



SYMPOSIUM

The Weis-Fogh Number Describes Resonant Performance Tradeoffs in Flapping Insects

Ethan S. Wold^{*.1}, Ellen Liu[†], James Lynch[‡], Nick Gravish[‡] and Simon Sponberg^{ID*.†}

^{*}School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA 30332, USA; [†]School of Physics, Georgia Institute of Technology, Atlanta, GA 30332, USA; [‡]Mechanical and Aerospace Engineering, University of California San Diego, San Diego, CA 92161, USA

From the symposium “Evolution, Physiology, and Biomechanics of Insect Flight” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 2–6, 2024 in Seattle.

¹E-mail: ewold3@gatech.edu

Synopsis Dimensionless numbers have long been used in comparative biomechanics to quantify competing scaling relationships and connect morphology to animal performance. While common in aerodynamics, few relate the biomechanics of the organism to the forces produced on the environment during flight. We discuss the Weis-Fogh number, N , as a dimensionless number specific to flapping flight, which describes the resonant properties of an insect and resulting tradeoffs between energetics and control. Originally defined by Torkel Weis-Fogh in his seminal 1973 paper, N measures the ratio of peak inertial to aerodynamic torque generated by an insect over a wingbeat. In this perspectives piece, we define N for comparative biologists and describe its interpretations as a ratio of torques and as the width of an insect’s resonance curve. We then discuss the range of N realized by insects and explain the fundamental tradeoffs between an insect’s aerodynamic efficiency, stability, and responsiveness that arise as a consequence of variation in N , both across and within species. N is therefore an especially useful quantity for comparative approaches to the role of mechanics and aerodynamics in insect flight.

Introduction

Flapping insects are capable of remarkable aerial feats of speed and maneuverability, having captured the fascination of scientists for centuries. Insect-scale flapping locomotion is particularly energetically expensive (Ellington 1999), suggesting that insects may utilize elastic energy storage in their thorax to reduce large flight power requirements. Most insects fly using indirect actuation, in which the flight musculature attaches to the surface of a thin exoskeletal shell as opposed to directly to the wing hinge itself (Gau et al. 2019). Deformations of this elastic shell move the wings indirectly via the wing hinge, which converts the linear displacement of the muscles to angular wing movement (Fig. 1B). This configuration gives insects the ingredients of a spring-mass-damper: inertial wings, damping from the air, and elasticity from the thorax. Thus, insects produce mechanical oscillations, with a reso-

nant frequency that theoretically represents the most efficient frequency at which to flap (Sotavalta 1952; Greenewalt 1960; Weis-Fogh 1973; Gau et al. 2022). Many studies have examined the aerodynamics of flapping flight, utilizing nondimensional numbers that capture the relationship between wing kinematics and fluid dynamic properties (Ellington 1984c; Dickinson et al. 1999; Sane and Dickinson 2001; Sane 2003; Lentink and Dickinson 2009b; Chin and Lentink 2016). But since the original descriptions of indirect flight actuation and scaling, much less focus has been given to the interplay of structural mechanics of the elastic thorax and aerodynamic forces on the wings.

Perhaps no single individual contributed more to our understanding of insect flight than Torkel Weis-Fogh, whose seminal works include the discovery of resilin in the insect cuticle (Weis-Fogh 1960), clap-and-fling mechanisms of lift production (Weis-Fogh 1973),

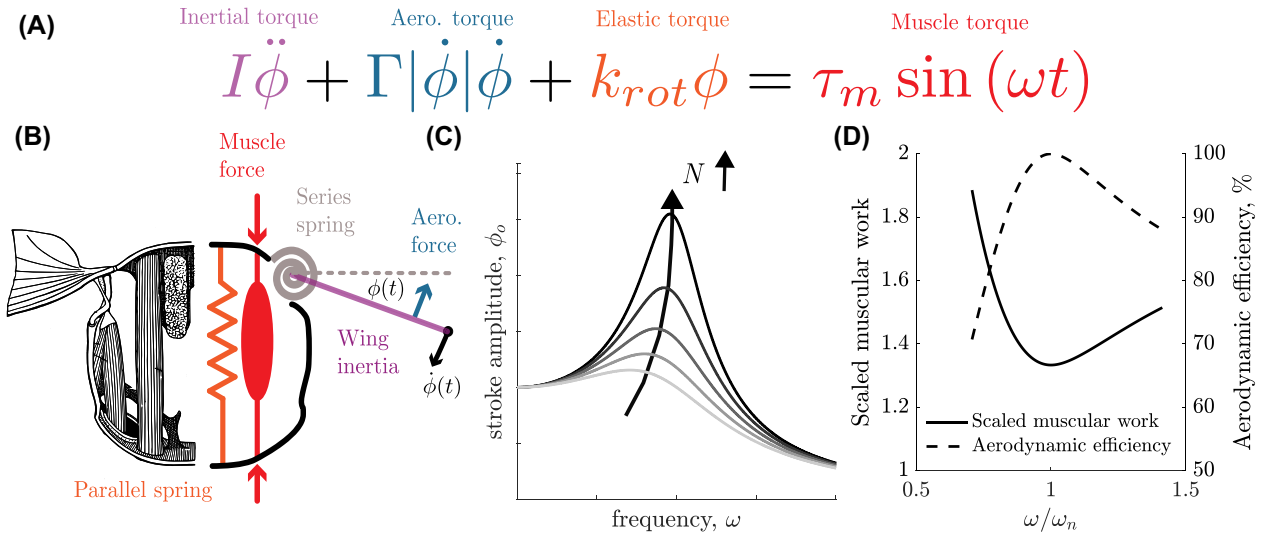


Fig. 1 (A) Forced spring-mass-damper equation for a flapping insect with velocity-squared aerodynamic damping where I is the wing inertia, Γ is the aerodynamic damping parameter, k_{rot} is the rotational thorax stiffness, τ_m is the muscle torque amplitude, and ω is the wingbeat frequency. (B) Cross-section of the insect flight apparatus and a discretized schematic showing the action of internal and external forces on the thorax-wing system (modified from Lynch et al. 2021). Series elasticity is much less than parallel (thoracic) stiffness for large insects such as moths and bees (Ando and Kanzaki 2016; Gau et al. 2022; Pons and Beatus 2022a). While this can modify resonance properties to some degree, we focus on the essential elements for creating resonant flapping flight. (C) Resonance curve of an insect, with darker curves corresponding to higher values of N . (D) Per-cycle positive muscular work and aerodynamic efficiency as a function of normalized frequency (driving frequency divided by resonant frequency) with a constant $N = 2$ for the equation in (A). At resonance ($\omega/\omega_n = 1$), positive muscular work is minimized and aerodynamic efficiency is maximized.

and application of steady-state aerodynamic theory to hovering animals (Weis-Fogh 1972). In his influential 1973 paper, Weis-Fogh introduced a non-dimensional number, N , describing the ratio of peak inertial to peak aerodynamic torques generated over a wingstroke to show that aerodynamically efficient hovering flight requires elastic energy storage in the thorax (Weis-Fogh 1973). This paper, along with the earlier work of Greenewalt (1960) and Sotavalta (1952), gave rise to the conceptual model of insects as elastic oscillators (Fig. 1A), taking advantage of resonance to reduce the large power requirements of flapping flight. We have previously named N the Weis-Fogh number, as an homage to Weis-Fogh's contributions to the field of insect flight (Lynch et al. 2021, 2024; Wold et al. 2024).

In recent years, a resurgence of interest in the resonant mechanics of flapping flight has resulted in comparative study of resonance across insect species. Comparative measurement of thorax stiffness (Gau et al. 2019; Jankauski 2020; Casey et al. 2023; Pons et al. 2023) and damping has enabled direct characterization of resonance, and the degree to which insects benefit from elastic energy savings. In particular, evidence from Lepidoptera has suggested that not all insects may flap at resonance (Gau et al. 2022). Operating at an off-resonance frequency may convey control benefits for in-

sects that modulate wingbeat frequency transiently to maneuver in the air (Gau et al. 2021). Such a tradeoff between efficiency and frequency modulation is a fundamental consequence of energy flow through a resonant system because, at resonance, the energy input each cycle (from muscle in an insect) is small compared to the total mechanical energy in the system (Box 2).

The growing interest in the resonance of insect flight systems has indicated a need for a simple metric that enables comparison of resonance across species, connecting morphology and kinematics to complex notions of stability, efficiency, and responsiveness (Box T1). N uniquely accomplishes this by relating an insect's body mechanics and flapping aerodynamics, capturing interactions between wing shape, movement, and the surrounding air. This contrasts with common dimensionless numbers such as the Reynolds, Strouhal, and Rossby numbers in insect flight that focus primarily on fluid properties and a characteristic length or frequency (Taylor et al. 2003; Chin and Lentink 2016). Originally motivated by Weis-Fogh as a matter of mathematical convenience, N has deep implications for flight dynamics and control, and highlights important parallels between oscillator physics and insect physiology. In this perspectives piece, we discuss the physical meaning of N and document its variation across insect species. We

then demonstrate how N provides a window into tradeoffs incurred by insects by virtue of being resonators. Low N insects benefit from increased aerodynamic efficiency and responsiveness at the expense of stability in unsteady environments. The performance tradeoffs associated with N cannot only explain its relatively small range across insects (typically $1 < N < 10$), but also how variation in N within this range may reflect significant difference in performance and adaptation over evolutionary time to enable different behavioral, ecological, and life history diversity.

Box T1: Terminology

Here we define three key terms as they are used in this paper to refer to aspects of resonant insect flight performance.

Aerodynamic efficiency: ratio of aerodynamic work per cycle used to support an insect's body weight in relation to total work done by the muscle per cycle to support all costs of locomotion (Weis-Fogh 1973; Lynch et al. 2021; Wold et al. 2024).

Responsiveness: The ability of an insect to change its kinematics within some time (response time) due to internal forces applied by the flight muscles (Dudley 2002; Wold et al. 2023; Lynch et al. 2024).

Stability: The ability of an insect to maintain its steady-state wingbeat trajectory in the face of external perturbations (Williams and Biewener 2015; Lynch et al. 2024).

Physical meaning and measurement of N

It is first useful to define N and how it conceptually links biomechanical properties (spring-driven and wing inertial forces) and aerodynamics. N has two related physical interpretations that enable translation to aspects of insect performance. Each provides different insights for the comparative biomechanics and performance of species that use indirect wing actuation.

N as a ratio of torques

N is defined as the ratio of peak inertial to peak aerodynamic torque over a wingbeat. Conceptually, this is the ratio between the effort it takes for an animal to accelerate the mass of the wing vs the effort to circulate the air around its wing. Because power is the product of torque and angular velocity, N also describes the balance of the two principal power costs for an insect: wing inertia and aerodynamics (Box 2). A larger N indicates a larger relative inertial power cost, while a small N indicates a larger relative aerodynamic power cost. Inertial

costs are generally thought of as “wasteful” in that they do not contribute to weight support or thrust, so high N insects would be increasingly inefficient without offsetting inertial costs with elastic energy storage (Dickinson and Lighton 1995). Consequently, larger N insects also have a larger capacity to benefit from elastic energy storage than lower N insects. In this way, N measures the maximum potential benefit of thorax elasticity without requiring direct stiffness measurements. Potential selective pressures favoring large or small N are multifactorial and will be discussed later, but these power relationships highlight the basic energetic implications of N for an insect.

Weis-Fogh originally used N to argue that thorax elasticity is necessary for insects to realize high aerodynamic efficiency. Most flying insects actuate their wings indirectly by deforming an elastic exoskeleton with their main power muscles (Gau et al. 2019) (Box 2). In the absence of meaningful thorax elasticity, muscles must produce sufficient torque to balance torques due to wing inertia and aerodynamic damping. Weis-Fogh normalized these torques by the peak aerodynamic torque and plotted them as a function of non-dimensional wing angle (wing angle divided by peak wing angle) (Weis-Fogh 1973) (Fig. 2A). N emerges from this construction as the maximum normalized inertial torque, which occurs at stroke reversal. Integrating the torques with respect to wing angle, one can compute an insect's aerodynamic efficiency: the fraction of total *positive* aerodynamic work over a wingstroke that is devoted to the “useful” task of body weight support, expressed as $\eta = \int_+ \hat{\tau}_{\text{aero}} d\hat{\phi} / \int_+ (\hat{\tau}_{\text{aero}} + \hat{\tau}_{\text{inertial}}) d\hat{\phi}$. Total positive mechanical work is defined as the sum of useful aerodynamic work and the “wasteful” inertial work done to accelerate and decelerate the wing mass (Box 2). The distinction of positive-only work is important and reflects the fact that the metabolic cost of negative work production by muscle is assumed to be over an order of magnitude less than the metabolic cost of positive work production (Asmussen 1953; Weis-Fogh 1972). Doing so reveals that an insect's aerodynamic efficiency decreases monotonically with N , so that insects with larger N need to require substantially more muscular work to maintain hover (Weis-Fogh 1973) (Fig. 2B). Weis-Fogh used this relationship as strong evidence for elastic energy exchange in the thorax of insects with moderate to high N , since without it, such insects would be unsustainably inefficient.

N as resonance curve sharpness

A second interpretation of N relates to an insect's resonance curve (Box 2, Fig. 1C). The wingbeat stroke amplitude vs frequency curve has a characteristic reso-

Box 2: Indirect actuation and resonance in flapping flight

Insects have been modeled using a spring-mass-damper equation with nonlinear aerodynamic damping in place of the usual linear viscous damping (Fig. 1A). Aerodynamic damping for insects is generally modeled as a force with magnitude proportional to the square of wing velocity, which is the case for Reynolds number flow $\gg 1$ (Re range for insects here is $O(10^3) - (10^4)$) (Willmott and Ellington 1997; Dudley 2002). The presence of the absolute value in the damping term ensures that the direction of the damping force vector always opposes wing motion. Due to the orientation of an insect's body with respect to the wingstroke plane, damping on the wing does play an important role in lift and thrust generation. As such, damping in models of aerodynamic resonance should not be thought of as wasteful dissipation, but as potentially useful energy exchange.

Like all other spring-mass-damper systems, flapping insects experience the phenomenon of resonance, in which certain frequencies are energetically favorable over other frequencies. This frequency preference is captured by a resonance curve, which plots the oscillation amplitude of some performance variable (in Fig. 1C, stroke angle ϕ), against the frequency of oscillation. The resonance frequency (ω_n) is the frequency at which the amplitude is maximized. While we use the term “resonance frequency” generally in this paper, there are different resonant frequencies that maximize different performance variables (i.e., stroke angle, stroke angular velocity, for example see Pons and Beatus 2022a; Wold et al. 2024 for more information). However, in many groups of insects, these different resonance frequencies are very close to one another (Pons and Beatus 2022a; Wold et al. 2024), and the description of resonance below is a reasonable approximation.

Conceptually, resonance captures the per-cycle transformation between inertial and elastic energy. The spring-wing model of an insect receives input from a sinusoidal muscle torque, which must balance the sum of a torques due to aerodynamic damping, wing inertia torque, and thorax elasticity. The resonant frequency is that at which inertial and elastic torques instantaneously balance one another, so that muscle must only produce sufficient torque to produce aerodynamics. In this sense, the system is operating at an energetic optimum, since muscular energy must only be supplied to offset irrecoverable losses from fluid dissipation. This can be seen in Fig. 1D, where the input energy from muscle is at a minimum at the resonant frequency. As a consequence, it is energetically challenging to modulate flapping frequency by changing the frequency of the driving force (ω). In insects well-modeled by Fig. 1A flapping at resonance, frequency modulation will take multiple cycles and a temporary reduction of oscillation amplitude, since the input energy per cycle is not large enough to overcome the combined energies of inertia, damping, and elasticity (Gau et al. 2021, 2022). The larger the gap between the wingbeat and resonance frequency, the larger the input energy per cycle will be relative to the total mechanical energy, and thus frequency modulation will be less and less onerous.

While spring-mass-damper equations are written in terms of forces or torques acting on a mass or wing, flight performance of insects is often discussed in terms of work and power. Each term in Fig. 1A corresponds to a per-wingstroke mechanical work, when integrated with respect to wing angle. The aerodynamic work is the work required to generate circulation of air around the wing, thus producing lift and supporting body weight. The inertial work is the work required to accelerate and decelerate the wing in a vacuum, and thus does not contribute to body weight support. For this reason, inertial work is often thought of as wasteful (Weis-Fogh 1972, 1973; Lynch et al. 2021). Depending on whether the insect is flapping at resonance, elastic storage may offset some or all of this wasteful inertial work. Accordingly, Weis-Fogh defined the aerodynamic efficiency of an insect as the ratio of aerodynamic work that is used to support body weight in relation to total work done by the flight muscles (Weis-Fogh 1973). This efficiency is maximal at resonance and decreases when inertial and elastic work do not balance one another (both above and below resonance) (Fig. 1D).

nant peak, and its sharpness, the steepness of the falloff in amplitude around the resonant frequency, is dictated by N (Fig. 1C). Larger N insects have sharper resonance curves, thus having a narrower range of frequencies over which they can benefit from larger resonant efficiency. By contrast, insects with smaller N (Fig. 1C, gray lines) have a range of frequencies over which wingbeat amplitude does not change drastically with frequency, but also have a lesser capacity for gen-

erating high-amplitude wingbeats with the same input muscle force. The resonance curve interpretation of N is analogous to the commonly used quality factor (Q) in engineering used to describe resonance curve width (Weaver Jr et al. 1991); however, N and Q are strictly speaking not equivalent. Q is a system-level property that does not change unless parameters such as mass, stiffness, or damping coefficient change (Weaver Jr et al. 1991). Due to the nonlinearity of aerodynamic

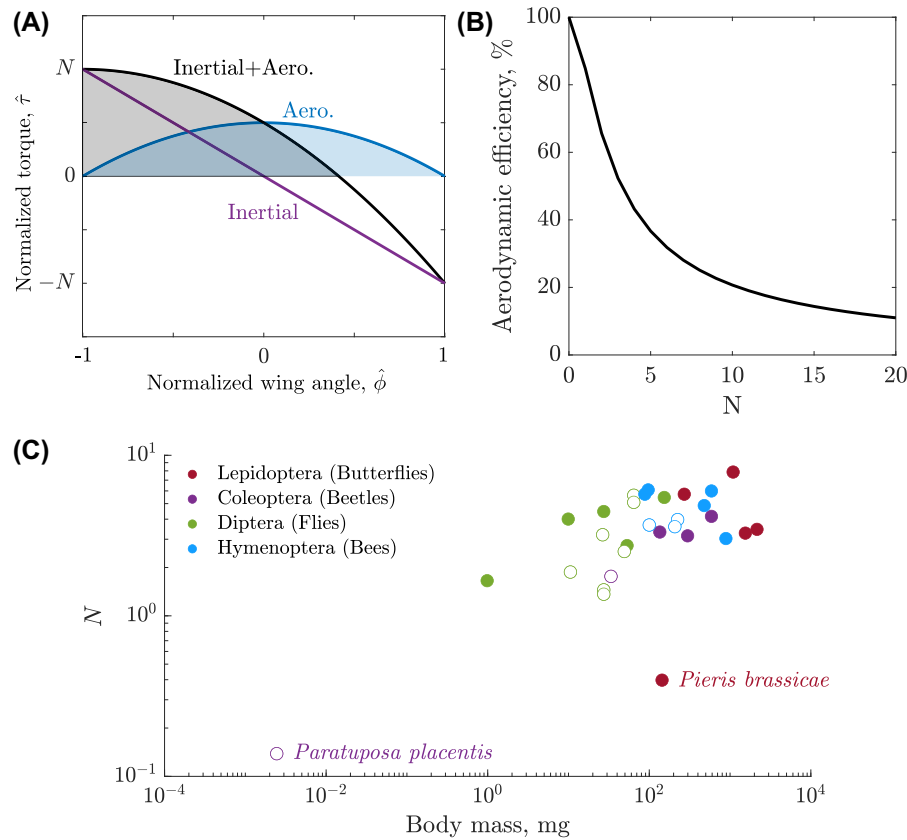


Fig. 2 (A) Normalized torques as a function of nondimensional wing angle for an insect with no thorax elasticity (inspired by Weis-Fogh 1973). Shaded areas correspond to positive aerodynamic work (blue) and positive summed aerodynamic and inertial work (gray), the ratio of which is aerodynamic efficiency. (B) Aerodynamic efficiency falls off monotonically with N for an insect with no thorax elasticity. (C) N as a function of body mass for insect species from four orders (modified from Lynch et al. 2021). Species names are listed for the two insects with $N < 1$. Data are taken from Weis-Fogh (1973), Ellington (1984a), and Farisenkov et al. (2022). Open circles are computed with power measurements (i.e., Equation (1)), while closed circles are computed using torque measurements (i.e., Equation (2)).

damping torques, N also varies depending on wingbeat amplitude.

Measuring N

N can be computed directly if one has a good estimate for inertial and aerodynamic forces generated by an insect over a wingstroke. Inertial torque about the wing hinge can be expressed as $\tau_{\text{inertial}} = I\ddot{\phi}(t)$, where I is the inertia of the wings and the added mass of air around the wings and $\phi(t)$ is the time-varying stroke angle (Weis-Fogh 1973; Lynch et al. 2021; Gau et al. 2022) (Fig. 1A). To maintain analytical tractability, Weis-Fogh employed the simplest possible model of aerodynamics, in which the magnitude of the aerodynamic damping force is proportional to the square of the wing tip velocity: $\tau_{\text{aero}} = \Gamma \dot{\phi}(t)|\dot{\phi}(t)$, (Fig. 1A). Here, Γ is a constant that depends on wing shape and fluid parameters, representing an average drag coefficient over a stroke (Weis-Fogh 1973; Whitney and Wood 2012). Applying the fi-

nal assumption that $\phi(t)$ is perfectly sinusoidal with amplitude ϕ_o and frequency ω , N can be expressed as the following:

$$N = \frac{\max(\tau_{\text{inertial}})}{\max(\tau_{\text{aero}})} = \frac{I\phi_o\omega^2}{\Gamma\phi_o^2\omega^2} = \frac{I}{\Gamma\phi_o}. \quad (1)$$

This simple expression can be computed across species with knowledge of detailed wing shape and aerodynamic properties. However, for many species, an accurate estimate of the average wing drag coefficient or location of the center of pressure may not be available, which is required to compute Γ . Often, these quantities are taken from other insects and assumed to generalize, estimated roughly from geometry, or from dynamically scaled-up robo-physical models (Weis-Fogh 1973; Jafferis et al. 2016; Lynch et al. 2021). A similar and mathematically equivalent formula for N can be derived by considering the ratio of cycle-averaged inertial and aerodynamic power, which are more common outputs of blade-element or computation fluid dynamics

models of flapping insects (Lynch et al. 2024; Wold et al. 2024).

$$N = \frac{4 \bar{P}_{\text{inertial}}}{3 \bar{P}_{\text{aero}}}. \quad (2)$$

The simple model that underlies the definition of N captures the effects of the most important kinematic variables for flight power (i.e., frequency and amplitude) in a way that preserves analytical tractability and comparative measurement across taxa. However, it is important to note that the assumptions of a purely sinusoidal wingstroke and a constant drag coefficient are significant at the level of an individual insect's aerodynamics. Many insects generate significantly non-sinusoidal wingstrokes (Willmott and Ellington 1997; Farisenkov et al. 2022; Wold et al. 2023). Furthermore, changes in other kinematic variables (i.e., angle-of-attack) modify the damping coefficient Γ throughout a wing stroke (Han et al. 2015), and other unmodeled aerodynamic forces such as rotational and unsteady forces certainly act on a flapping wing (Sane 2003; Chin and Lentink 2016). Non-sinusoidal wingstrokes may manifest in complex, nonlinear resonance which cannot be captured by a single peak and may still be advantageous to insects (Pons et al. 2023). This does not undermine the utility of N as a tool to evaluate differences in resonant mechanics between organisms or groups of organisms subject to the same assumptions. While there is more to aerodynamics than what is captured by velocity-squared damping with a constant coefficient, it is a standard representation of the principal forces acting on the wing (Willmott and Ellington 1997) and allows for analysis of broad trends in resonance across taxa through N , similar to how the Rossby number has been used in flight biomechanics (Lentink and Dickinson 2009a, 2009b; Chin and Lentink 2016).

Regardless of the exact method used to compute N , we suggest that special attention be paid to key assumptions involved. Perfectly sinusoidal wingstrokes are assumed at some level in every method outlined above. Computing N from power measurements (Equation (2)) as opposed to torques may be easier for many insects, since inertial and aerodynamic power can often be taken from published blade-element models or kinematics-based estimates of flight power (Dickinson and Lighton 1995; Willmott and Ellington 1997; Aiello et al. 2021a). However, the simple formula in Equation (1) along with the definition of Γ (Whitney and Wood 2012; Lynch et al. 2021; Gau et al. 2022) mostly depends on wing morphological and kinematic variables. If one assumes all other parameters are constant, perhaps with ground-truthing in a subset of species, computing N from Equation (1) may allow for easier broad comparison across taxa than Equation (2), which may require

3D kinematics or a new model for each additional insect of interest.

Natural variation and scaling of N

Using the equations above and combining the observations of Weis-Fogh with other independent estimates of N from the literature, we were able to provide an initial comparison across insects. Unlike engineered systems whose Q factor can vary by many orders of magnitude (Poot and Van Der Zant 2012; Lynch et al. 2021, 2024), we see that N falls between 1 and 10 across a wide range of flapping animals (Fig. 2C). Given the parallels between N and Q , it seems unlikely that many insects should have a $N < 0.5$, which would imply an overdamped system that struggles to generate energetically efficient wingbeats (overdamped systems are defined by $Q < 0.5$). Fittingly, 0.5 seems to be an approximate lower bound for N in insects. Of the species for which data are available, only a single butterfly species and a tiny bristle-winged beetle appear to have $N < 1$. In the most extreme case of the tiny beetle, other aerodynamics mechanisms are likely at play given the low Reynolds number regime in which these insects fly (Miller and Peskin 2004, 2009; Farisenkov et al. 2022). Thus, insects with $N < 1$ (or potentially insects with $N > 10$) may require specialized adaptation in kinematics or wing morphology to maintain efficient flight. In addition to the cases in Fig. 2C, other miniature insects such as mosquitos may be promising subjects of future study, as recent estimates of inertial power suggest they may have $N \ll 1$ (Liu et al. 2024). The performance-related pressures that may drive variation in N within this restricted range will be discussed in the following sections.

Since N has only been measured across a relatively small subsample of insects (Fig. 2C), few studies have been conducted on its evolutionary implications. N is a composite trait that depends on wing and kinematic properties. Unraveling the tempo and mode of evolution of N and its constituents may be particularly informative for insect flight evolution, but overly broad comparisons may prove limited due to the number of factors that could drive variation in N . However, zooming in on strategically chosen model clades (Abzhanov et al. 2008; Aiello et al. 2021a, 2021b) or species for which much is known about wing morphology, kinematics, and performance, offers a promising avenue to link N to larger scale patterns in life history and ecology.

Given the restricted variation in N across insects that vary drastically in both body mass and wingbeat frequency, is there an explanation grounded in first-principles that predicts Weis-Fogh numbers that lie within an order of magnitude of one another? Steady

fluid forces (lift and drag) experienced by a wing moving through air are both proportional to the projected area of the wing and the cube of wing length. Inertial forces are proportional to wing mass and the square of wing length. Using the standard assumptions that area and mass are proportional to the square and cube of length, respectively, both inertial and aerodynamic forces should scale roughly with the fifth power of wing length. Wingbeat amplitude does not typically scale with wing length and is physically limited at 180° . It follows that the ratio of these forces should be close to one, with small deviations from isometry resulting in values of N above or below one (Fig. 2C). This scaling argument bears resemblance to reasoning for why animals operate within a restricted range of Strouhal and Rossby numbers (Taylor et al. 2003; Lentink and Dickinson 2009a, 2009b; Chin and Lentink 2016), but uniquely ties together the interactions between aerodynamic forces and wing inertia.

Aerodynamic efficiency favors low N

Despite the scaling arguments for N remaining close to 1, it is certainly possible that larger deviations could occur and even small changes in N could have large performance consequences. The close connection between N and aerodynamic efficiency may provide a mechanistic basis for this bounding and suggest a tradeoff in the variation of observed N . Weis-Fogh showed that in the absence of thorax elasticity, aerodynamic efficiency falls off with N , but that ideal (resonant) thorax elasticity can recover these energy losses and enable 100% efficient flight (Weis-Fogh 1973) (Fig. 2B). However, a recent extension of the Weis-Fogh analysis that includes the effects of internal losses within the thorax itself demonstrates that even a perfectly resonant insect suffers from decreasing aerodynamic efficiency as N increases (Lynch et al. 2021).

The thorax of flapping insects dissipates energy as it deforms; however, it does this in a frequency-independent manner (Gau et al. 2019; Wold et al. 2023). This is a separate form of damping from aerodynamics and viscous dissipation that does not directly influence N but has important implications. Frequency-independent (structural) damping associated with bulk deformations of dry materials has now been found in the exoskeleton of different insects (Dudek and Full 2006; Gau et al. 2019; Wold et al. 2023), and contrasts with the usual viscous damping model that is applied to biomaterials that dissipate more energy with faster deformations. While viscous damping depends on velocity and hence frequency during oscillatory movement and the magnitude of the aerodynamic dissipation depends on velocity-squared (and hence frequency

squared), structural damping is constant across frequencies. Structural losses are parameterized by the structural damping factor, γ , which can be incorporated into Weis-Fogh's aerodynamic efficiency equation as another term in the denominator. Doing so shows that the presence of any dissipation in the thorax results in an efficiency that falls off sharply with N (Lynch et al. 2021) (Fig. 3A). Thus, even an insect operating at perfect resonance will favor a lower N to maximize aerodynamic efficiency for even a small unavoidable degree of structural damping. Realistic values of γ for moths indicate that an insect flapping at resonance with $N = 4$ could suffer as much as a 50% aerodynamic efficiency loss, compared to the same insect with no internal damping (Fig. 3A). Thus, the interactions between N and other properties such as resonant frequency and internal damping result in an efficiency space that favors a low N .

Weis-Fogh's original efficiency argument compared the case of no thorax elasticity to the case of ideal, resonant thorax elasticity. But what about intermediate cases, where thorax elasticity offsets some, but not all inertial power costs, like in the hawkmoth *Manduca sexta* (Gau et al. 2022)? Recently, we generalized Weis-Fogh's efficiency argument to explicitly incorporate imperfect thorax elasticity, illustrating how N interacts with a system with resonant mechanics (Wold et al. 2024) (Fig. 3B). Doing so requires defining a two-dimensional efficiency space where N and the squared ratio of resonant and wingbeat frequencies ($\hat{K} = \omega_n^2/\omega^2$) dictate the aerodynamic efficiency of an insect. \hat{K} measures the ratio of an insect's resonant and wingbeat frequencies, where $\hat{K} = 1$ is the case where the insect flaps at resonance and all inertial power costs are offset by elastic energy storage (Box 2). In this extended formulation, the degree to which an animal's efficiency decreases with N depends on how close it is to its resonant peak. In the case where $\hat{K} \approx 0$, the problem reduces to the original Weis-Fogh plot (Fig. 2B). However, at perfect resonance $\hat{K} = 1$, high efficiency is achieved regardless of N . Thus, the interactions between N and \hat{K} result in a rich efficiency space, which may constrain insects' flight behavior depending on their combination of resonant properties. For instance, insects with a large N may require operation closer to resonance (\hat{K} close to 1) in order to fly with high efficiency or must abdicate significant efficiency for frequency modulation capacity off of resonance (Fig. 3B). This updated framework illustrates the interplay of N and other resonant properties of an insect, and can now be applied comparatively to insects believed to operate off of their resonant peak.

In the superfamily of bombycoid moths, we recently demonstrated that sister families hawkmoths (Sphingi-

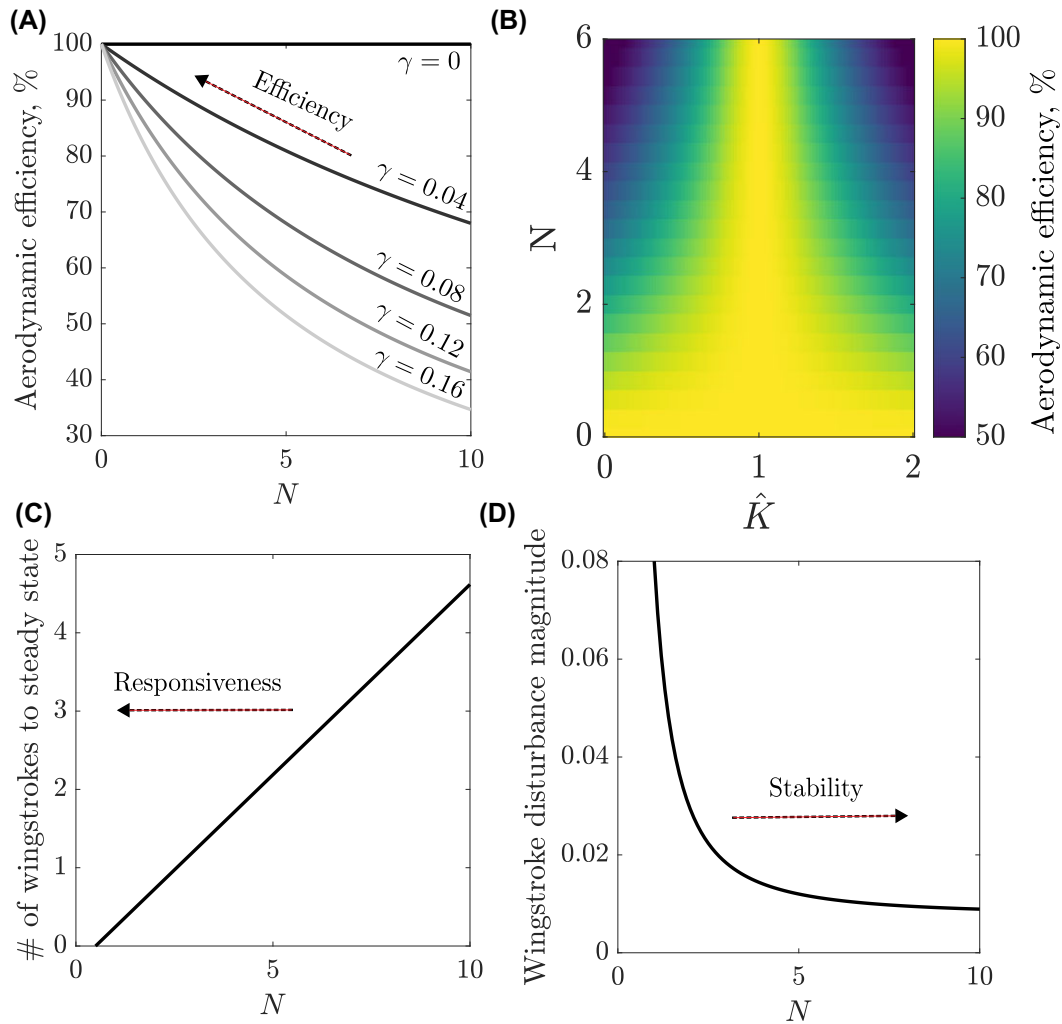


Fig. 3 (A) For an insect flapping at resonance, aerodynamic efficiency can only be 100% with no internal damping ($\gamma = 0$) (Lynch et al. 2021). For realistic, nonzero internal damping ($\gamma > 0$) efficiency decreases monotonically with N . (B) Two-dimensional efficiency space for insects flapping on or off of resonance (Wold et al. 2024). At resonance ($\hat{K} = 1$) efficiency is 100% regardless of N . However, off of resonance ($\hat{K} \neq 1$) efficiency decreases with increasing N . (C) Simulations reveal that the number of wingstrokes required to reach full amplitude steady-state oscillations increases linearly with N (Lynch et al. 2024). (D) Constant flow perturbation experiments on a robophysical flapper reveal that wingbeat trajectories are increasingly distorted at lower N (Lynch et al. 2024).

dae) and silkmoths (Saturniidae) diverge in N , and this divergence results in hawkmoths having poorer aerodynamic efficiency when compared to silkmoths (Wold et al. 2024). This makes sense when considering that silkmoths do not have functional mouthparts and do not feed as adults, and therefore fly under an extremely limited energy budget (Janzen 1984; Aiello et al. 2021a, Jacobs and Bastian 2016). Hawkmoths are nectarivorous and hover-feed from flowers, potentially requiring an ability to modulate wingbeat frequency transiently in the air (Roth et al. 2016; Gau et al. 2021). Taken together, differences in N between these two groups appear to match clade-specific performance and life history traits, causing energy-limited silkmoths to flap more efficiently and hawkmoths to balance a tradeoff

between efficiency and frequency modulation. While this is a single study, we hope that it inspires further comparative work in linking resonant properties like N to performance across diverse taxa.

Low N favors responsiveness at the cost of stability

Variation in N may also have performance implications related to tradeoffs in responsiveness and stability (Box T1). Agile flight requires responsiveness such that when the insect attempts to modulate its wing kinematics by modulating muscle force, the system is sensitive to the change and rapidly adjusts its dynamics to perform the maneuver. This property is essential to perform evasive behaviors to evade predators and avoid

obstacles in complex environments. Insects also must ensure that perturbations such as a gust of wind, do not catastrophically affect lift production and or produce extreme distortions to their wingbeat trajectories (Hedrick et al. 2009; Ortega-Jimenez et al. 2013; Matthews and Sponberg 2018).

Responsiveness

N has a direct implication for a critical parameter of responsiveness: The timescale over which the wing is able to respond to a control input from the flight muscles. Simulations of flapping wings with varying N demonstrate that low N systems can modulate their wing kinematics more quickly than high N systems (Lynch et al. 2024). It is easier to modulate the kinematics of a wing with relatively less inertia. The number of wingbeats required to achieve steady state flapping from rest increases linearly with N , such that high N systems will take many more wingbeats to start, stop, or modulate kinematics to a new steady-state (Fig. 3C). While this suggests that larger N insects face a responsiveness deficit (Fig. 3C), they may be able to overcome this by modulating N transiently via subtle actions of steering muscles. Steering muscles attach directly to the wing hinge and their effects on stroke kinematics may not be as easily overcome by large inertial forces as the indirect flight power muscles (Dickinson and Tu 1997; Deora et al. 2017).

Stability

Large relative inertial forces lead to large changes in the angular momentum of the wing during a wingstroke, making any perturbative force on the wing less significant. External flows, such as those experienced when flying in crosswinds or collisions, may have a more significant effect on the wing kinematics of a low N insect, causing them to deviate from the steady-state wing trajectory and making it difficult to maintain stable hover or steady flight. Recent experiments from a dynamically scaled, robophysical flapping wing with elasticity have demonstrated empirically this relationship between perturbation magnitude and N (Lynch et al. 2024) (Fig. 3D). At lowest N , kinematics deviate substantially from a perfect sinusoid. The kinematics smooth out as N increases, but maintain a lower amplitude than would be the case without external flow (Fig. 3D). Thus, while low N insects may be more aerodynamically efficient, even relatively simple flow environments may present them with a control problem. Due to tradeoffs between aerodynamic efficiency, stability, and responsiveness between high and low N , variation in N even within an order of magnitude may hold significant performance implications for an in-

sect. These tradeoffs also highlight the importance of robophysical models for testing the performance consequences of different parameters when considering both resonant mechanics and aerodynamics. We hypothesize that insects may have tuned N over evolutionary time to match different environmental conditions or energetic demands, or behaviors.

Modulation of N

Thus far, we have discussed the value of N for specific species. But organisms may be able to modulate their N via different behaviors or through selection over evolutionary time. As can be seen from Equation 1, simply changing steady-state wingbeat amplitude is sufficient to change N , allowing an insect to transiently modify its resonance curve. While quantitative studies on changing N are lacking, realistic angle-of-attack and wing pitch trajectories likely modulate N by making the aerodynamic damping coefficient time-varying (Dickinson et al. 1999; Jafferis et al. 2016). In these cases, N from Equation 1 does not capture the nuances of aerodynamic force and power production. N may be able to be inferred by simulating a model with more complicated aerodynamics or empirically measuring the resonance curve of dynamically scaled robotic wings. A large degree of series elasticity in the wing hinge can also dramatically widen an insect's resonance curve, decreasing the effective N (Pons and Beatus 2022b, 2022a). While the wing hinge of large insects like moths is quite stiff, at the scale of *Drosophila* and below, it appears to be more compliant, thus increasing series-elastic effects on the resonance curve (Gau et al. 2022; Pons et al. 2023). In addition, small insects like dipterans may be able to modulate series elasticity of their wing hinge via precise movements of steering muscles, thus dynamically altering N during flight (Deora et al. 2017; Melis et al. 2023).

Thus far, we have discussed resonant efficiency and frequency modulation in the context of *synchronous* insects, which set their wingbeat frequency with the frequency of the neural drive to their flight muscles. However, many clades of insects such as Diptera, Coleoptera, and Hymenoptera are *asynchronous*, generating 5–20 wingbeats with a single neural signal (Gau et al. 2023). Doing so renders their wingbeat frequency emergent from interactions between their muscle dynamics and body mechanics. This has led to the prediction that they flap at their resonant frequency, although this remains largely untested except through indirect observations (Greenewalt 1960; Jankauski 2020; Casey et al. 2023). Asynchronous insects still have resonance curves; however, interpreting their N values may require additional nuance. For example, elas-

ticity in tiny insects like *Drosophila* is dominated by the active stiffness of their flight muscle as opposed to the exoskeleton, resulting in nonlinearities that enable more complex resonant phenomena than cannot be captured in the simplest spring-wing models (Pons et al. 2023).

Asynchronous insects are likely capable of some frequency modulation during flight, and to a larger degree during other behaviors (Altshuler et al. 2005; Peters et al. 2017; Combes et al. 2020). For instance, many bee species perform multiple different modes of buzzing for communication, thermogenesis, flight, and pollination (Hrncir et al. 2008; Pritchard and Vallejo-Marín 2020). Switching between these buzzing modes is important because they serve different functions. “Buzz pollination” is critical for dislodging pollen granules from flower anthers (Jankauski et al. 2022; Vallejo-Marín 2022). Many of the non-flight buzzing modes are accomplished without full deployment of the wings, drastically altering inertial and damping forces. Thus, asynchronous frequency modulation likely occurs through the modulation of resonant properties of the wing or thorax as opposed to neural driving frequency. Doing so may result in a changing N to match performance demands associated with different behaviors or a relatively constant N across buzzing modes to maintain favorable energetics.

Conclusions and future avenues

We have shown that N is relatively easy to measure and can convey important performance information for flapping flight, including aerodynamic efficiency, responsiveness, and stability. The framework provided by N can help us analyze these performance characteristic tradeoffs to help us further understand how insects of diverse flight strategies are able to fly successfully in complex environments. The restricted range $1 < N < 10$ for most insects reflects limitations on both low and high N . The existence of irrecoverable internal damping in the thorax and a propensity of some insects to flap off of their resonant peak favors low N . Low N systems also benefit from faster response times to control inputs from musculature but suffer from greater instability in perturbative environments. Thus, low N insects achieve efficiency and responsiveness at the expense of stability. It may also not be that insects favor a particular N but rather a range of N values they can achieve by modulating their wing stroke kinematics or the series elasticity of their wing hinge (via movements of steering muscles). Variation in N even within a single order of magnitude has critical performance implications and consequently may be an important target for selection over evolutionary time.

Exceptions to the $1 < N < 10$ range may be indicative of specialized adaptations for resonant flight, and may be promising systems for further exploration. For example, there are already outliers in the range of N being from 1 to 10 such as *Paratuposa placentis* and *Pieris brassicae* whose N is low due to their specialized wing structure. *Paratuposa placentis* has a bristled wing that decreases the wing inertia leading to low N (Farisenkov et al. 2020, 2022) while some butterflies such as *Pieris brassicae* have large wings leading to large aerodynamic damping causing $N < 1$ (Weis-Fogh 1973; Ellington 1984b, 1984c). These two examples suggest that $N < 1$ insects must adapt wing morphology, kinematics, or both to sustain efficient flight without the help of elastic energy storage.

N cannot be easily experimentally manipulated in freely behaving insects, making it difficult to precisely link performance tradeoffs with the different properties that affect N . However, N can be systematically varied in a dynamically scaled robophysical flapping system by varying wing, fluid, and driving force parameters (Dickinson et al. 1999; Lynch et al. 2021, 2024). Particularly relevant are new robophysical systems that take a driving force input as opposed to a wing trajectory input, allowing kinematics to emerge from motor and wing dynamics. N can also be estimated in these systems without a formula by sweeping over a range of driving frequencies and measuring the width of an empirical resonance curve. In combination with an external flow perturbation, for example, this setup can be used to examine effects of N on flapping performance in unsteady conditions (Lynch et al. 2021). We suggest that future efforts focus on testing the effects of N on unstudied aspects of flight performance, such as flight in varying flow speeds, or the effects of currently unmodeled properties of insect wings on N , such as wing flexural compliance.

N holds great promise for expanding our understanding of insect flight mechanics, control, and evolution. Capturing the interactions between an insect’s wing morphology, kinematics, and aerodynamics, N distinguishes itself from other dimensionless numbers in animal locomotion. Furthermore, the original arguments developed by Weis-Fogh for linking N to aerodynamic efficiency have proven ripe for expansion in depth and realism to incorporate effects such as internal damping and varying thorax elasticity. By assessing the performance tradeoffs over a range of N values in computational models, robophysical springwings, and across taxa, we can make further progress in understanding how insects balance efficiency, responsiveness, and stability against the backdrop of remarkable morphological, behavioral, and environmental diversity.

Funding

This work was supported by US National Science Foundation RAISE grant no. IOS-2100858 to S.S. and N.G. and 1554790 (MPS-PoLS) and a Dunn Family Professorship to S.S. as well as the US National Science Foundation Physics of Living Systems SAVI student research network (GT node grant no. 1205878).

Conflict of interest

We have no conflicts of interest to report.

Data availability statement

No new data were generated or analysed in support of this research.

References

- Abzhanov A, Extavour CG, Groover A, Hodges SA, Hoekstra HE, Kramer EM, Monteiro A. 2008. Are we there yet? Tracking the development of new model systems. *Trends Genet* 24:353–60. <https://doi.org/10.1016/j.tig.2008.04.002>.
- Aiello BR, Sikandar UB, Minoguchi H, Bhinderwala B, Hamilton CA, Kawahara AY, Sponberg S. 2021a. The evolution of two distinct strategies of moth flight. *J R Soc Interface* 18:20210632. <https://doi.org/10.1098/rsif.2021.0632>
- Aiello BR, Tan M, Bin Sikandar U, Alvey AJ, Bhinderwala B, Kimball KC, Barber JR, Hamilton CA, Kawahara AY, Sponberg S. 2021b. Adaptive shifts underlie the divergence in wing morphology in bombycoid moths. *Proc Biol Sci* 288:20210677. <https://doi.org/10.1098/rspb.2021.0677>
- 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* 102:18213–8. <https://doi.org/10.1073/pnas.0506590102>
- Ando N, Kanzaki R. 2016. Flexibility and control of thorax deformation during hawkmoth flight. *Biol Lett* 12:20150733. <https://doi.org/10.1098/rsbl.2015.0733>
- Asmussen E. 1953. Positive and negative muscular work. *Acta Physiol Scand* 28:364–82. <https://doi.org/10.1111/j.1748-1716.1953.tb00988.x>
- Casey C, Heveran C, Jankauski M. 2023. Experimental studies suggest differences in the distribution of thorax elasticity between insects with synchronous and asynchronous musculature. *J R Soc Interface* 20:20230029. <https://doi.org/10.1098/rsif.2023.0029>.
- Chin DD, Lentink D. 2016. Flapping wing aerodynamics: from insects to vertebrates. *J Exp Biol* 219:920–32. <https://doi.org/10.1242/jeb.042317>.
- Combes SA, Gagliardi SF, Switzer CM, Dillon ME. 2020. Kinematic flexibility allows bumblebees to increase energetic efficiency when carrying heavy loads. *Sci Adv* 6:1–10. <https://doi.org/10.1126/sciadv.aay3115>.
- Deora T, Gundiah N, Sane SP. 2017. Mechanics of the thorax in flies. *J Exp Biol* 220:1382–95. <https://doi.org/10.1242/jeb.128363>.
- Dickinson MH, Lehmann F-O, Sane SP. 1999. Wing rotation and the aerodynamic basis of insect flight. *Science* 284:1954–60. <https://doi.org/10.1126/science.284.5422.1954>.
- Dickinson MH, Lighton JRB. 1995. Muscle efficiency and elastic storage in the flight motor of *Drosophila*. *Science* 268:87–90. <https://doi.org/10.1126/science.7701346>.
- Dickinson MH, Tu MS. 1997. The function of dipteran flight muscle. *Comp Biochem Physiol A Physiol* 116:223–38. [https://doi.org/10.1016/S0300-9629\(96\)00162-4](https://doi.org/10.1016/S0300-9629(96)00162-4).
- Dudek DM, Full RJ. 2006. Passive mechanical properties of legs from running insects. *J Exp Biol* 209:1502–15. <https://doi.org/10.1242/jeb.02146>.
- Dudley R. 2002. *The biomechanics of insect flight: form, function, evolution*. Princeton, New Jersey: Princeton University Press.
- Dudley R. 2002. Mechanisms and implications of animal flight maneuverability. *Integr Comp Biol* 42:135–40. <https://doi.org/10.1093/icb/42.1.135>.
- Ellington CP. 1984a. The aerodynamics of hovering insect flight. VI. Lift and power requirements. *Phil Trans R Soc Lond B* 305:145–81. <https://doi.org/10.1098/rstb.1984.0054>.
- Ellington CP. 1984b. The aerodynamics of hovering insect flight. II. Morphological parameters. *Phil Trans R Soc Lond B* 305:17–40. <https://doi.org/10.1098/rstb.1984.0050>.
- Ellington CP. 1984c. The aerodynamics of hovering insect flight III: kinematics. *Philos Trans R Soc Lond B Biol Sci* 305:41–78.
- Ellington CP. 1999. The novel aerodynamics of insect flight: applications to micro-air vehicles. *J Exp Biol* 202:3439–48. <https://doi.org/10.1242/jeb.202.23.3439>.
- Farisenkov SE, Kolomenskiy D, Petrov PN, Engels T, Lapina NA, Lehmann F-O, Onishi R, Liu H, Polilov AA. 2022. Novel flight style and light wings boost flight performance of tiny beetles. *Nature* 602:96–100. <https://doi.org/10.1038/s41586-021-04303-7>.
- Farisenkov SE, Lapina NA, Petrov PN, Polilov AA. 2020. Extraordinary flight performance of the smallest beetles. *Proc Natl Acad Sci USA* 117:24643–5. <https://doi.org/10.1073/pnas.2012404117>.
- Gau J, Gemilere R, (FM Subteam) L-V, Lynch J, Gravish N, Sponberg S. 2021. Rapid frequency modulation in a resonant system: aerial perturbation recovery in hawkmoths. *Proc Biol Sci* 288:20210352. <https://doi.org/10.1098/rspb.2021.0352>.
- Gau J, Gravish N, Sponberg S. 2019. Indirect actuation reduces flight power requirements in *Manduca sexta* via elastic energy exchange. *J R Soc Interface* 16:20190543. <https://doi.org/10.1098/rsif.2019.0543>.
- Gau J, Lynch J, Aiello B, Wold E, Gravish N, Sponberg S. 2023. Bridging two insect flight modes in evolution, physiology and robophysics. *Nature* 622:767–74. <https://doi.org/10.1038/s41586-023-06606-3>.
- Gau J, Wold ES, Lynch J, Gravish N, Sponberg S, Sponberg S. 2022. The hawkmoth wingbeat is not at resonance. *Biol Lett* 18:1–5.
- Greenewalt CH. 1960. The wings of insects and birds as mechanical oscillators. *Proc Am Philos Soc* 104:605–11.
- Han J-S, Kim J-K, Chang JW, Han J-H. 2015. An improved quasi-steady aerodynamic model for insect wings that considers movement of the center of pressure. *Bioinspir Biomim* 10:046014. <https://doi.org/10.1088/1748-3190/10/4/046014>.
- Hedrick TL, Cheng B, Deng X. 2009. Wingbeat time and the scaling of passive rotational damping in flapping flight. *Science* 324:252–5. <https://doi.org/10.1126/science.1168431>.
- Hrncir M, Gravel A-I, Schorkopf DLP, Schmidt VM, Zucchi R, Barth FG. 2008. Thoracic vibrations in stingless bees (*Melipona seminigra*): resonances of the thorax influence vi-

- brations associated with flight but not those associated with sound production. *J Exp Biol* 211:678–85. <https://doi.org/10.1242/jeb.013920>.
- Jacobs D, Bastian A. 2016. Predator-prey interactions: co-evolution between bats and their prey. Cham, Switzerland: Springer.
- Jafferis NT, Graule MA, Wood RJ. 2016. Non-linear resonance modeling and system design improvements for underactuated flapping-wing vehicles. *Proc IEEE Int Conf Robot Autom* 2016-June:3234–41. <https://doi.org/10.1109/ICRA.2016.7487493>.
- Jankauski M, Casey C, Heveran C, Busby MK, Buchmann S. 2022. Carpenter bee thorax vibration and force generation inform pollen release mechanisms during floral buzzing. *Sci Rep* 12:1–10. <https://doi.org/10.1038/s41598-022-16859-z>.
- Jankauski MA. 2020. Measuring the frequency response of the honeybee thorax. *Bioinspir Biomim* 15:046002. <https://doi.org/10.1088/1748-3190/ab835b>.
- Janzen DH. 1984. Two ways to be a tropical big moth: santa Rosa saturniids and sphingids. *Oxford Surv Evol Biol* 1: 85–144.
- Lentink D, Dickinson MH. 2009a. Rotational accelerations stabilize leading edge vortices on revolving fly wings. *J Exp Biol* 212:2705–19. <https://doi.org/10.1242/jeb.022269>.
- Lentink D, Dickinson MH. 2009b. Biofluiddynamic scaling of flapping, spinning and translating fins and wings. *J Exp Biol* 212:2691–704. <https://doi.org/10.1242/jeb.022251>.
- Liu Y, Liu L, Sun M. 2024. Power requirements in hovering flight of mosquitoes. *Phys Fluids* 36:021907. <https://doi.org/10.1063/5.0191111>.
- Lynch J, Gau J, Sponberg S, Gravish N. 2021. Dimensional analysis of spring-wing systems reveals performance metrics for resonant flapping-wing flight. *J R Soc Interface* 18:20200888. <https://doi.org/10.1098/rsif.2020.0888>.
- Lynch J, Wold ES, Gau J, Sponberg SN, Gravish N. 2024. Energetic and control tradeoffs in spring-wing systems. *arXiv:2403.03398*.
- Matthews M, Sponberg S. 2018. Hawkmoth flight in the unsteady wakes of flowers. *J Exp Biol* 221:jeb179259. <https://doi.org/10.1242/jeb.179259>.
- Melis JM, Siwanowicz I, Dickinson MH. 2023. Machine learning reveals the control mechanics of the insect wing hinge. *Biorxiv*.
- Miller LA, Peskin CS. 2004. When vortices stick: an aerodynamic transition in tiny insect flight. *J Exp Biol* 207:3073–88. <https://doi.org/10.1242/jeb.01138>.
- Miller LA, Peskin CS. 2009. Flexible clap and fling in tiny insect flight. *J Exp Biol* 212:3076–90. <https://doi.org/10.1242/jeb.028662>.
- Ortega-Jimenez VM, Greeter JSM, Mittal R, Hedrick TL. 2013. Hawkmoth flight stability in turbulent vortex streets. *J Exp Biol* 216:4567–79. <https://doi.org/10.1242/jeb.089672>.
- Peters JM, Gravish N, Combes SA. 2017. Wings as impellers: honey bees co-opt flight system to induce nest ventilation and disperse pheromones. *J Exp Biol* 220:2203–9. <https://doi.org/10.1242/jeb.149476>.
- Pons A, Beatus T. 2022a. Distinct forms of resonant optimality within insect indirect flight motors. *J R Soc Interface* 19:20220080. <https://doi.org/10.1098/rsif.2022.0080>.
- Pons A, Beatus T. 2022b. Elastic-bound conditions for energetically optimal elasticity and their implications for biomimetic propulsion systems. *Nonlinear Dyn* 108:2045–74. <https://doi.org/10.1007/s11071-022-07325-6>.
- Pons A, Perl I, Ben-Dov O, Maya R, Beatus T. 2023. Solving the thoracic inverse problem in the fruit fly. *Bioinspir Biomim* 18:046002. <https://doi.org/10.1088/1748-3190/accc23>.
- Poot M, Van Der Zant HSJ. 2012. Mechanical systems in the quantum regime. *Phys Rep* 511:273–335. <https://doi.org/10.1016/j.physrep.2011.12.004>.
- Pritchard DJ, Vallejo-Marín M. 2020. Floral vibrations by buzz-pollinating bees achieve higher frequency, velocity and acceleration than flight and defence vibrations. *J Exp Biol* 223: jeb220541. <https://doi.org/10.1242/jeb.220541>.
- Roth E, Hall RW, Daniel TL, Sponberg S. 2016. Integration of parallel mechanosensory and visual pathways resolved through sensory conflict. *Proc Natl Acad Sci USA*. 113:12832–7. <https://doi.org/10.1073/pnas.1522419113>.
- Sane SP. 2003. The aerodynamics of insect flight. *J Exp Biol* 206:4191–208. <https://doi.org/10.1242/jeb.00663>.
- Sane SP, Dickinson MH. 2001. The control of flight force by a flapping wing: lift and drag production. *J Exp Biol* 204:2607–26. <https://doi.org/10.1242/jeb.204.15.2607>.
- Sotavalta O. 1952. Flight-tone and wing-stroke frequency of insects and the dynamics of insect flight. *Nature* 170:1057–8. <https://doi.org/10.1038/1701057a0>.
- Taylor GK, Nudds RL, Thomas ALR. 2003. Flying and swimming animals cruise at a Strouhal number tuned for high power efficiency. *Nature* 425:705–7. <https://doi.org/10.1038/nature02047.1>.
- Vallejo-Marín M. 2022. How and why do bees buzz? Implications for buzz pollination. *J Exp Bot* 73:1080–92. <https://doi.org/10.1093/jxb/erab428>.
- Weaver Jr W, Timoshenko SP, Young DH. 1991. *Vibration problems in engineering*. Chichester, UK: John Wiley & Sons.
- Weis-Fogh T. 1960. A rubber-like protein in insect cuticle. *J Exp Biol* 37:889–907. <https://doi.org/10.1242/jeb.37.4.889>.
- Weis-Fogh T. 1972. Energetics of hovering flight in hummingbirds and in *Drosophila*. *J Exp Biol* 56:79–104. <https://doi.org/10.1242/jeb.56.1.79>.
- Weis-Fogh T. 1973. Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift production. *J Exp Biol* 59:169–230.
- Whitney JP, Wood RJ. 2012. Conceptual design of flapping-wing micro air vehicles. *Bioinspir Biomim* 7:036001. <https://doi.org/10.1088/1748-3182/7/3/036001>.
- Williams CD, Biewener AA. 2015. Pigeons trade efficiency for stability in response to level of challenge during confined flight. *Proc Natl Acad Sci USA* 112:3392–6. <https://doi.org/10.1073/pnas.1407298112>.
- Willmott AP, Ellington CP. 1997. The mechanics of flight in the hawkmoth *Manduca sexta* I. Kinematics of hovering and forward flight. *J Exp Biol* 200:2705–22. <https://doi.org/10.1242/jeb.200.21.2705>.
- Wold ES, Aiello BR, Harris M, bin Sikandar U, Lynch J, Gravish N, Sponberg SN. 2024. Moth resonant mechanics are tuned to wingbeat frequency and energetic demands. *bioRxiv*. <https://doi.org/10.1101/2024.01.30.578003>.
- Wold ES, Lynch J, Gravish N, Sponberg S. 2023. Structural damping renders the hawkmoth exoskeleton mechanically insensitive to non-sinusoidal deformations. *J R Soc Interface* 20:20230141. <https://doi.org/10.1098/rsif.2023.0141>.