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The hawkmoth wingbeat is not at resonance

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Flying insects have elastic materials within their exoskeletons that could reduce the energetic cost of flight if their wingbeat frequency is matched to a mechanical resonance frequency. Flapping at resonance may be essential across flying insects because of the power demands of small-scale flapping flight. However, building up large-amplitude resonant wingbeats over many wingstrokes may be detrimental for control if the total mechanical energy in the spring-wing system exceeds the per-cycle work capacity of the flight musculature. While the mechanics of the insect flight apparatus can behave as a resonant system, the question of whether insects flap their wings at their resonant frequency remains unanswered. Using previous measurements of body stiffness in the hawkmoth, *Manduca sexta*, we develop a mechanical model of spring-wing resonance with aerodynamic damping and characterize the hawkmoth's resonant frequency. We find that the hawkmoth's wingbeat frequency is approximately 80% above resonance and remains so when accounting for uncertainty in model parameters. In this regime, hawkmoths may still benefit from elastic energy exchange while enabling control of aerodynamic forces via frequency modulation. We conclude that, while insects use resonant mechanics, tuning wingbeats to a simple resonance peak is not a necessary feature for all centimetre-scale flapping flyers.

1. Introduction

Flapping-wing flight is one of the most energetically expensive modes of locomotion in nature [1,2]. However, insects that beat their wings indirectly through deformations of their thorax could reduce the energetic cost of flight by flapping at a frequency matched to their bodies' resonance frequency [3]. In this arrangement, wing kinetic energy during a wingstroke is stored in spring-like structures and returned at stroke reversal to reaccelerate the wing. In seminal studies from the 1960s, Weis-Fogh identified the elastic materials necessary for resonance in the thorax of many species [4]. However, only recently have bulk measurements of thoracic stiffness under physiological conditions been made [5], enabling the characterization of the resonant frequency of insect spring-wing systems.

Evidence suggests that insects use elastic energy exchange, but insect wingbeat frequencies may not precisely match the resonant frequency of the flight system. Estimates of flight power requirements [1,6] combined with measurements of elastic structures in the flight system [5] indicate that elastic energy exchange can offset the high inertial costs of flapping-wing flight. However, the presence of elastic energy exchange does not mean that an insect's wingbeat frequency will equal the resonant frequency of its body. Static measurements of bulk elasticity suggest that dragonfly wingbeat frequencies (29 Hz) exceed their resonance frequency (20 Hz) [7]. However, unlike many insects such as bees,

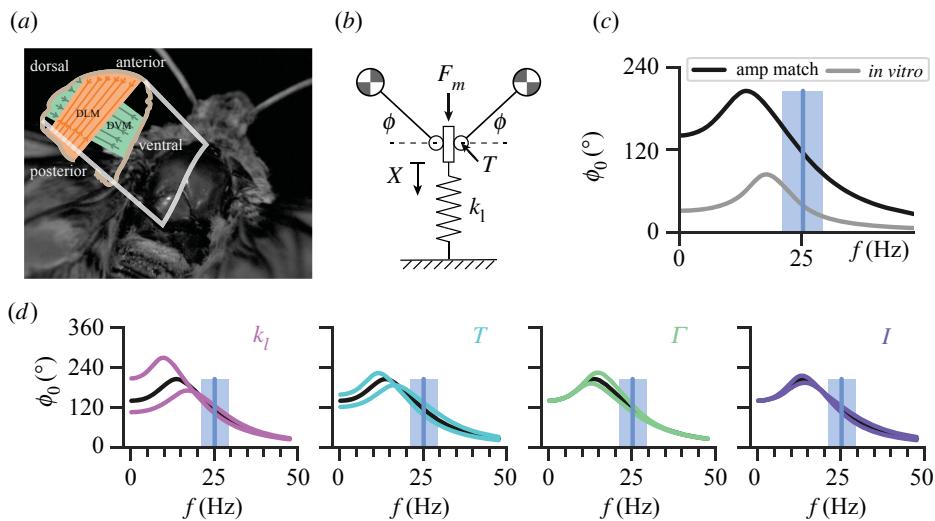


Figure 1. Hawkmoths' wingbeats are not at resonance. (a) Dorsal view of *Manduca sexta* highlighting the thorax. (Inset) cross-sectional view of second thoracic segment along the white line. The downstroke (DLM) and upstroke (DVM) muscles attach to the exoskeleton to indirectly generate wing movement. (b) Mechanical representation of insect flight system. Muscle force F_m displaces a linear spring with stiffness k_1 , acting through a transmission T to drive wing motion. For (c–d), blue lines mark typical hawkmoth wingbeat frequency (25.2 Hz) and blue regions denote frequency modulation range (8.25 Hz) during perturbation recovery [9]. (c) *Manduca sexta* resonance curve for amplitude matched (black) and *in vitro* (grey) force amplitude. (d) Sensitivity analysis where coloured lines denote the resonance curve generated with the corresponding 0.5th and 99.5th percentile parameter values.

flies, beetles and moths, dragonfly flight muscles directly actuate the wing hinge and do not use indirect thoracic deformations to move the wing. This indirect actuation introduces a large parallel-elastic element that dominates stiffness in the system [5]. Measurements of an intact honeybee thorax found a resonance peak far above wingbeat frequencies in response to external forcing, although unphysiological boundary conditions likely artificially elevated this resonance frequency by unrealistically constraining and therefore stiffening the thorax [8].

The relationship between wingbeat and resonance frequencies has specific energetic and control implications. The benefit that an harmonic oscillator gains from operating at resonance scales with the Q -factor, the 'steepness' of the resonant peak. A system with high Q has higher efficiency at resonance, but the benefits fall sharply as flapping frequency diverges from resonance. Additionally, operating at resonance can lead to performance constraints, especially a limited capacity for frequency modulation [9]. In flying insects, the Weis-Fogh number, $N = (\max F_{\text{inertia}})/(\max F_{\text{aero}})$ is analogous to the Q -factor [10] and has been measured to be between 1 and 10 for most insects [10,11]. These N values indicate a relatively shallow but significant resonant peak, at least compared to some engineered resonant systems ($Q \gg 10$) [12]. Nonetheless $N > 1$ indicates resonant behaviour and the potential loss of efficiency if insects flap at frequencies off of resonance.

The idea of resonance tuning in insect flight first arose in asynchronous insects, but—regardless of energetics—the stretch-activation of asynchronous muscles may prevent a deviation from resonance [13,14]. In these systems, reducing wing inertia increases wingbeat frequency as would be predicted for a resonant system. Wingbeat frequency may be more constrained. By contrast, the synchronous *Manduca sexta* uses large-amplitude frequency modulation (32% range) at the wingstroke timescale [9]. Without a clear picture of how muscular, inertial and elastic components integrate to establish a resonant system, it remains an open question how

insects resolve the competing demands for energy-efficient yet manoeuvrable flight. To address this question, we developed a model of insect spring-wing mechanics and test whether *M. sexta* operates at resonance.

2. Methods

To determine the hawkmoth resonance frequency, we modelled the flight system (figure 1a,b) as a parallel linear spring (thorax, k_1) coupled to a rotational wing inertia (I) and velocity-squared, aerodynamic damping (Γ) through a linear transmission (T) to capture the indirect actuation of the insect flight system,

$$\frac{F_m}{T} = I\ddot{\phi}(t) + \Gamma|\dot{\phi}(t)|\dot{\phi}(t) + \frac{k_1}{T^2}\phi(t), \quad (2.1)$$

where F_m is muscle force applied to the thoracic exoskeleton and $\phi(t)$ is the time-varying wingbeat sweep angle. For more detailed justification of this equation, see electronic supplementary material, information S1. Parameters were calculated based on existing literature as described in the electronic supplementary material (table 1 and figure 1b [14–16]). Stiffness was derived from material testing of the intact thorax deformed along its natural line of action at amplitudes matching *in vivo* conditions [5]. Because active muscle can also store and return energy, we estimated the contribution of the antagonistic pair of flight muscles as twice the active stiffness of the main downstroke [17] muscles (DLM) found by fitting a stiffness to workloop data [18]. Modelling elastic elements in the wing-thorax-flight muscle system as a lumped parameter parallel element has precedence [5,19]. Similar simplified aerodynamics models have been validated in a dynamically scaled robophysical flapper and robotic systems like the Robobee [10,16,20]. Additionally, data suggest that the hawkmoth wing–thorax transmission is linear [7,21].

Given that spring-wing flight systems are nonlinear (equation (2.1)), we used numerical simulations to assess emergent peak-to-peak wingbeat amplitude, which we term ϕ_0 . We varied sinusoidal forcing frequency over a range encompassing typical wingbeat frequencies. We used an initial F_m of 0.5 N,

Table 1. Model parameter values and description.

parameter	value	description
I	$5.69 \pm 0.34 \times 10^{-8} \text{ kg m}^2$	inertia
Γ	$3.69 \pm 0.33 \times 10^{-8} \text{ kg m}^2$	aerodynamic damping parameter
k_l	$4078 \pm 510 \text{ N m}^{-1}$	thorax linear stiffness, including active muscle
T	$2230 \pm 110 \text{ m}^{-1}$	transmission ratio
F_m	0.5 N	zero-to-peak muscle force amplitude
F_m^*	2.25 N	zero-to-peak muscle force amplitude, adjusted

matching measurements of *M. sexta* under physiological conditions [18].

3. Results

With this model, we found the resonance frequency to be 17.73 Hz, well below both average wing frequencies of approximately 25 Hz and the physiological range of 21.1–29.3 Hz during perturbation recovery [9]. However, we measured an output peak-to-peak wing amplitude of only 40.30° at 25 Hz (figure 1c). The low wingbeat amplitude likely reflects the unexpectedly low power observed in isolated DLM experiments. Tu & Daniel [18] found that the DLMs produced a body mass-specific power of 2.82 W kg⁻¹, which is at least an order of magnitude lower than kinematics-based estimates of flight power requirements [6]. Other muscles such as the upstroke dorsoventral flight muscles (DVMs) likely also contribute, but it remains likely that isolated muscle experiments underestimate true *in vivo* power.

To address this underestimation of force and power in our original model parameters, we increased force amplitude until ϕ_0 matched physiological peak-to-peak wingbeat amplitudes of 117° at 25 Hz [6]. We then used this amplitude of $F_m^* = 2.25 \text{ N}$ (a 4.5 x increase) for all frequencies. With this new model, we identified a resonance frequency of 13.61 Hz (figure 1c). Regardless of which model is used, hawkmoths operate significantly above their resonance frequency. From our simulations, we calculated a Q of 7.04, which agrees with previous estimates from kinematic data of 10 for hawkmoths [1]. To further validate our model, we estimated that thorax elastic energy exchange offsets between 37 and 58% of *Manduca*'s inertial power requirements based on the model parameters, and this energy return agrees with previous empirical estimates [5]. Our model therefore captures known mechanical resonant properties of the moth flight apparatus to the extent that prior data are available.

The conclusion that *M. sexta* operates above resonance was robust to uncertainty in each model parameter. To show this, we propagated error due to individual-to-individual variation in biological measurements to the four lumped parameters (T , I , Γ and k_l) in the equations of motion (equation 2.1; table 1). We then generated gain curves for

the 0.5th and 99.5th percentile values for each parameter (figure 1d). Changes in stiffness had the largest impact on the resonance peak (9.70–17.03 Hz), followed by transmission ratio (11.80–16.52 Hz), damping (12.71–14.72 Hz) and inertia (13.3–14.01 Hz). In all cases, typical wingbeat frequencies remained well above resonance. Since we likely overestimate the contribution of active muscle stiffness, reducing it would only further decrease the resonant frequency below wingbeat frequency. Even when stiffness and transmission ratio are varied simultaneously to maximally increase the model's resonant frequency, the resonant frequency only reaches 20.24 Hz.

Finally, we simulated the necessary change in parameter values that would enable resonance tuning. Thoracic stiffness would need to increase by 130% to 9438 N m⁻¹, requiring an increase in peak elastic force of 2.46 N and a total force of 4.34 N. Stiffer active muscle could contribute some of this stiffness but is insufficient because 2 N alone exceeds prior measurements of peak DLM force production [18]. Series-elastic elements in the wing could add stiffness or introduce coupled resonance modes. However, we observe the *Manduca* thorax to be highly backdrivable, such that articulating the wings causes large concomitant deformations of the thorax. If series elasticity were significant, wing articulation would substantially deform the series-elastic elements, diminishing thorax deformation. Furthermore, the phase lag between scutum and wing displacement has been measured to be approximately 1 ms in *Manduca* and is a key manifestation of series-elastic behaviour [22]. This is an order of magnitude shorter than the quarter-cycle phase lag between muscle force and wing displacement caused by parallel-elastic resonance, which in in *Manduca* is 10 ms. We therefore conclude that series-elastic effects negligibly affect stiffness in *Manduca*.

T would have to decrease to 1370 rad m⁻¹ to produce flight at resonance. Given known muscle strains, this transmission ratio would require peak-to-peak stroke amplitudes of only 72°, which is far below wingbeat amplitudes observed during flight [6]. No values of Γ nor I increased the resonance frequency to 25 Hz. Typically, decreasing damping increases resonance frequency, but at $\Gamma=0$ resonance was only 19.13 Hz. As I decreased initially, resonance frequency increased, but a further reduction in I led to an overdamped system without a resonance peak because the Weis-Fogh number fell below 1 [10]. Other forms of damping, especially frequency-independent damping known to exist in insect exoskeleton [5,23], could reduce resonance frequencies, but this structural damping is an order of magnitude (2.4 WKg⁻¹) less than aerodynamic damping (11–39 WKg⁻¹) [5].

Our model has only a few parameters, but they must be measured accurately in the insect of interest. While measurements of thoracic stiffness and transmission are not yet available for other synchronous or asynchronous species, the same general model used here could extend to these cases. In addition to potential limitations explored in the sensitivity analysis, we use a phenomenological muscle model and simplified bulk thoracic stiffness. While these seem justified for *M. sexta*, it is possible that nonlinear resonance modes, specialized anatomical structures like the dipteran wing hinge 'clutch' [2] and history-dependent muscle dynamics [24] could complicate resonance, especially in specific species. However, the model's simplicity makes it extremely versatile and allows it to serve as a template for added complexity as better insect data become available.

4. Discussion

We conclude that hawkmoths do not flap their wings at their mechanical resonance frequency. Instead, steady state wingbeat frequencies are 80% higher than the resonance frequency (figure 1d). The lack of resonance tuning does not prevent hawkmoths from benefiting from elastic energy exchange. The passive thorax returns the maximally beneficial amount of elastic energy over a single wingstroke [5,6], despite operating off the resonance peak. Furthermore, while operating at a resonance frequency may allow an insect to maximize its output wingstroke amplitude for a given muscle force amplitude, other performance metrics may be optimized at different frequencies. For example, aerodynamic efficiency is maximized at the undamped natural frequency, not the resonant frequency. We also find that the hawkmoth wingbeat frequency exceeds its undamped natural frequency of 19 Hz by over 30%. It remains unclear what measure of efficiency is most susceptible to selective pressures in insects.

In addition to energetics, off-resonance wingbeat frequencies explain how hawkmoths rapidly modulate wingbeat frequency by $\pm 16\%$ from wingstroke to wingstroke during perturbation recovery [9]. If hawkmoths had been flying at resonance, then a rapid shift in wingbeat frequency would require dissipation of substantial built-up elastic energy. These results suggest that off-resonance wingbeats in hawkmoths enable frequency control while retaining the benefits of elastic energy exchange.

Beyond hawkmoths, the capacity for off-resonance wingbeats may be a distinguishing factor between synchronous and asynchronous insects. Asynchronous insects generate wingbeats via a delayed stretch response in their flight muscles. This stretch-activation causes the contraction frequency of asynchronous muscle to scale linearly with the resonance frequency of an attached external load [12]. After accounting for boundary conditions, direct measurements of the honeybee thorax suggest that wingbeat frequencies match resonance [8]. These results suggest that it may be impossible for asynchronous wingbeats to rapidly deviate

from resonance. Instead, asynchronous insects use small accessory muscles to stiffen the thorax, adjusting the resonance frequency of the wing-thorax system to shift wingbeat frequencies [13].

To overcome the high energetic costs of flapping-wing flight, insect-scale robots are often tuned to resonance and give up control via frequency modulation [20]. However, recent evidence showed that shifting wingbeat frequencies away from resonance can increase yaw torque production in the Robobee [25]. Our results suggest that off-resonance actuation may unlock potential for engineered systems to achieve the manoeuvrability of synchronous insects.

Generally, our work suggests that resonance is not a necessary feature of centimetre-scale flapping-wing flight. The few parameters that inform our model allow for flight both at and away from resonance; the parameters that are realized in insects may depend on control–efficiency tradeoffs or fundamental physiological differences between species.

Data accessibility. The data are provided in the electronic supplementary material [26].

Authors' contributions. J.G.: conceptualization, data curation, formal analysis, investigation, methodology, software, validation, visualization, writing—original draft and writing—review and editing; E.S.W.: data curation, formal analysis, methodology, validation, visualization, writing—original draft and writing—review and editing; J.L.: conceptualization, formal analysis, methodology, writing—original draft and writing—review and editing; N.G.: conceptualization, funding acquisition, project administration, supervision, writing—original draft and writing—review and editing; S.S.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—original draft 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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