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Insects select flight speeds that coincide with low metabolic energy expenditure

Abstract

Aerodynamic theory predicts a U-shaped relationship between mechanical power and airspeed. Empirical data from birds and bats support a similar U-shaped metabolic power-speed curve, reflecting the underlying muscle mechanics. However, data on insects' flight energetics remain limited and sometimes conflicting, with some studies reporting airspeed-independent metabolic rates and others suggesting U-shaped relationships. To evaluate whether a consistent metabolic power-speed relationship exists across insect orders, we quantified the energetic cost of tethered flight across a range of airspeeds (0–4ms^{-1}) in four species – bumblebee (*Bombus terrestris*), desert locust (*Schistocerca gregaria*), blowfly (*Calliphora vicina*) and privet hawkmoth (*Sphinx ligustri*).

Clear curvilinear relationships between mass-specific metabolic power and airspeed were observed across all species: U-shaped in *Bombus* and *Schistocerca*; and skewed U-shaped in *Calliphora* and *Sphinx*. The speed corresponding to the minimum mass-specific metabolic cost of transport coincided with reported preferred flight speed ranges in all species. This suggests that these species are physiologically attuned to fly at speeds that minimise flight energetics and economy. Despite substantial differences in phylogeny, wing morphology and muscle physiology, these findings provide experimental evidence for airspeed-dependent metabolic power curves in insects and highlight the importance of flight energetics in speed selection.

Introduction

Aerodynamic theory predicts that the mechanical power required for flight follows a U-shaped relationship with airspeed: induced power dominates at low speeds while profile and parasite power increase at higher airspeeds (1). This U-shaped mechanical power-speed relationship has been demonstrated in birds. For example, the mechanical power output of the principal flight muscle, the pectoralis muscle, is highest at slow and high speeds during wind tunnel flight (2, 3). Since the mechanical power is generated by metabolically fuelled muscle contractions, it is expected that metabolic power should follow a similar relationship with airspeed, albeit dependent on factors such as efficiency (i.e. mechanical power output/metabolic power input) and the postural cost of flight (i.e. the metabolic cost required to maintain wing and body position independent of aerodynamic power; (1, 4). Empirical data support this prediction: in birds (5) and bats (6, 7), metabolic power varies with airspeed in an approximately U-shaped relationship, consistent with aerodynamic theory (1) and muscle mechanical performance (3). Nevertheless, in some species (e.g. barnacle goose (*Branta leucopsis*; (8); fish crow (*Corvus ossifragus*; (9)) a U-shaped relationship has not been observed, possibly due to the relatively narrow sustained flight speed range that precludes measuring metabolic power curve using indirect calorimetry.

Understanding the metabolic power-speed relationship is crucial for interpreting flight behaviour since energy balance and the time taken to undertake a journey all influence optimal flight strategies(10). Two characteristic speeds can be determined from the metabolic power-curve: the minimum power speed (U_{mp}), which maximises flight duration for a given amount of energy, and the maximum range speed (U_{mr}), which minimises the metabolic cost of transport (11).

Despite extensive research into the physiology and biomechanics of animal flight, relatively little is known about the metabolic power requirements of forward flight in the most numerous and diverse volant class – the insects. Most flight energetics data are available for hovering flight (12) and only a few studies have examined how metabolic power varies with flight speed. This gap may reflect the technical challenges of measuring metabolic rate in small, untrainable animals. Comparison with aerodynamic power output, which is predicted to follow a broadly U-shaped trajectory in *Drosophila* (13), *Bombus* (14) and *Manduca sexta* (15), offers an indirect insight into flight energetics, yet empirical validation of the metabolic energy input remains elusive in most species.

Some studies have reported that metabolic rate is independent of airspeed in *Bombus* spp. (16), while others have found a U-shaped relationship in the buff-tailed bumblebee (*Bombus terrestris*), during both free- and tethered flight (17), in the common drone fly (*Eristalis tenax*) (18), and in honeybees (19). Additionally, metabolic power has been shown to increase with airspeed in locusts (20).

The aim of this study was to establish the general pattern of the flight metabolic–speed curve in a range of insect species, representing different orders, flight styles, types of flight muscle (asynchronous and synchronous) and wing morphologies during tethered wind tunnel flights. While tethered insects may not fully support their body weight, previous work indicates that the overall shape of the metabolic power speed relationship is unchanged compared to free-flight (17). Specifically, we tested the following hypotheses: (i) that insect flight energetics vary in a U-shaped relationship with airspeed and (ii) that preferred flight speeds in the field align with the range of speed that encompasses minimal power output (U_{mp}) and cost of locomotion (U_{mr}).

Methods

Animals

Insects were procured from local suppliers either as pupae (blowfly (*Calliphora vicina* (Robineau-Desvoidy 1830), privet hawkmoth (*Sphinx ligustri* (Linnaeus 1758)): Worldwide Butterflies, Dorset, UK) or as adults (desert locust (*Schistocerca gregaria* (Forsskål 1775), *Bombus terrestris* (Linnaeus 1758): Koppert UK Ltd, Suffolk, UK). Animals were maintained in the laboratory with *ad libitum* access to food and water. Mean body mass ± standard deviation was: *Bombus*: 180 ± 40 mg, N = 7; *Schistocerca:* 1555 ± 251 mg, N = 8; *Sphinx*: 1328 ± 139 mg, N = 5; *Calliphora*: 56 ± 10 mg, N = 6.

Tethering and Wind Tunnel Setup

Tethering was accomplished by attaching a small magnet (diameter 3 mm; height 1 mm) to the thorax using cyanoacrylate glue (*Schistocerca*, *Sphinx* & *Bombus*) or beeswax (height < 1 mm) (*Calliphora*), enabling the insect to be suspended on a stiff stainless steel rod (diameter 1.6 mm) in the working section (100mm wide, 105 mm high, 175mm long) of a custom-built, temperature-controlled benchtop closed-circuit wind tunnel (air flow

characteristics reported in(17)). All insects were dorsally tethered except *Schistocerca*, which was ventrally tethered (21).

Flight was initiated by increasing the tunnel air velocity *via* a variable power supply, and adjusting body pitch angle relative to the oncoming airflow *via* a longitudinal rotation of the tether to match literature reported flight postures across the speed range (*Bombus* 15 – 40°*; Schistocerca*; 0 - 15°; *Calliphora*: 0 - 40°; *Sphinx*: 15 - 40°(21-24). Preliminary trials indicated that there were differences in preferred ambient temperature between species, whereby *Bombus* and *Calliphora* performed longer sustained flights at a lower temperature. Therefore, working section temperature was regulated at 20 °C for *Calliphora* (25) and *Bombus* (26) and 30 °C for *Schistocerca* (21) and *Sphinx* (27) *via* a temperature controlled circulator system (5750P41A10E ¾ HP, PolyScience, IL, USA) which circulated fluid through a heat exchanger in the airflow path.

Metabolic Measurements

Air was extracted from the working section of the wind tunnel, passed through a CO_2 analyser (FoxBox, Sable Systems Inc., NV, USA) and returned to the working section, downstream of the extraction location. Insects were flown at multiple randomly selected airspeeds during a single experiment, each followed by a period of rest to allow the rate of CO_2 production to return to baseline resting levels. Each animal was flown once at each specific speed. The concentration of CO_2 was recorded *via* a data acquisition system (Lab Chart and PowerLab, ADInstruments, Oxford, UK) at a sample frequency of 1000 Hz. Fight metabolic rate ($\dot{V}_{CO_2}$, ml min^{-1}) was calculated from the slope of the increasing CO_2 concentration within the tunnel corresponding to the flight period. The system was calibrated by injecting a known volume (0.2 ml) of 100% CO_2 into the excurrent airflow from the analyser, *via* a hypodermic needle(16, 17).

Body mass-specific metabolic power (P_{i}^{*}) was calculated from $\dot{V}_{\mathrm{CO_2}}$ (28) using a species-specific flight respiratory exchange ratio from the literature: *Calliphora*: 1.00 (29); *Schistocerca*: 0.82 (20); *Sphinx*: 0.79 (12); *Bombus*: 1.00 (30). Body mass-specific metabolic cost of transport (COT_{met}^{*}; J kg^{-1} m^{-1}) was calculated to assess relative flight economy across the speed range.

Statistical analysis

To assess whether P_i^* varied with airspeed, metabolic rate-speed relationships were analysed using linear-mixed effects models with individual included as a random effect to take account of repeated measurements on individuals. Four candidate models were considered: linear, quadratic, cubic, and a model derived from aerodynamic theory describing the relationship between mechanical power (*P*) and speed (*U*): $P = c_1 + c_2U^{-1} + c_3U^3$, where c_n are constants (15). The aerodynamic model reflects the theoretical decomposition of aerodynamic power into induced, profile and parasite components. Assuming metabolic power is proportional to mechanical power (i.e. constant efficiency), this functional form was also fitted to the metabolic data. Models were fitted in Python (version 3.14) and compared using the small-sample corrected Akaike's Information Criterion (AICc). The model with the lowest AICc was considered the best supported by the data and was used for subsequent analyses. For *Bombus*, hovering observations were included when fitting empirical models. However, because the aerodynamic model includes a U^{-1} term, it was only fit to forward flight observations. As models were therefore fitted to different data sets, AICc-based model selection was restricted to models fitted to the full data set, and the aerodynamic model fit is reported separately.

The minimum P_i^* and the airspeed at which it occurred (minimum power speed, U_{mp}) were estimated from the fitted relationship between P_i^* and airspeed. The maximum range speed (U_{mr}) was determined from the airspeed at which a line from the origin was tangent to the fitted curve, corresponding to the minimum COT_{met}^*. Confidence intervals for U_{mp}, U_{mr} and P_i^* were estimated using cluster bootstrap resampling of individuals (5000 replicates). Factorial aerobic scope (i.e., maximum P_i^* / minimum P_i^*) was calculated using the fitted model. The relationship between COT_{met}^* and airspeed were obtained by dividing the fitted P_i^* and airspeed relationship by airspeed, rather than fitting a separate model to the COT_{met}^* data. Confidence envelopes for COT_{met}^* were obtained by applying this transformation to predictions from bootstrap replicates of the fitted metabolic power-speed model.

Results

Mass-specific metabolic rate (P_i^*) varied curvilinearly with airspeed in all species (Fig. 1). Model selection indicated that the aerodynamic model provided the best fit for *Sphinx*, whereas the quadratic model provided the best fit for *Bombus*, *Calliphora* and *Schistocerca*. In *Schistocerca*, the aerodynamic model and quadratic model received similar support (ΔAICc = 0.39), indicating that they both fit the data comparatively well. In *Bombus*, the hovering data were retained for the linear and quadratic models, whereas the aerodynamic model was fit only to the forward flight data and the results reported in Supplementary Information (Tables S1, S2). In *Bombus* and *Schistocerca* the relationship was U-shaped across the speed-range studied. In *Calliphora* and *Sphinx*, the relationship was skewed U-shaped: *Calliphora* showed an asymmetrical curve with a steeper increase in P_i^* at higher speeds, while *Sphinx* showed a steeper rise at lower speeds.

The minimum mass-specific metabolic power ($P_{i,min}^*$) and minimum power speed U_{mp} were: *Bombus* 186.5 [146.5-240.4] W kg^{-1} at U_{mp} of 1.79 [95% CI 1.20-2.23] m s^{-1}; *Schistocerca* 73.6 [62.7-89.6] W kg^{-1} at U_{mp} of 2.43 [2.01-2.73] m s^{-1}; *Calliphora* 147.1 [113.8-171.3] W kg^{-1} at U_{mp} of 1.34 [1.21-1.47] m s^{-1}; and *Sphinx* 115.4 [77.3-140.8] W kg^{-1} at U_{mp} of 2.99 [2.77-3.69] m s^{-1} (Table S3). For *Sphinx*, the upper 95% CI is limited to the range of measured airspeeds.

Mass-specific metabolic cost of transport, COT_{met}^*, showed a skewed U-shaped relationship with airspeed in all species, with a steeper rise at lower speeds (Fig. 1). In all species the minimum COT_{met}^* occurred within the range of airspeeds tested. The estimated P_i^* at the maximum range speeds (U_{mr}) were: *Bombus* 231.0 [168.7-319.9] W kg^{-1} at U_{mr} 2.83 [2.48-3.39] m s^{-1}; *Schistocerca* 86.4 [71.4-105.0] W kg^{-1} at U_{mr} 3.39 [3.16-3.75] m s^{-1}; *Calliphora* 158.3 [121.6-188.4] W kg^{-1} at U_{mr} 1.57 [1.44-1.69] m s^{-1}; and *Sphinx* 125.2 [80.5-149.6] W kg^{-1} at U_{mr} 3.63 [3.05-3.69] m s^{-1} (Table S3). For *Sphinx*, the upper 95% CI is limited to the range of measured airspeeds.

Factorial aerobic scope across the speed range in *Bombus* was 2.13, in *Schistocerca* 1.30, in *Calliphora* 6.40 and in *Sphinx* 1.80 (Table S3).

Discussion

Quantification of metabolic rate during flight in a range of insect species provides strong evidence to support the hypothesis that P_{i}^{*} varies with flight speed. Metabolic power-speed relationships in both tethered and free-flying *Bombus terrestris*(17), free-flying *Eristalis tenax* (18), tethered *Schistocerca gregaria* (20) and data compiled from several studies on both free and tethered honeybees (*Apis mellifera*) flights (31) also support our findings that P_{i}^{*} does vary with airspeed. This finding, contrasts with an earlier complete dataset on a free flying insect species (*Bombus spp.*), where no clear change P_{i}^{*} occurred with varying airspeed, though the authors noted that a shallow U-shaped curve was observed in some individual bees (16). Therefore, we deduce that the general pattern of airspeed-dependence of metabolic power observed in vertebrates is also present in various flying insect species. Nevertheless, the shape of the curve describing flight energetics does vary with species, ranging from a U-shaped to a skewed U-shaped curve, which may have important ecological implications. However, this variation could also result from the speed range over which flight could be induced in the laboratory – for example, a skewed U-shaped curve may simply represent a truncated U-shaped curve. In addition, inter-specific differences in wing morphology (e.g. wing loading and aspect ratio), are expected to influence the relative contributions of induced and parasite power, and therefore the shape of the power-speed relationship. In *Bombus* and *Schistocerca* the metabolic power-speed curve follows a U-shape, as has been observed in flying vertebrates (4, 32) and as is expected from the relationship between mechanical power and flight speed (3). However, in *Calliphora* and *Sphinx*, the U-shaped relationship did not extend to low speeds and high speeds, respectively. This is discussed below.

i) Economical insect flight energetics

a) Bombus

Bombus P_{i}^{*} overlaps the range previously reported (250 – 500 W kg^{-1}; (16, 33, 34), and confirms that hovering and high-speed flight incur a higher energetic costs than intermediate-speed forward flight (16). This aligns with estimates of the mechanical power

requirements across the speed range (14). The U-shaped curve in tethered *Bombus* contrasts with an earlier reports of speed-independent P_{i}^{*} in freely flying bumblebees (16). We speculate that the true relationship between metabolic power and speed may have been obscured in that study (16) due to the use of different castes and species, whereas our study and that of Senior et al. (17) used a single worker caste. We measured a factorial aerobic scope of 2.13 for *Bombus*; however, studies involving loaded flights indicate that metabolic rate can be increased further still, to accommodate the energetic demands of carrying nectar and pollen (35). Foraging requires travel to and from the nest, across considerable distances. Radar-tracked bumblebees have been shown to fly up to 7 km per day when foraging (36), highlighting the ecological importance of flight energetics. Our finding that U_{mr} (U_{mr} = 2.83 m s^{-1}), occurs within the preferred flight speed range in free-flying *Bombus* (2.1 - 4.2 m s^{-1}) (37), provides evidence for a behavioural adaptation that minimises energy use during foraging. Natural foraging flight speed may reach 7 m s^{-1} (38) which, by extrapolation of U-shaped flight power relationship, is expected to be metabolically expensive. This indicates that factors other than minimising metabolic energy expenditure may also affect flight behaviour, though when loaded it may be advantageous to fly faster than when unloaded(39). Nevertheless, there appears to be a strong selection pressure in *Bombus* for low metabolic flight costs across the wide preferred speed range, thereby conferring benefits to foraging energetics, with knock-on benefits to the survival of both the individual and the success of the colony.

b) <u>Schistocerca</u>

Schistocerca P_{i}^{*} (73 – 100 W kg^{-1}) falls within the range previously reported during tethered flight (54 – 163 W kg^{-1}; (20, 40). The observed U-shaped relationship indicates that increased effort is required at the extremes of the speed range. While our tethered protocol resulted in flight behaviour at airspeeds as low as 1.67 m s^{-1}, previous studies suggest that a minimum airspeed of approximately 3 m s^{-1} is required for tethered *Schistocerca* to generate sufficient lift to support body weight (41). Therefore, at speeds below 3 m s^{-1} P_{i}^{*} may include an energetic component associated with additional thrust generation, as the animal attempts to accelerate to the minimum flight speed. Preferred free-flight speeds are reported at 3.5 – 4.2 m s^{-1} (21), which is similar to the speed corresponding to the minimum COT_{met}^{*} (U_{mr} 3.39 m s^{-1}), and align with field estimates of migratory flight speeds (42). This suggests that

minimising metabolic cost per unit distance travelled is a key factor for speed selection in flying locusts, a finding that is consistent with optimisation of long-range migratory flights.

c) Calliphora

Calliphora flight energetics follow a pronounced skewed U-shaped relationship with airspeed, consistent with estimates of the mechanical power requirements of *Drosophila* flight (13), another Dipteran that, despite c.100x smaller body mass, shares similar flight kinematics (43). The skewed U-shaped metabolic power-speed relationship (as opposed to a U-shaped curve) may reflect the limited range of speeds over which data were collected (44), rather than that the absence of a U-shaped relationship altogether. However, it has also been argued that in smaller species of flying animals, the power curve is inherently more asymmetrical (skewed U-shaped) as their minimum power requirements are similar to those of hovering (45, 46).

Minimising the cost of flight again appears to be a key determinant of speed selection. During free-flight, *Calliphora* exhibits *a* mean horizontal flight speed of 1.2 ± 0.5 m s^{-1}, with a maximum voluntary speed of 2.4 m s^{-1} (47). The speeds corresponding to both minimum power (U_{mp} 1.34 m s^{-1}) and minimum COT^{*}_{met} (U_{mr} 1.57 m s^{-1}) lie within the range of typical voluntary flight speeds reported for freely flying flies, suggesting that routine flight speeds are closely aligned with those that minimise energetic cost. In contrast, the maximal voluntary speed of 2.4 m s^{-1} would incur a substantially higher energetic cost, corresponding to a 1.7-fold higher COT^{*}_{met} than when flying at U_{mr}. Our inclusion of high-speed data (>2.4 m s^{-1}), also elicited in a previous study on lift production (48), provides an opportunity to quantify the energetic implications of strenuous flight performance, without requiring additional experimental manipulations such as adding loads (35) or changing air density (49). This contrasts with the other species studied in this paper, where their maximum flight speeds are beyond the capabilities of the wind tunnel. Interestingly, *Calliphora* exhibits a very large 6.4x factorial aerobic scope – the highest of the species quantified in this paper, and substantially higher than values reported in birds [e.g. 1.13x in the cockatiel (*Nymphicus hollandicus*) (4) and 1.31x in the budgerigar (*Melopsittacus undulates*) (32)]. However, within the preferred speed range of *Calliphora*, the aerobic scope is 1.44x, which is comparable to other flying taxa. The increase in metabolic rate at high flight speeds could be the result of an increase in the

mechanical power requirements of flight, a reduction in the overall mechanical efficiency of flight, or a combination of these effects. We speculate that *Calliphora*'s intrinsic reserve of metabolic power may support the energetic demands of strenuous flight, such as flying in turbulent air flows, performing sharp manoeuvres (43) and accelerating (47).

d) Sphinx

The decline in flight metabolic power with increasing forward speed in *Sphinx*, as indicated by the skewed U-shaped P_i^* curve, is surprising from an energy optimisation perspective, given that hawkmoths are highly specialised for feeding while hovering (50). In contrast to *Bombus*, flight economy in *Sphinx* is attuned to high-speed forward flight, making low speed flight relatively costly. Our fitted mass-specific metabolic power curve for *Sphinx* was broadly congruent with published hovering data. Extrapolation of the fitted model to slow flight speeds indicated that the reported hovering mass-specific metabolic power in a comparably sized freely hovering sphingid hawkmoth (418 ± 125 W kg^{-1}; (12) would occur at a predicted airspeed of 0.83 m s^{-1} (≈0.6-1.2 m s^{-1} across the reported range), i.e. a forward speed close to hovering.

While high-speed flight is relatively inexpensive, previous reports suggest that the preferred flight speed in *Sphinx* is surprisingly slow, at 1.8 m s^{-1} (51). In contrast, the similarly sized tobacco hawkmoth (*Manduca sexta*) has a preferred flight speed of 3.2 m s^{-1} (51), which aligns closely with the speed at which minimum COT_{met}^* occurs in *Sphinx* (U_{mr} = 3.63 m s^{-1}). In fact, the reported preferred speed in *Sphinx* (51) appears unusually slow compared to other hawkmoths. By plotting a line of best fit between preferred speed and body mass across 5 other species (51), we estimate a preferred speed in *Sphinx* of 2.8 m s^{-1} (Fig. 1H), which is similar to our quantified U_{mr}. This discrepancy raises the possibility that *Sphinx* does fly unusually slowly in the field, or that preferred speed is strongly influenced by laboratory conditions (52). Bearing in mind this limitation, minimising the cost of locomotion again appears to be a key criterion of hawkmoth flight speed selection.

ii) Ecological significance of flight speed selection

This study highlights the critical role of flight speed in insect flight energetics and provides unique insight into the physiological basis of the behavioural ecology. Our findings provide valuable new data for modelling approaches that aim to predict patterns of animal movement and the effects of environmental perturbations. Our experimentally derived metabolic power curves can be used to estimate flight costs and foraging economy, and to predict migratory flight speeds.

The relatively shallow metabolic power-speed curves in *Bombus* and *Schistocerca* indicate that they have physiological and/or morphological adaptions that support a relatively stable energetic cost of flight over a relatively wide speed range, consistent with the extended foraging trips and migratory flights in these species. However, the most energetically favourable strategy may not actually be the one favoured in the field. For example, skylarks (*Alauda arvensis*) fly faster than the predicted U_{mr} during migration but, as also observed for most birds (53), conform to U_{mp} during short flights (54). Flight speed in birds seems flexible and context-dependent, as also observed in Kuhl's pipistrelle bat *Pipistrellus kuhlii* (55). Our data indicate that flight speed selection has a strong metabolic basis, with the speed that minimises the cost of locomotion generally falling in the range of observed speeds in the field. Whether insect flight speed selection varies during flights with different motivations, e.g. foraging, migration, courtship, and seasonal and loaded flight, remains less clear. For example, *Bombus terrestris* has been observed foraging at speeds up to 7 m s^{-1} (38), indicating that energetic economy may not always be the principal determining factor in speed selection. Our laboratory-based approach to quantifying flight energetics has provided a basis for further field studies that should investigate the free-ranging speeds that insects use, and whether the patterns of speed selection observed in vertebrates also occurs in this enormously morphologically and physiologically diverse invertebrate class.

iii) Effects of tethering on flight energetics

Tethering may cause an underestimation of flight metabolic rate by ~ 55% (56), likely because tethered insects fail to generate sufficient lift to support their body weight (57). Furthermore, the tethering attachment and stiff-wire apparatus may disrupt local airflow across the insect body and wings, potentially causing increased drag at higher speeds. Despite

these limitations, tethering remains essential for physiological or biomechanical studies as many insects are unable to sustain flight in confined spaces, such as the working section of a wind tunnel. In this study, tethering was required for most species, since most could not maintain forward flight within the confined space without repeatedly colliding with the tunnel walls. A notable exception is *Bombus*, which could perform free-flight, but was also tethered to ensure consistent experimental conditions across all species. A companion study by the authors (17) demonstrates that whilst the magnitude of P_{i}^{*} at any given speed may be reduced during tethering, the overall shape of the metabolic power-speed relationship is unaffected. In contrast, deciphering the effects of tethering on the shape of the metabolic power-speed curve is not possible for the other species in this paper. Confidence in our inferred trajectories of P_{i}^{*} across airspeeds in *Bombus, Calliphora* and *Sphinx* comes from the remarkable similarity to the overall shape of the modelled (13, 14) and measured (15) mechanical power-speed relationships for untethered flight. This similarity suggests that the U-shaped pattern of power generation is preserved during both free- and tethered flight even if the absolute magnitude of P_{i}^{*} is reduced by tethering. While the overall shape of the metabolic-power speed relationship is similar in free- and tethered- flight, (17), the lower magnitude of tethered P_{i}^{*} shifts the estimated U_{mr} to slower speeds, and therefore caution is warranted in drawing conclusions about flight behaviour in the field from tethered-flight energetics measurements. Despite the constraints of tethering, the consistency of the shape-of the metabolic power-speed curve between tethered and free-flights in *Bombus* indicates that this approach is effective for quantifying the overall shape of the relationship between flight energetics and speed in insects that could not otherwise be studied in free-flight.

Conclusion

Our characterisation of the airspeed-dependence of metabolic rate across a range of insect species supports the existence of a U- or skewed U-shaped metabolic power curves in insects. These findings show clear parallels with flight energetics in vertebrates, reflecting the shared physical constraints associated with powered flight. Minimising the metabolic cost of flight emerges as a key criterion in insect flight speed selection, offering new insights into the physiological underpinnings of insect behaviour, ecology and evolution.

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Figure 1. Metabolic requirements of insect flight across a speed range. Mass-specific metabolic power (P_{i}^{*}; W kg^{-1}) and mass-specific cost of transport (COT_{met}^{*}; J kg^{-1} m^{-1}) are

shown as a function of airspeed for bumblebee, *Bombus terrestris* (A, E), desert locust, *Schistocerca gregaria* (B, F), blowfly, *Calliphora vicina* (C, G), and privet hawk moth, *Sphinx ligustri* (D, H). Each marker represents a datapoint from a single individual. Reported preferred flight speeds are indicated by the grey shaded regions. The minimum power speed (U_{mp}) is indicated by the green symbol with 95% confidence intervals shown by the green shaded region; the maximum range speed (U_{mr}) is indicated by the purple symbol and 95% confidence intervals shown by the purple-shaded region. Solid lines represent the best-supported model fits (based on AICc; Table S1), with upper and lower 95% confidence intervals indicated by the dashed lines.