The evolution of two distinct strategies of moth flight

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Across insects, wing shape and size have undergone dramatic divergence even in closely related sister groups. However, we do not know how morphology changes in tandem with kinematics to support body weight within available power and how the specific force production patterns are linked to differences in behaviour. Hawkmoths and wild silkmoths are diverse sister families with divergent wing morphology. Using three-dimensional kinematics and quasi-steady aerodynamic modelling, we compare the aerodynamics and the contributions of wing shape, size and kinematics in 10 moth species. We find that wing movement also diverges between the clades and underlies two distinct strategies for flight. Hawkmoths use wing kinematics, especially high frequencies, to enhance force and wing morphologies that reduce power. Silkmoths use wing morphology to enhance force, and slow, high-amplitude wingstrokes to reduce power. Both strategies converge on similar aerodynamic power and can support similar body weight ranges. However, inter-clade within-wingstroke force profiles are quite different and linked to the hovering flight of hawkmoths and the bobbing flight of silkmoths. These two moth groups fly more like other, distantly related insects than they do each other, demonstrating the diversity of flapping flight evolution and a rich bioinspired design space for robotic flappers.

1. Introduction

The evolution of flapping flight is foundational to the success of many insects [1] and is key for foraging, mate finding, courtship, predator avoidance and migration. To conduct these behaviours, significant selective pressures are placed on the flight performance of aerial organisms. Both wing morphology and movement can strongly impact the aerodynamics of a flying animal or machine [2,3]. For example, robotic flapping-wing micro air vehicles (FW-MAVs) have greater power efficiency and control than fixed-wing and rotary-wing aircraft of similar size [4,5]. Since the origin of flapping flight in insects, a wide diversity of wing morphologies (size, shape and mechanics), movements and flight behaviours have evolved [6–9]. A central question in the evolution of flapping flight is whether divergent strategies (combinations of wing shape, size and kinematics) arise to achieve similar flight performance. A comparison of disparate species across Insecta shows that not all insects use the same flapping flight strategies. Butterflies direct vortices in different directions on upstroke and downstroke [10,11], while a fly (Drosophila melanogaster) and a hawkmoth (Manduca sexta) produce lift on both upstroke and downstroke [3,12,13]. Mosquitoes use exceptionally high-frequency wingstrokes coupled...
with rapid wing rotations [14] and dragonflies directly actuate the forewing and hindwing independently [15].

Less explored than these disparate comparisons is how closely related sister groups sharing morphological and physiological features diverse to fill different aeroeological niches. Do changes primarily occur in size, shape or kinematics to adapt single flight strategies to multiple behaviours or do all three change in tandem (different overall strategies) when new life histories and behaviours evolve? Considering diversification in closely related but divergent clades is an opportunity to test how wing size, shape and movement evolve together and interact to produce species-specific aerodynamics. However, these multiple factors contributing to aerodynamic performance make it challenging to link the evolutionary patterns of wing morphology and movement to interspecific differences in flight behaviour and aerodynamics as well as translate these patterns to the design and movement of engineered robotic flappers.

Hawkmoths (Sphingidae) and wild silk moths (Saturniidae) are diverse sister clades separated by approximately 60 Ma of evolution [9,16,17]. We recently showed that wing shape and size diverges between the families through an adaptive shift [9] coincident with the inter-familial divergence in life history [18–20] and flight behaviour [18–20]. However, wing morphology diverged between the clades in a way that belies simple intuition about how shape should affect performance based on the behavioural demands of each family [9]. Hawkmoths are active, fast fliers [20], well known for their ability to sustain long-duration bouts of hover [21–24], where some species can track flower oscillations up to frequencies of 14 Hz [24,25]. Yet, hawkmoths evolved small wings of high aspect ratio (AR), non-dimensional radius of the second moment of area (\( r_s \)) and wing loading (\( W_s \)), metrics typically associated with power reduction and a high lift-to-drag ratio [9,26]. These metrics are also associated with poor maneuverability in fixed-wing aircraft, although animal fliers partially control flight more like rotary-blade systems where force vectors are modulated by wing rotations [27,28]. In contrast to the smoother flight of hawkmoths, silkmoth flight is often described as erratic or bobbing [18,29,30], which is thought to be advantageous for predator avoidance. Adult silkmoths also lack functional mouth parts and rely entirely on the strictly finite energy stores gathered during the larval period for their entire adult life stage [19]. Yet, silkmoths evolved wing morphology that is advantageous for maneuverability (low AR, \( W_s \), and \( r_s \)) and, despite relying on a fixed energy budget as adults, the clade did not evolve wing morphology that is advantageous for power reduction [9]. It remains unclear if these shifts in wing morphology led to shifts in flight performance between the clades and how wing movement evolves in tandem and interacts with wing morphology to generate sufficient force to balance body weight while not exceeding the available power.

We hypothesize that each clade has evolved a distinct strategy for flight that relies on correspondingly distinct wing sizes, shapes and movements. If so, silkmoths and hawkmoths with comparable body masses should have similar wingstroke-averaged aerodynamic forces, but may differ in their within-wingstroke patterns of force production. Alternatively, the adaptive shift in wing morphology between the two clades [9] has a minimal impact on flight performance. A third alternative is that wing movement is conserved across the two clades and the divergence in wing morphology alone plays a role in flight performance, leading to the evolution of divergent flight performance between the two clades. While differences between Saturniidae and Sphingidae in wingbeat frequency and observations of erratic versus hovering flight suggest that kinematics play a role, morphology and movement have not been integrated in aerodynamic comparisons of the sister clades. To assess the interplay of shape, size and kinematics, we first quantify three-dimensional wing kinematics during forward flight from live specimens of five species from each sister family and combine these with our prior analysis of wing shape and size evolution [9]. We then use a blade element model [12,13,31] that can be applied across species to estimate the quasi-steady aerodynamic force production and power requirements and separate the contributions of wing size, shape and kinematics. As the notoriously agile hawkmoths evolved small wings of shapes advantageous for power reduction, we predict that the evolution of wing movement in this group aids in force production and flight control; both can be accomplished through high-frequency wingstrokes. We predict that the evolution of silkmoth wing movement reduces the power requirements of flight, which can occur through high-amplitude wingstrokes [32–34]. Alternatively, silkmoths have not evolved any means of reducing power, which could be an additional factor contributing to the short silkmoth adult lifespan. Revealing how species of each clade have evolved sufficient force generation within an available power budget through interspecific differences in wing shape, size and movement will also unveil multiple, and possibly unique, combinations of aerodynamic variables within a bio-inspired design space that could be implemented in future robotic fliers tuned to various behavioural and performance metrics.

2. Material and methods

Details of the mathematical notation used in this study are in electronic supplementary material, table S1.

2.1. Live specimens
Live specimens of five different species from each sister family (10 total species) were used in this study (electronic supplementary material, table S2). Species from the hawkmoth (Sphingidae) family include: Eumorpha achemon, Amphion floridensis, Hyles lineata, Paonias myops and Smerinthus ophthalmica. Species from the silkmoth (Saturniidae) family include: Actias luna, Automeris io, Antheraea polyphemus, Hylaphora caryata and Eacles imperialis.

2.2. Body and wing measurements and morphometrics
Body and wing morphologies were digitized for each live specimen using StereoMorph (v. 1.6.2) [35] in R (v. 3.4.2) following our previous methodology [9]. For all individuals, total body mass (\( m_0 \)) was measured directly after the individual was flown.

Morphology was analysed in Matlab (v. R2018b - 9.5.0.944444) following [9]. To generate a combined wing shape from the overlap of the fore- and hindwings, the forewings long axis was rotated to be perpendicular to the body long axis. In hawkmoths, the long axis of the hindwing was also oriented perpendicular to the body long axis. In silkmoths, hindwing orientation was left in its natural position obtained when the wings are splayed open and the moth is at rest. This position was chosen while reviewing videos of silkmoth flight; the long axis of the hindwing is always oriented posteriorly and nearly parallel with the body long axis (see electronic supplementary material, movies). All wing morphology parameters (see
2.3. High-speed recordings of moth flight
Flight experiments were conducted in a 100 × 60.96 cm working section of an open-circuit Eiffel-type wind tunnel (ELD, Inc., Lake City, MN, USA). See [37] for tunnel details.

Moths were enticed to fly by providing a wind speed of 0.7 ms\(^{-1}\). Flight bouts were filmed at 2000 frames s\(^{-1}\) for hawkmoths and 1000 frames s\(^{-1}\) for silkmoths using three synchronized high-speed cameras (resolution: 1280 × 1024 pixels) (Mini UX 100; Photron, San Diego, CA, USA). The wind tunnel was illuminated with six 850 Nm infrared lights (Larson Electronics, Kemp, TX, USA) and a neutral density-filtered white LED ‘moon’ light (Neewer CW-126) [24]. Room lights were also turned on for the diurnal species (A. floriensis).

Videos were digitized and calibrated in XMALab [38]. A total of seven landmarks were digitized on the moth: rostral tip of the head (between the antennae), junction between the thorax and abdomen, caudal tip of the abdomen, left and right forewing hinges, right wing tip and a point on the trailing edge of the wing (see electronic supplementary material, table S3 for individual kinematics).

2.4. Blade element model summary
A third-order Fourier series was fitted to all kinematics for every wingstroke. Representative wing shape, size and kinematics for each species were calculated by averaging the wing shapes and time-varying Fourier-fitted kinematics over all wingstrokes of all individual moths.

Species-specific aerodynamic forces were evaluated using a quasi-steady blade element model, estimating the total aerodynamic force as contributions from translational and rotational motion and the force due to added mass [12,13,31,39] and based on hawkmoth (Manduca sexta) lift and drag coefficients [13]. This type of first-principles model provides flexibility to directly test how different combinations of wing morphology and kinematics impact aerodynamic force and power across a larger number of species and allows us to directly explore how the different force components (translational, rotational and added-mass) contribute to the overall aerodynamic force profile. A trim search then found equilibrium conditions to balance force and moment over a wingstroke. Trim conditions are given in electronic supplementary material, table S4.

The wing inertial force was also calculated. Since these are internal forces to the moth, they cannot produce a net force over full steady wingstroke periods, but it is possible that there is an indirect contribution of wing inertial forces on aerodynamics via their movement of the body. However, the wing kinematic measurements were relative to the body and we transformed all forces to the body-attached frame. Thus, any relative motion between the wings and body due to inertial forces and its effect on the aerodynamics is naturally captured.

Total aerodynamic power is the sum of induced, profile and parasite powers [33], and we also calculate the inertial power. A detailed formulation of the blade element model is in the electronic supplementary material.

3. Results
3.1. Hawkmoths and silkmoths evolved divergent wing and body morphology
We quantified several morphological features and compared them with our previous work to ensure that the previously identified inter-clade differences in wing and body morphometrics are consistent. Variables include wing area (S), the non-dimensional radius of the second moment of wing area (\(r_2\)), wing aspect ratio (AR), wing loading (\(W_s\)) and total body mass (\(m_t\)) (summary data: electronic supplementary material, table S2).

Hawkmoth and silkmoth wing morphology is well separated in morphospace (figure 1a–c). A MANOVA where AR, \(W_s\) and \(r_2\) are the response variables and clade is the factor reveals significant differences between clades (\(F = 34.5, p < 0.0001\)). AR, \(W_s\) and \(r_2\) are all greater in hawkmoths than in silkmoths by factors of 1.6, 3.7 and 1.1, respectively. Variation in body mass (\(m_t\)) spans similar ranges within each family. For a given body mass, S is significantly greater in silkmoths than in hawkmoths (figure 1d), as indicated by an ANCOVA between the slopes of each clade (hawkmoth regression: \(r^2 = 0.9565, F = 263.7, p < 0.0001\); silkmoth regression: \(r^2 = 0.6273, F = 15.15, p = 0.0036\); ANCOVA: \(F = 26.551, p < 0.0001\)). These results recapitulate the broader adaptive shift that we found in wing and body morphology in prior work.

3.2. Hawkmoths and silkmoths evolved divergent wing kinematics
Wing movement can also strongly impact aerodynamics. We next determined if wing movement diverged between the clades. Analysis of three-dimensional kinematics across all 10 species revealed strong and consistent inter-clade differences for several variables (figure 2; electronic supplementary material, table S3; recorded kinematics: hawkmoths, electronic supplementary material, figure S4; silkmoths, electronic supplementary material, figure S5). Across the species considered here, hawkmoths fly with a 2.5 times greater average wing beat frequency (\(n\)) than silkmoths. Silkmoths fly with a 1.2 times greater average sweep amplitude (\(\theta_s\)) and 2.3 times greater average inclined (more vertical) stroke plane angle (\(\beta\)) than hawkmoths (electronic supplementary material, table S3). A MANOVA where \(n\), \(\theta_s\) and \(\beta\) are the response variables and clade is the factor reveals significant differences between clades (\(F = 32.546, p < 0.0001\)).

The within-wingstroke time-varying deviation angle (\(\theta\)) and feathering angle (\(\alpha\)) differed slightly between hawkmoths and silkmoths (figure 2a,b; electronic supplementary material, figures S4 and S5). On average, silkmoths had 1.5 times larger \(\theta\) amplitude, whereas hawkmoths had 1.2 times larger \(\alpha\) amplitude and 1.1 times smaller mean \(\alpha\). These differences are also evident when comparing an exemplar from each clade: E. achemon (hawkmoth) and A. polyphemus (silkmoth) (figure 2a).

3.3. Hawkmoths and silkmoths evolved convergent wingstroke-averaged aerodynamics and aerodynamic power requirements
Given that hawkmoths and silkmoths evolved differences in wing shape, size and movement, we assessed the overall aerodynamic force and power implications between the two clades. Again, while we focus on two exemplar species (figure 3a)—the hawkmoth, E. achemon, and the silkmoth, A. polyphemus—these trends are consistent across the species of each respective family (electronic supplementary material, figure S6). Despite the large morphological differences, hawkmoths and silkmoths have overlapping total body masses, suggesting that they produce comparable
aerodynamic forces at steady state. We found that all species were able to trim to equilibrium conditions using the observed wingstroke kinematic variation in each species and prior observed variation in $C_L$ and $C_D$ (electronic supplementary material, table S4). *Actias luna* was an exception in that its forces trimmed, but a small pitching moment persisted in the model. Thus, the combinations of wing shape, size and kinematics, despite being significantly divergent, produce comparable wingstroke-averaged aerodynamic forces (electronic supplementary material, figure S6). In addition, the peak magnitudes of the wing inertial forces are of the same order of magnitude as the aerodynamic forces across all species (electronic supplementary material, figure S10).

Similar average aerodynamic forces do not imply similar aerodynamic power across clades. Nonetheless, the power requirements of forward flight are also consistent within and between each clade. Total body mass-specific aerodynamic power requirements range from 15.06 to 18.32 W kg$^{-1}$ in hawkmoths and from 11.76 to 17.18 W kg$^{-1}$ in silkmots (figure 4a). However, there were differences in which component of aerodynamic power contributed greatest. Induced power ($P_{ind}$) was always the largest contributor to total power in hawkmoths and three silkmots species, but in two silkmots (*A. luna* and *A. polyphemus*) profile power ($P_{prof}$) was greater than $P_{ind}$ (figure 4a). Parasitic power ($P_{par}$) was negligible across all species (figure 4a), consistent with prior studies [33].

3.4. Hawkmoths and silkmots evolved divergent wingstroke-averaged inertial power requirements

While aerodynamic power requirements are similar between the species of each family, the inertial power requirements, the power required to accelerate and decelerate the wing mass, do differ between the families (electronic supplementary material, table S5). On average, the inertial power (body-mass specific) of hawkmoths (36.7 ± 12.8 W kg$^{-1}$) is approximately three times greater than that of silkmots (13.4 ± 3.3 W kg$^{-1}$). The difference is primarily driven by the large inter-clade difference in $n$ as inertial power scales with $n^3$. However, these inter-clade differences in inertial power probably do not contribute to larger inter-clade differences in power consumption. Most of the energy required to accelerate and decelerate the wing mass is believed to be

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**Figure 1.** Wing shape and size is divergent between hawkmoth and silkmot species. (a) A representative hawkmoth (*E. achemon*) and (b) silkmot (*A. polyphemus*) species used for a detailed comparison of wing kinematics and aerodynamics. Scale bar length = 1 cm. (c) Functionally relevant metrics of wing morphology and (d) wing size diverge between hawkmoths and silkmots.

**Figure 2.** Wing kinematics are divergent between hawkmoths and silkmots. (a) Within-wingstroke kinematics of the sweep ($\phi$), deviation ($\theta$) and feathering angles ($\alpha$) for each of the representative species: *E. achemon* (hawkmoth) and *A. polyphemus* (silkmot). (b) Summary kinematics of wingstroke amplitude ($\phi_{p-p}$), frequency ($n$) and stroke plane angle ($\beta$) for all 10 species used in this study. The key for species abbreviations for each symbol can be found in electronic supplementary material, table S1.
stored and returned through thoracic mechanics \cite{40,41}. Even if the inertial power requirement is not fully accounted for by elastic energy exchange, it is not surprising that the remaining power requirement is greater in hawkmoths than in silkmoths since most hawkmoth species regularly feed and replenish energy stores. Comparative work is lacking on thoracic mechanics and elastic energy storage, but, given that silkmoths lack functional mouthparts as adults, we hypothesize that thoracic mechanics might have also evolved to increase the ability to store and return elastic energy and thus reduce the energy expenditure needed to move the wing masses. We find this a particularly exciting avenue of future research.

3.5. Hawkmoths and silkmoths evolved interspecific differences in within-wingstroke aerodynamics

While the average powers and normalized forces converge, the within-wingstroke force profiles do show consistent differences between clades, reflecting different strategies for achieving body weight support and thrust. In hawkmoths, $F_{bz}$ is predominately negative (backwards) during the first...
half and positive during the second half of the wingstroke. In silkmoths, \( F_{b\text{x}} \) has significant positive and negative portions during both halves of the wingstroke (figure 3a; electronic supplementary material, figure S6). In hawkmoths, \( F_{b\text{z}} \) generally supports weight (negative) across the entire wingstroke and is of greater (more than twice) magnitude during the first half than during the second half wingstroke (figure 3a; electronic supplementary material, figure S6). In silkmoths, \( F_{b\text{z}} \) is also generally negative, but is usually of reduced magnitude during the second half stroke in comparison with hawkmoths; in two silkmoth species, \( F_{z\text{b}} \) becomes predominantly positive (figure 3a; electronic supplementary material, figure S6).

Although the magnitudes of rotational (\( F_{b\text{rot}} \)) and added mass (\( F_{b\text{adm}} \)) forces are generally larger in silkmoths than in hawkmoths (electronic supplementary material, figures S6 and S7), these forces tend to act in opposition, and, across all species, interspecific differences in total force (\( F_{b\text{total}} \)) are primarily due to translational force, \( F_{b\text{tra}} \) (electronic supplementary material, figures S6 and S7). The silkmoth \( A.\ io \) represents an exception to this as \( F_{\text{total}} \) is indeed impacted by \( F_{b\text{tra}} \) and \( F_{b\text{adm}} \) throughout the wingstroke (electronic supplementary material, figure S6). These results are consistent whether we consider the species-specific flight speeds or model all species at 2 m s\(^{-1}\) (electronic supplementary material, figure S8).

3.6. Quasi-steady blade element models separate the contributions of wing shape, size and kinematics in flight strategies

We created several intermediate models to separate contributions and assess how size, shape and kinematics impact aerodynamics. To do so, we focused on exemplar species from each clade (\( E.\ achemon \), \( A.\ polyphemus \)), which are representative of the general divergence in wing shape, size and movement between the clades. The base comparison reported above (model 1—figure 3a; electronic supplementary material, figure S7A-B) uses each species’ own wing shape and size, time-varying kinematics (\( \phi, \theta, \alpha, \beta, \chi \) and \( n \)) and recorded forward flight velocities. In model 2 (figure 3b; electronic supplementary material, figure S7C) kinematics and size are set to those of the hawkmoth \( E.\ achemon \) in both cases, leaving interspecific differences only in wing shape. In model 3 (figure 3c; electronic supplementary material, figure S7D), wing shape and size are set to those of \( E.\ achemon \), leaving interspecific differences only in wing kinematics. Finally, in model 4 (figure 3d; electronic supplementary material, figure S7E), wing shape and kinematics are set to those of \( E.\ achemon \), leaving interspecific differences only in wing size.

3.6.1. Wing shape

The \( E.\ achemon \) wing shape produces slightly larger net aerodynamic force than \( A.\ polyphemus \) shaped wings (model 2, figure 3b; electronic supplementary material, figure S7C). The increase in \( F_{b\text{total}} \) is primarily driven by the increased \( F_{b\text{tra}} \) (electronic supplementary material, figure S7C). While different in average and peak magnitude, the pattern of the \( F_{b\text{tra}} \) (as well as \( F_{b\text{rot}} \) and \( F_{b\text{adm}} \)) throughout the wingstroke was similar in both wing shapes (electronic supplementary material, figure S7C). The \( E.\ achemon \) wing shape produced larger \( F_{b\text{tra}} \) because of its larger radius of second moment of area than \( A.\ polyphemus \).

Figure 4. A comparison of the total aerodynamic power requirements of flight. Total aerodynamic power is the sum of induced power (\( P_{\text{ind}} \)), profile power (\( P_{\text{pro}} \)) and parasitic power (\( P_{\text{par}} \)). The total and component power is shown for (a) all species during forward flight at recorded speeds and (b) each sub-model of our two-species comparison in figure 3b–d.

![Figure 4](https://example.com/figure4.png)
3.6.2. Wing kinematics
The most apparent aerodynamic interspecific difference due to kinematics alone (model 3) is that A. polyphemus kinematics produces a lower force (five times smaller peak force) than E. achemon kinematics (figure 3c; electronic supplementary material, figure S7D). The reduction in $F_{\text{total}}$ is again determined primarily by differences in $F_{\text{tra}}$ (electronic supplementary material, figure S7D). The main cause of this difference is that $n$, and hence wing angular velocity, of E. achemon is approximately three times greater than that of A. polyphemus (figure 2; electronic supplementary material, table S3). Interspecific differences in kinematics are also responsible for interspecific differences in the sign of $F_{0}$ and $P_{s}$ in model 1 during the first half and second half of wing-stroke, respectively (figure 3a). To break this down further, we separated the contributions of stroke plane angle ($\theta$), wing angles ($\phi$ and $\alpha$) and $n$ (electronic supplementary material, figure S9). The interspecific sign flip in $F_{0}$ (figure 3a) occurs as a result of $n$ (electronic supplementary material, figure S9B), and the $P_{s}$ sign flip (figure 3a) occurs primarily from differences in lower $n$ and more vertical $\beta$ of A. polyphemus (electronic supplementary material, figure S9B,C).

3.6.3. Wing size
A. polyphemus has 2.5 times larger wings and, if all other variables are equal (model 4), it is not surprising that A. polyphemus wing size produces about six times larger forces (figure 3d; electronic supplementary material, figure S7E). As before, differences in $F_{\text{total}}$ are primarily due to differences in $F_{\text{tra}}$ (electronic supplementary material, figure S7E). However, the $F_{\text{rot}}$ and $F_{\text{fadm}}$ components of $F_{0}$ and $P_{s}$ are also nearly an order of magnitude larger in A. polyphemus sized wings than in E. achemon sized wings (electronic supplementary material, figure S7E). Overall, wing size has the predictable effect of scaling force components.

4. Discussion
4.1. The evolution of two distinct strategies for flapping flight
Silkmoths and hawkmoths have evolved two distinct strategies (combinations of wing shape, size and movement) for flapping flight (figure 5). Species of both families have evolved sufficient average force production and power reduction, but do so with distinctly different wing shapes, sizes and movements and different patterns of within-wingstroke force production. An adaptive shift in hawkmoth wing size and shape resulted in the divergence of wing morphology between the two clades [9]. In the present study, we now demonstrate that key wing movement features also diverge between clades, indicating that hawkmoth wing movements, which occur at frequencies more than three times greater than silkmoths (figure 2), might also be evolving around an adaptive peak.

In hawkmoths, sufficient force production is primarily due to the evolution of high $n$ (movement) (figure 2) because translational force production, the largest contributor to total force, is proportional to airflow velocity squared [32]. The evolution of higher $t_{z}$ wings (shifting more area distally) in hawkmoths also enhances the force and torque production (e.g. [42,43]) compared with silkmoths. Silkmoths achieve sufficient force production through relatively larger wings than hawkmoths (figure 1d) because wing area is proportional to translational force and larger wings will also produce greater wing tip velocities [32]. So, hawkmoths primarily use kinematics to enhance the force production, whereas silkmoths primarily use wing shape and size.

Both clades are also likely under selective pressure to reduce the power requirements of flight. Hawkmoths regularly sustain long-duration bouts of hovering, often associated with nectaring from flowers [21,23–25], which requires a high power output [33], while all silkmoths do not feed as adults, relying on limited energy reserves gathered as larvae [18,19]. Hawkmoths evolved high AR wings (shape) (19); figure 1c), reducing the induced power ($P_{\text{ind}}$) requirements of flight [44,45] in comparison with the evolution of low AR in silkmoths (figure 4b). Silkmoths evolved high-amplitude wingstrokes ($\phi_{\text{p-p}}$), also reducing $P_{\text{ind}}$ (figure 4b), which is inversely proportional to both wing size ($R$) and $\phi_{\text{p-p}}$ [32,34]. In total, silkmoths have a lower $P_{\text{ind}}$ than hawkmoths (figure 4a), offsetting the larger profile power ($P_{\text{pro}}$) incurred by the evolution of larger wings in silkmoths than hawkmoths, which ultimately results in similar overall power requirements between the clades (figure 4a). Thus, the evolution of hawkmoth wing shape and silkmoth wing movement are different means to reduce power.

Aerodynamic performance, therefore, emerges from the interaction of wing shape, size and kinematics, demonstrating an example of correlated evolution between the components of a complex locomotor system [46]. The ability for natural selection to act on both wing shape and kinematics to impact force generation and the power requirements of an animal demonstrates the potential decoupling of animal locomotor performance metrics. Because wing shape, size and movement can each independently affect aerodynamic performance, there are likely to be fewer purely morphological constraints forcing convergence. This may contribute to the diversity of wing shapes across extant aerial animals, even in closely related sister clades.

4.2. The evolution of two distinct aerodynamic strategies contributes to inter-clade differences in flight behaviour
4.2.1. Large, slow wings contribute to bobbing flight behaviour in silkmoths
While the two strategies contribute comparable average aerodynamic forces and power, inter-clade differences in within-wingstroke aerodynamics (figure 3e) probably contribute to differences in flight behaviour between the clades. Silkmoths often display erratic flight patterns [18,19,29,30] where vertical position is regularly changing throughout their flight bout. While all species produce sufficient $F_{0}$ for forward flight, silkmoths generally have more variation in $F_{0}$ between the first and second half of the wingstroke than hawkmoths (figure 3e; electronic supplementary material, figure S6). This is especially noticeable in A. polyphemus and A. luna, where $F_{0}$ switches sign to become positive during the second half of the wingstroke. Large, slow force fluctuations and asymmetry (figure 3e; electronic supplementary material, figure S6) do lead to greater fluctuations in body vertical velocity (electronic supplementary material, figures S4 and S5; table S3) and are likely to be the source of the bobbing. Such erratic motions in silkmoths might be useful in
The evolution of two distinct strategies for flight. A summary of how distinct divergence in wing shape, size and movement impacts flight performance in each clade.

4.2.2. Evolution of high wing beat frequency (n) could contribute to hawkmoth manoeuvrability

The divergence of n parallels the divergence of flight behaviour [18–20] and wing morphology [9] between hawkmoths and silkmoths. The evolution of high n might be the key to conducting high-speed manoeuvres in small flapping fliers with high AR wings like hawkmoths. While we do not directly measure manoeuvrability in this study, it is clear that hawkmoths have evolved a means to accomplish rapid manoeuvres while foraging [21,24,25]. Since moths use flapping wing mechanics, it may not be surprising that they diverge from manoeuvrability metrics often associated with fixed-wing systems. As opposed to fixed-wing cases, manoeuvrability of flapping relies on the generation of aerodynamic forces from wing movement to initiate directional change [47]. Therefore, an increase in n would allow for more frequent modification of force vectors, which could increase manoeuvrability. Further, increasing n will also enhance manoeuvrability by increasing the force and torque produced by a wing [48], which is exemplified in model 3 of this study (figure 3c). The diversification of n, which supports our previous estimates based on scaling relationships [9], could contribute to interspecific variation in flight control and manoeuvrability across species.

4.3. Hawkmoth and silkmoth aerodynamics are more similar to other flying insects than they are to each other

Despite being sister clades, the respective flight strategies of hawkmoths and silkmoths are more similar to other flying insects than they are to each other. The hawkmoth flight strategy is most similar to that of other high-frequency flappers such as flies. In both hawkmoths (figure 3a; electronic supplementary material, figure S6) and the fly D. melanogaster, vertical force is produced during both halves of the wingstroke [49,50]. The low-frequency flapping and time-varying aerodynamics of silkmoths are most similar to those of butterflies. Across multiple species of butterflies and silkmoths, vertical force produced during the downstrokes acts to offset body weight while vertical force during the upstroke contributes either minimal or negative body weight support (figure 3b) [10]. As silkmoths and butterflies converged in wing shape [8], relative size [8], kinematics [10] and aerodynamics [10], it is not surprising that many species of both groups also evolved erratic flight. Similarly, species of both clades also evolved similar aerodynamic power requirements [10]. As butterflies feed as adults and silkmoths do not, the convergent power requirements suggest that silkmoths have not evolved any adaptations for additional power reduction in comparison with butterflies. The combination of wing morphology and kinematics that have evolved in both silkmoths and butterflies might be constrained for this style of flight. Finally, bumblebee aerodynamics at slow flight speeds are similar to that of hawkmoths, but, at fast flight speeds, vertical force production is asymmetric between first and second wingstroke halves [51], similar to a silkmoth (figure 3a). The shift in bee aerodynamics is due to an increasingly more vertical stroke plane at greater flight speeds (similar to silkmoths) [52], further exemplifying how the evolution of divergent kinematics between hawkmoths and silkmoths contributes to inter-clade differences in aerodynamics and flight behaviour.

In conclusion, the divergence in flight strategy between the hawkmoth and silkmoth sister clades is just as strong as the evolutionary divergence between distant clades. Through a strong divergence in wing shape, size and movement,
hawkmoths and silkmoths have evolved two independent flight strategies. This study thus demonstrates that even closely related clades with recently shared ancestry can still undergo strong divergence in flight strategies. The change in wing size and shape corresponds to an adaptive shift between silkmoths and hawkmoths [9], which is now reflected in their kinematics and performance. These sister groups are ideal ‘model clades’ [53] for exploring the morphological, neuromechanical and behavioural diversification of insect flight. Finally, while the design of human-engineered flapping fliers is often inspired by insect flight, a rich design space might be better inspired by the many strategies that even closely related insects take to achieve similar but flexible flight behaviours. Rapid manoeuvres through a cluttered environment and long sustained bouts of flight are two examples of such behaviours that can be incorporated into an FW-MAV. Indeed, this work illuminates a rich morphological and kinematic bio-inspired design space where different combinations of wing size, shape and movement can be implemented in FW-MAV design to improve flight performance fine-tuned to specific application.

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