. 2000 System dynamics and mechanical vibrations. Berlin, Germany: Springer.
50. Zahn M. 1979 Electromagnetic field theory. New York, NY: Wiley.
51. Graham RL, Knuth DE, Patashnik O. 1994 Concrete mathematics: a foundation for computer science. Reading, MA: Addison-Wesley.
52. Berret B, Chiovetto E, Nori F, Pozzo T. 2011 Evidence for composite cost functions in arm movement planning: an inverse optimal control approach. PLoS Comput. Biol. 7, e1002183. (doi:10.1371/journal.pcbi.1002183)
53. Srinivasan M, Ruina A. 2006 Computer optimization of a minimal biped model discovers walking and running. Nature 439, 72–75. (doi:10.1038/nature04113)
54. Abbott BC, Bigland R, Ritchie JM. 1952 The physiological cost of negative work. J. Physiol. 117, 380–390. (doi:10.1113/jphysiol.1952.sp004755)
55. Rajasekar S, Sanjuan MAF. 2016 Nonlinear resonances. Cham, Switzerland: Springer.
56. Ellington CP. 1984 The aerodynamics of insect flight. IV. Aerodynamic mechanisms. Phil. Trans. R. Soc. Lond. B 305, 79–113. (doi:10.1098/rstb.1984.0052)
57. Bishop RED, Johnson DC. 2011 The mechanics of vibration. Cambridge, UK: Cambridge University Press.
58. Beatus T, Cohen I. 2015 Wing-pitch modulation in maneuvering fruit flies is explained by an interplay between aerodynamics and a torsional spring. Phys. Rev. E 92, 022712. (doi:10.1103/PhysRevE.92.022712)
59. Ishihara D, Horie T. 2016 Passive mechanism of pitch recoil in flapping insect wings. Bioinspir. Biomim. 12, 016008. (doi:10.1088/1748-3190/12/1/016008)
60. Altshuler DL, Dickson WB, Vance JT, Roberts SP, Dickinson MH. 2005 Short-amplitude high-frequency wing strokes determine the aerodynamics of honeybee flight. Proc. Natl Acad. Sci. USA 102, 18 213–18 218. (doi:10.1073/pnas.0500590102)
61. Vance JT, Roberts SP. 2014 The effects of artificial wing wear on the flight capacity of the honey bee Apis mellifera. J. Insect. Physiol. 65, 27–36. (doi:10.1016/j.jinsphys.2014.04.003)
62. Muijres FT, Iwasaki NA, Elzinga MJ, Melis JM, Dickinson MH. 2017 Flies compensate for unilateral wing damage through modular adjustments of wing and body kinematics. Interface Focus 7, 20160103. (doi:10.1098/rsfs.2016.0103)