

A COMPARISON OF MECHANICAL AND ENERGETIC ESTIMATES OF FLIGHT COST FOR HOVERING SPHINX MOTHS

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SUMMARY

Mechanical power output, based on measured power input, is compared with calculated values for aerodynamic and inertial power output in sphinx moths ranging from 350 to 3400 mg. Aerodynamic power output, calculated from momentum and blade-element aerodynamic theories, scales with the 1.08 power of body mass, amounting to about 40% of the mechanical power output of large moths to about 15% in the smallest individuals. Calculated value for the inertial power cost of hovering represents a larger fraction of the mechanical power output than the aerodynamic cost in all moths, with the value increasing as body mass decreases. Independent estimates of inertial power output based on metabolic data are similar to those obtained from calculations of the moment of inertia for the wings. These data suggest that inertial power output represents the largest power requirement for hovering sphinx moths, and that elastic torques do not significantly reduce the mechanical power output. Higher mass-specific power input of small sphinx moths appears to be the result of greater mass-specific inertial power requirements. Estimates of flight cost based on morphology and flight mechanics of sphinx moths yield values for mechanical power output which are similar to values estimated from their flight metabolism.

INTRODUCTION

A recent study by Torkel Weis-Fogh (1973) has provided a quantitative basis for estimating the aerodynamic and inertial power output of hovering animals based on aerodynamic theory. While providing a lucid overview of the subject, his approach is complicated by a variety of assumptions and the need for accurate information about the morphology and wing stroke characteristics of the hovering animals. Moreover, several assumptions implicit in the blade-element theory, which forms the basis of Weis-Fogh's analysis, limit its usefulness in interpreting force generation in slow-flying insects due to the importance of unsteady aerodynamics (see Ellington, 1978; Rayner, 1979, for further discussion). The theory has been difficult to evaluate because metabolic data for hovering animals is relatively scarce and, in most cases, the morphology of the animals used in metabolic experiments is only approximately known.

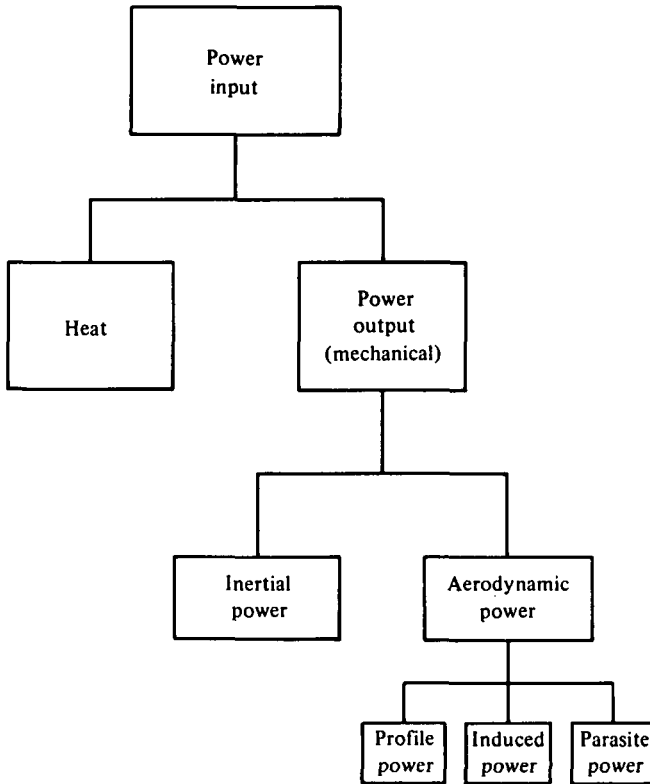


Fig. 1. Pathway for energy expenditure in a flying insect. Mechanical power output represents the sum of aerodynamic and inertial power requirements. Aerodynamic power output is a combination of the power required to accelerate air through the wing disc (induced power), the power required to overcome wing drag (profile power), and body drag (parasite power). For hovering animals, since there is no forward speed, parasite power requirements are negligible.

Sphinx moths are excellent animals for studying hovering flight because they hover continuously in a confined space. In the past decade, several studies of the energetic cost of hovering of sphingids have been reported (Heinrich, 1971; Heinrich & Casey, 1973; Casey, 1976*a, b*; Bartholomew & Casey, 1978). Detailed analysis of wing stroke characteristics revealed by high-speed cinematography indicates that the flight dynamics of *Manduca sexta* (Johan) during hovering conform to the characteristics of 'normal hovering' described by Weis-Fogh (1973).

The flight cost for a hovering insect represents all energy not directly converted to heat as a result of muscle inefficiency and is a result of several different factors (Fig. 1), the sum of which may be called the mechanical power output. Included in the mechanical power output is the energy expended to overcome the aerodynamic drag forces. These are the profile power output (power necessary to overcome the drag of the wings) and the induced power output (the power necessary to accelerate air downward through the wing disc to counteract the gravitational force). A third aerodynamic power cost required to overcome drag on the body (parasite power), is insignificant during hovering since there is no forward speed (Pennycuik, 1969). \square

In addition to the aerodynamic power requirements, which represent work done on the surrounding air, a further component of the flight cost is the inertial power output (the power necessary to accelerate and decelerate the wing mass). The importance of inertial power to the flight cost of hovering insects is disputed. Sotovolta (1947, 1952) suggests that inertial forces represent the major power requirements for medium and large insects. In contrast, Weis-Fogh (1961, 1965, 1972, 1973) suggests that inertial power requirements are counteracted by an elastic system present in the insect thorax.

The central position of the total mechanical power output, between the flight metabolism and the various mechanical factors which determine its magnitude, makes it possible to estimate $P_{o,m}$ by two entirely different means. Physiologists measuring energy metabolism can estimate the mechanical power output by assuming an efficiency for the flight muscles. Students of aerodynamics and fluid mechanics can use one of several methods (Ellington, 1978), to calculate the mechanical costs involved based on morphometric and wing stroke data.

It is generally assumed that the metabolism of hovering sphinx moths during flight is related to flight effort, yet no complete evaluation of the flight effort is currently available for sphinx moths. The present analysis was undertaken in an attempt to explain two sets of observations which on the surface appear paradoxical. First, hovering sphinx moths have among the highest mass-specific power inputs ever measured (Casey, 1976*a*) yet their calculated aerodynamic power requirements for hovering are among the lowest (Weis-Fogh, 1973; Rayner, 1979). Second, the mass-specific power input of hovering sphingids is inversely related to body mass (Bartholomew & Casey, 1978), while the mass-specific aerodynamic power requirements are independent of body mass (Weis-Fogh, 1961, 1973, 1977; Lighthill, 1974). In a recent study, Bartholomew & Casey (1978) reported energy metabolism and morphometric data of hovering sphinx moths over a wide size range, and wing-beat frequencies of the moths from the same experiments. The present analysis uses data of Bartholomew & Casey (1978) coupled with aerodynamic theories (Pennycuick, 1969; Weis-Fogh, 1973; Ellington, 1978) to quantify the components of mechanical power output of hovering sphingids. Mechanical power output is also estimated from data on flight metabolism in an attempt to make generalizations about the effect of body size on hovering flight cost within a group of geometrically similar animals. Finally, the relative importance of inertial power output in relation to body size is examined, based on two different methods of calculation.

MATERIALS AND METHODS

Symbols and terminology. The various parameters used in this analysis along with their symbols are given in Table 1. Any power output terms utilize a double subscript (eg. $P_{o,a}$, $P_{o,m}$) where the subscript 'o' is used to designate output. This terminology is used to avoid confusion with such terms as P_i , which has been used to designate the power input or metabolic rate (Tucker, 1973; Casey, 1976*a*), the inertial power output (Weis-Fogh, 1972, 1973) or the induced power (Pennycuick, 1969; Rayner, 1979). Mechanical power output is calculated as the product of power input \times muscle efficiency ($P_{o,m} = P_i \times E_m$). A second estimate of mechanical power output, cal-

Table 1. *Symbols and notation used in the present study. Symbols followed by an asterisk (e.g., $P_{o,a}^*$) denote mass-specific values*

P_i	Power input (flight metabolism)
E_m	Efficiency of energy conversion in flight muscle
E_f	Flight efficiency ($P_{o,a} \div P_i$)
$P_{o,m}$	Mechanical power output (flight metabolism $\times E_m$)
$P_{o,in}$	Induced power output (calculated, momentum theory)
$P_{o,pro}$	Profile power output (calculated, blade-element theory)
$P_{o,a}$	Aerodynamic power output ($P_{o,in} + P_{o,pro}$)
$P_{o,i}$	Inertial power output (mechanical estimate)
$P_{o,m} - P_{i,a}$	Inertial power output (metabolic estimate)
$P_{o,a}/P_{o,m}$	Dynamic efficiency (metabolic)
$P_{o,a}/P_{o,a+i}$	Dynamic efficiency (mechanical)
$P_{o,a+i}$	Mechanical power output (assuming no elastic torque)

culated as the sum of the aerodynamic and inertial power components, is indicated as $P_{o,a+i}$. This parameter represents the total mechanical power output only if elastic torques are negligible (see Weis-Fogh, 1972, 1973, for further discussion).

Data and calculations. The data (Table 2) comprise morphometric and wing stroke data of Bartholomew & Casey (1978, Table 8) together with previously unpublished data of these authors, for the same moths. Efficiency of the flight muscles during hovering is assumed to be 0.2, and independent of body size. The stroke amplitude (θ) is assumed to be 2.09 radians and independent of body mass (Weis-Fogh, 1973). Metabolism of support systems (see Tucker, 1973) is assumed to represent an insignificant fraction of the metabolic cost of hovering, since standard metabolism of resting moths is more than two orders of magnitude lower than metabolism in hovering moths (Zebe, 1954; Bartholomew & Casey, 1978). Ventilation in sphinx moths appears to be a direct result of thoracic deformations associated with wing movement (Weis-Fogh, 1967), and circulation appears to be controlled in relation to heat stress during flight (Heinrich, 1970).

The induced power requirements of the hovering moths were calculated by the momentum theory of helicopter aerodynamics (Pennycuick, 1968), using a wing disc area calculated from the stroke angle (θ) of the wings (Ellington, 1978). Profile power output (Weis-Fogh's uncorrected value), was calculated according to blade-element theory (Weis-Fogh, 1973). Inertial power output, moment of inertia, and dynamic efficiency were calculated by the method of Weis-Fogh (1973).

RESULTS

Aerodynamic power. Calculated values for all power components are given in Table 3. Aerodynamic power components during hovering are shown in relation to body mass in Fig. 2. The induced power component corrected for the area swept by the wings is about 16% greater than the momentum jet estimate. The total induced power requirements vary from about 5 mW for a 0.3 g sphinx moth to about 40 mW in a 4 g moth. Profile power calculated by entirely different methods and theory is similar both in magnitude and in scaling to induced power (Fig. 2*b*). Both components scale with an exponent of about 1.1, and consequently the mass-specific aerodynamic

Table 2. *Morphologic, wing stroke and derived parameters for hovering sphinx moths*

Moment of inertia (I) and the ratio of maximal inertial to aerodynamic work (N) calculated by the method of Weis-Fogh (1973). Other data from Bartholomew & Casey (1978)

	Body mass (g)	Wing Length (mm)	Wing stroke frequency (s ⁻¹)	Wing weight (mgf)	Moment of inertia (g·cm ² × 10 ⁴)	N
<i>Manduca rustica</i>	2.92	62	—	171	5.68	4.6
<i>M. rustica</i>	2.70	60	29	144	4.40	5.6
<i>M. corallina</i>	1.31	54	29	91	2.25	5.7
<i>M. corallina</i>	1.29	53	32	88	2.09	7.8
<i>M. corallina</i>	1.39	54	25	91	2.26	4.4
<i>M. corallina</i>	2.48	65	26	146	4.87	5.0
<i>M. lefeburei</i>	0.57	43	33	31	0.49	5.2
<i>Protambulyx strigilis</i>	1.12	53	—	75	1.78	7.1
<i>P. strigilis</i>	1.26	60	—	76	2.31	4.9
<i>Erinnyis ello</i>	1.21	40	24	47	—	—
<i>Pachylia ficus</i>	3.22	67	—	152	5.79	4.8
<i>Madoryx oculus</i>	1.49	37	43	46	—	—
<i>M. oculus</i>	1.90	46	41	68	1.21	5.3
<i>Perigonia lusca</i>	0.86	30	66	25	0.19	8.1
<i>P. lusca</i>	0.51	27	—	72	0.44	—
<i>Enyo ocypete</i>	0.57	27	—	26	—	—
<i>E. ocypete</i>	0.36	26	—	25	0.14	10.0
<i>E. ocypete</i>	0.33	25	—	25	0.13	12.1
<i>E. ocypete</i>	0.39	27	56	30	0.18	14.0
<i>E. ocypete</i>	0.40	27	—	17	0.12	6.5
<i>Oryba achemenides</i>	2.23	56	41	104	2.76	8.1
<i>O. achemenides</i>	3.39	57	39	121	3.35	6.2
<i>Pachygonia drucei</i>	0.70	37	48	35	0.41	9.1
<i>Xylophanes libya</i>	0.56	39	48	29	0.37	6.9
<i>X. chiron</i>	0.95	39	—	38	0.49	5.7
<i>X. pluto</i>	0.83	43	—	50	0.78	8.3
<i>X. pluto</i>	0.88	41	40	30	0.42	4.2
<i>X. pluto</i>	0.78	37	50	23	—	5.9

power (the sum of $P_{o,tn}$ * and $P_{o,pro}$ *) is essentially the same for all sphingids regardless of body size.

Mechanical power output and dynamic efficiency. Assuming that sphinx moths hover at similar flight-muscle efficiencies, the metabolic data of Bartholomew & Casey (1978) are converted to estimates of the total mechanical power requirements for flight (Table 3). Mechanical power output ($P_{o,m}$) varies from about 35 mW in a 0.335 g moth to 235 mW in a 3.4 g moth (Table 3). Since $P_{o,m}$ of moths are multiples of the metabolic rate during flight, they show similar scaling properties, varying with body mass to the 0.77 power (Fig. 3). Also shown in Fig. 3 are the summed components of aerodynamic power (profile and induced powers). In general, aerodynamic power requirements represent only a small portion of the mechanical power requirements.

The dynamic efficiency (η) for hovering flight of sphinx moths ($P_{o,a}/P_{o,m}$) indicates the relative magnitude of aerodynamic to total mechanical power requirements. For all sphinx moths, aerodynamic cost amounts to less than half of the mechanical power output. The mean for all sphinx moths (Table 3) is 25% + 9.3 s.d. Fig. 3 gives the

Table 3. *Calculated power requirements (mW) for hovering sphinx moths*

Species	$P_{o,m}$	$P_{o,tn}$	$P_{o,pro}$	$P_{o,a}$	$P_{o,a+t}$	$P_{o,m}$		$P_{o,a}$	
						$P_{o,a}$	$P_{o,t}$	$P_{o,m}$	$P_{o,a+t}$
<i>Manduca rustica</i>	149	33	25	58	145	91	87	0.39	0.40
<i>M. rustica</i>	168	33	23	56	168	112	112	0.33	0.33
<i>M. corallina</i>	56	12	10	23	66	33	43	0.41	0.35
<i>M. corallina</i>	166	11	10	21	86	144	64	0.13	0.25
<i>M. corallina</i>	79	12	10	22	53	57	31	0.28	0.42
<i>M. corallina</i>	166	25	19	44	118	122	74	0.26	0.37
<i>M. lefeburei</i>	48	4	4	8	22	49	14	0.17	0.36
<i>Protambulyx strigilis</i>	68	9	11	20	75	48	54	0.38	0.27
<i>P. strigilis</i>	—	9	15	24	64	—	40	—	0.37
<i>Erinnyis ello</i>	63	14	—	—	—	—	—	—	—
<i>Pachylia ficus</i>	216	35	25	60	158	155	97	0.28	0.38
<i>Madoryx oecus</i>	139	20	—	—	—	—	—	—	—
<i>M. oecus</i>	124	23	18	41	115	83	74	0.33	0.35
<i>Perigonia lusca</i>	81	11	8	19	76	62	58	0.23	0.24
<i>P. lusca</i>	—	6	5	10	—	—	—	—	—
<i>Enyo ocypete</i>	44	7	—	—	—	—	—	—	—
<i>E. ocypete</i>	47	6	3	9	41	39	33	0.17	0.20
<i>E. ocypete</i>	42	3	2	5	32	36	29	0.13	0.17
<i>E. ocypete</i>	35	4	3	7	42	29	35	0.18	0.15
<i>E. ocypete</i>	—	4	3	7	22	—	15	0.21	0.24
<i>Oryba achemenides</i>	238	24	27	51	212	187	161	0.21	0.24
<i>O. achemenides</i>	235	44	33	77	267	157	190	0.33	0.29
<i>Pachygonia drucei</i>	71	6	6	12	56	59	44	0.17	0.22
<i>Xylophanes libya</i>	45	4	7	11	41	34	29	0.25	0.38
<i>X. chiron</i>	—	10	7	17	51	—	34	—	0.33
<i>X. pluto</i>	55	7	7	14	58	42	45	0.25	0.24
<i>X. pluto</i>	91	8	7	15	35	76	20	0.17	0.43
<i>X. pluto</i>	75	—	6	—	—	—	—	—	0.32

difference in scaling for aerodynamic and mechanical power outputs. Dynamic efficiency is positively correlated with body mass, indicating that as body size decreases a larger fraction of the mechanical power output appears to be used for other than, overcoming aerodynamic power requirements (Fig. 3). In the smallest sphingids, $P_{o,a}$ accounts for only about 15–20% of the total mechanical power output, while for moths having body mass in excess of 2 g, the efficiency increases to between 30 and 40% (Table 3).

Inertial power. In addition to power required to overcome aerodynamic drag forces, power must be expended to accelerate and decelerate the wing mass at the extremes of the stroke. Weis-Fogh (1972, 1973) has used $P_{o,a+t}$ as an estimate of mechanical power output, pointing out that if there are significant elastic torques occurring during the wing stroke, these torques will tend to compensate for inertial power costs and result in $P_{o,a+t}$ representing an overestimation of the mechanical power requirements. Therefore, it is useful to compare calculated values of inertial power requirements ($P_{o,i}$) based on mechanical and wing stroke data with estimates based on $P_{o,m} - P_{o,a}$. The latter value should help determine whether calculated values of inertial power output are reasonable, thereby providing information as to whether or not an elastic system is operational. This is basically the approach used by Weis-Fogh (1973; Table 5).

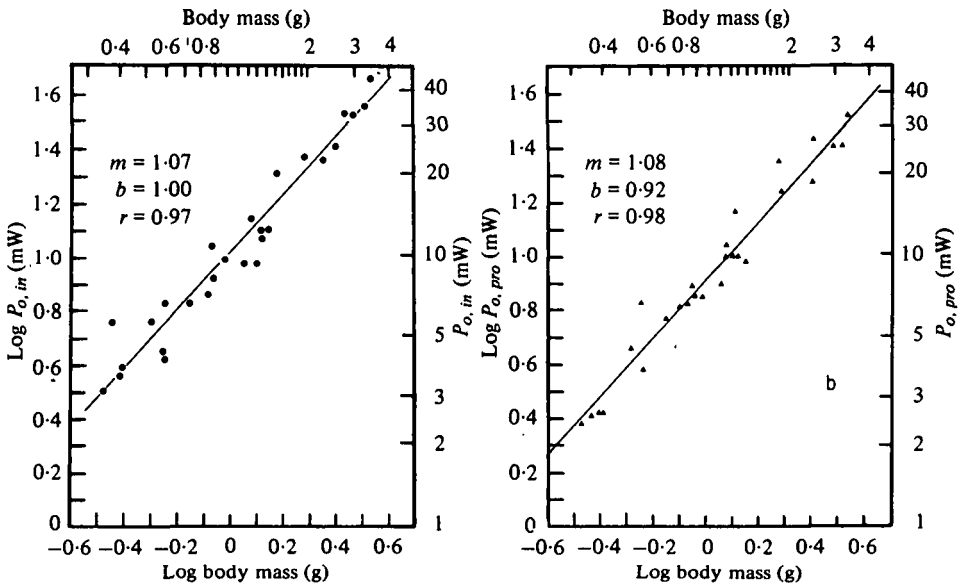


Fig. 2. (a) The relation of induced power output of sphinx moths to body mass. Lines in this and in subsequent figures are fitted by linear regression, where $\log y = m \log X + b$, r = correlation coefficient. (b) The relation of profile power to body mass in sphinx moths calculated by blade-element theory.

Inertial power outputs obtained by the two methods are generally similar (Table 3). Both parameters exhibit exponents on body mass of less than 1.0 (Fig. 4 *a, b*), indicating that as body size decreases, mass-specific inertial power requirements for a small sphinx moth are greater than for a large moth. As shown in Fig. 5, the estimates of flight cost based on calculations of mechanical power requirements ($P_{o,a+i}$) are very similar to those which are obtained from metabolic data ($P_{o,m}$), suggesting that calculations of $P_{o,i}$ are realistic and that elastic torques are not significant in reducing the $P_{o,i}$ of hovering sphinx moths. The dynamic efficiencies obtained by the two methods are generally similar, and both sets of data decrease as body mass decreases (Fig. 6).

DISCUSSION

Aerodynamic power output. The mechanism of lift production by hovering insects has been disputed. The presence of unsteady aerodynamics during the wing stroke has led to criticism of both the momentum and blade-element theories as being too simple (Ellington, 1977, 1978; Rayner, 1979). However, for the present discussion this controversy is of little consequence, since calculated values for aerodynamic power output are approximately the same regardless of the theory used to calculate them. Since the induced power at maximum represents only about 20% of the total mechanical power output (Table 3), a change of 20% in $P_{o,in}$ results in only about a 4% change in $P_{o,m}$. Any errors which are introduced are liable to be systematic (all values of $P_{o,in}$ scale with mass to approximately the 1.1 power, regardless of the method of calculation), and therefore should not affect the scaling argument.

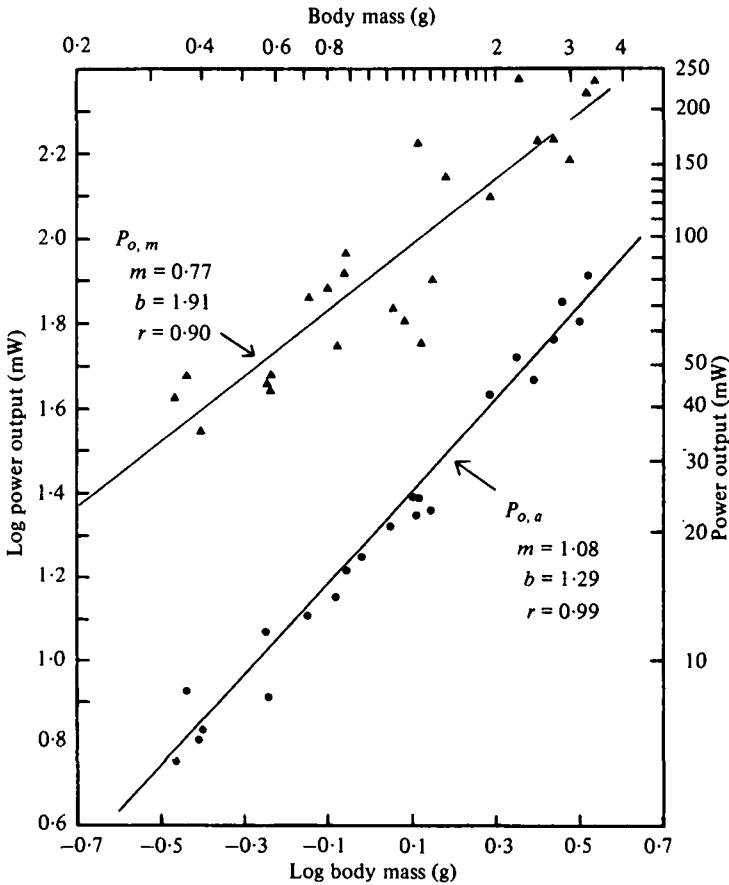


Fig. 3. The relations of aerodynamic power output (the sum of induced and profile power from Figs. 2 a, b) and total mechanical power output (derived from metabolic data) to body mass in sphinx moths.

Aerodynamic power requirements of hovering sphinx moths account for a smaller fraction of the metabolic rate as body size decreases. Flight efficiency ($P_{o,a}/P_i$) decreases from 7.4% in a 4 g sphinx moth to 3.3% in a 0.3 g sphingid. Assuming that the mechanical power output is an accurate index of the total power requirements and that the efficiency of flight muscle to convert energy into work does not vary systematically with size, these results suggest that small moths expend larger fractions of their mechanical power output on inertial power requirements.

Inertial power output. The similarity (Fig. 4 a, b) between calculated inertial power output ($P_{o,i}$) and the mechanical energy not accounted for by aerodynamic power requirements ($P_{o,m} - P_{o,a}$) suggests that inertial power requirements represent a greater cost for hovering sphinx moths than do aerodynamic power requirements. This conclusion is strengthened by the fact that aerodynamic and inertial power requirements scale differently with body mass, and when added together provide an explanation for the observed inverse relationship between mass-specific power input and body mass of hovering sphinx moths, both within and between species (Casey

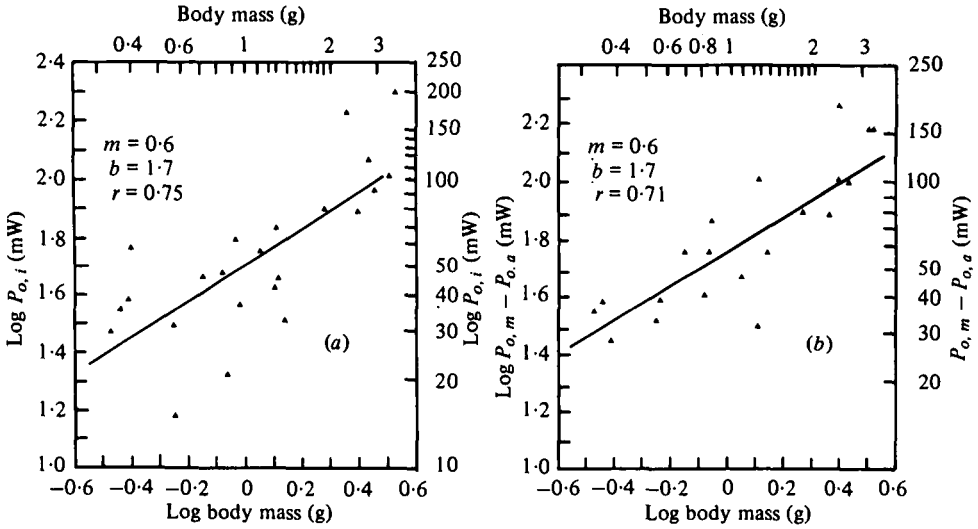


Fig. 4. (a) The relation of inertial power output ($P_{o,i}$) to body mass in sphinx moths in the absence of elastic torques. $P_{o,i}$ was calculated based on the moment of inertia of the wings. (b) The relation of inertial power output estimated as the difference between total mechanical and aerodynamic power requirements (Fig. 3), to body mass in sphinx moths.

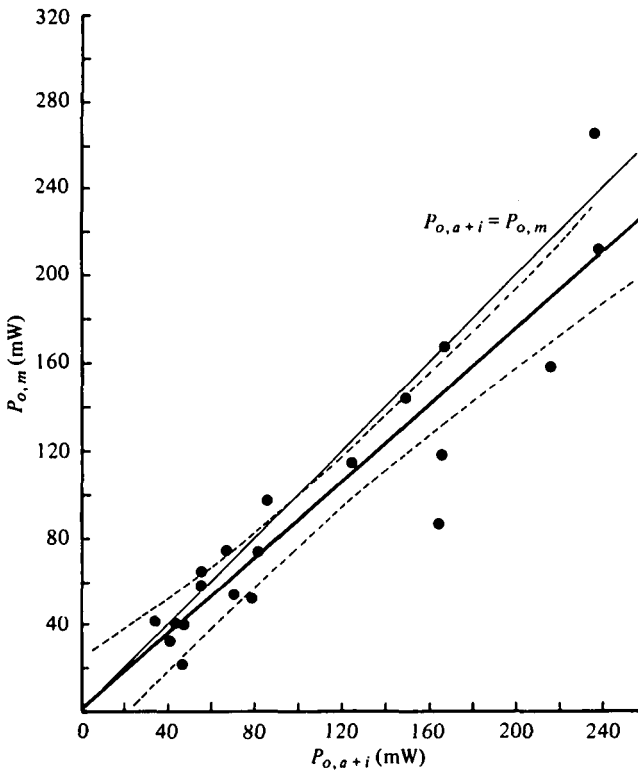


Fig. 5. The relations of total mechanical power output of hovering sphinx moths based on flight mechanics ($P_{o,a+i}$), to metabolic data ($P_{o,m}$). Curved lines indicate 95% confidence interval.

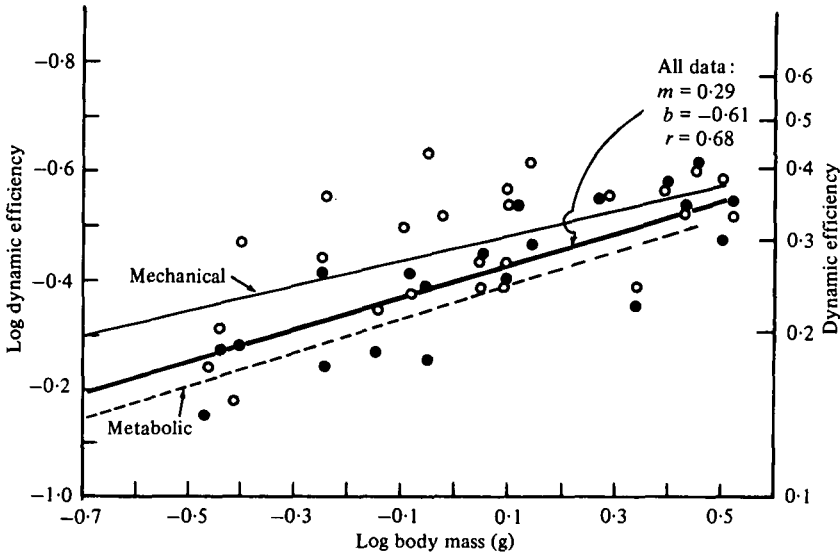


Fig. 6. A comparison of the relations of dynamic efficiency, the ratio of aerodynamic power to total mechanical power output of hovering sphinx moths, to body mass. Open circles = metabolic estimate ($P_{o,a}/P_{o,m}$). Filled circles = mechanical estimate ($P_{o,a}/P_{o,a+t}$). Heavy line indicates the regression of all data in relation to body mass. At the 95% confidence level the two regression lines are not significantly different ($F = 1.47$; $P > 0.05$).

1976*b*; Bartholomew & Casey, 1978). Since mass-specific aerodynamic power requirements are essentially size-independent ($P_{o,a}^*$ scales with $M^{0.08}$), metabolic measurements suggest a larger quantity of energy 'wasted' overcoming wing inertia as body size decreases within the sphingids, and mechanical estimates of dynamic efficiency by the method of Weis-Fogh (1973) are consistent with this interpretation.

The findings of the present study are not consistent with Weis-Fogh's suggestion that sphinx moths utilize an elastic system in the pterothorax to reduce inertial power requirements. The relatively low metabolic rates and high power requirements of dipterans and hymenopterans examined (Weis-Fogh, 1973; his table 5) have forced the conclusion that an elastic system must be operational in order for estimates of muscle efficiency to be reasonable. In sphinx moths, however, high metabolic rates coupled with low aerodynamic power requirement argue for the opposite conclusion; namely, that inertial power costs for hovering must be substantial. If this were not the case, muscle efficiency of sphingids would be half or less that of hovering Diptera, Hymenoptera and humming-birds.

Admittedly, the estimates of the moment of inertia and inertial power cost calculated in this study are crude, and based on several assumptions. More detailed study of the mechanical properties of the thorax of sphingids and of insects in general is clearly warranted. It is therefore of interest that C. P. Ellington (personal communication) has calculated the moment of inertia for the wings of *M. sexta*. For both wings it is equal to $0.185 m_w R^2$, where m_w is the total wing mass of fore and hind wings and R is the wing length. Weis-Fogh's (1973) equation 27 therefore underestimates the moment of inertia – and, as a consequence, the inertial power output – by 9%. Furthermore,

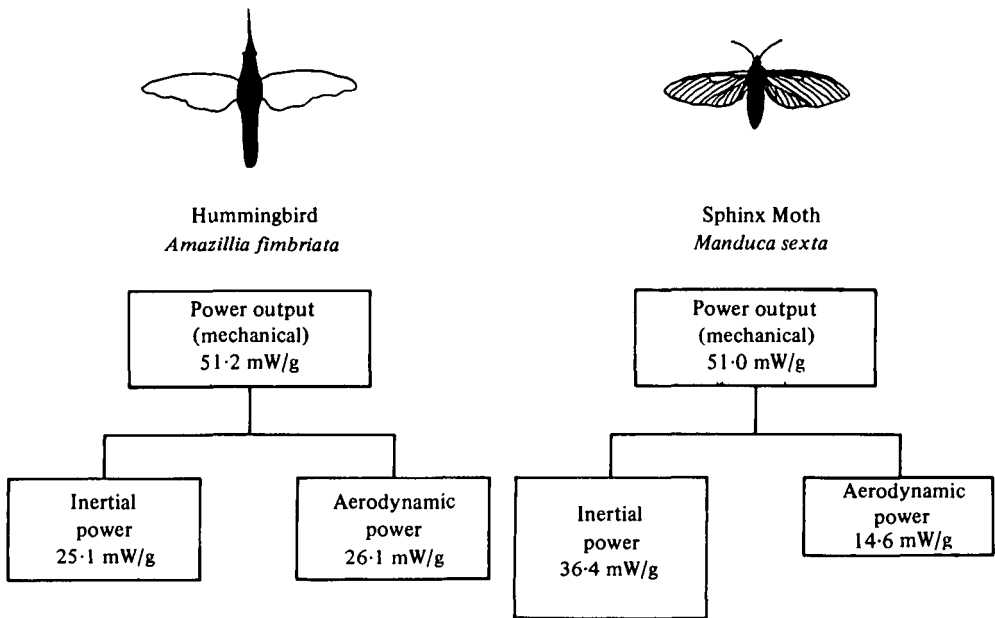


Fig. 7. A comparison of mechanical power output of 3.7 g: hummingbird, *Amazilia fimbriata* and a 1.28 g sphinx moth, *Manduca sexta*. Data for induced power (*A. fimbriata*) from Rayner (1979), data for profile and inertial power from Weis-Fogh (1973). Inertial power for *M. sexta* assuming 10% underestimate of the moment of inertia (see text); induced power from Rayner (1979); profile power from Weis-Fogh (1973).

the average deviation between the moment of inertia estimated by Weis-Fogh's equation 27 and measured values (Sotavalta, 1947, 1952) obtained by cutting and weighing strips of wings was -11% (see Weis-Fogh, 1973; table 3). If sphingids in general have greater inertial power requirements than calculated in this study, the conclusions of the importance of inertial power requirements and the lack of elastic storage are strengthened. For a large sphingid this amounts to a decrease of about 2% in the mechanical estimate of dynamic efficiency. Nevertheless, even if inertial power requirements for sphingids were systematically overestimated by 50%, the conclusion that inertial power requirements represent a significant portion of the total mechanical power requirements of hovering sphinx moths would remain intact.

Mechanical power output. As a first approximation, mechanical and metabolic data yield similar estimates of the flight cost of hovering sphinx moths over a wide size range (Fig. 6). The differences may be due to inaccuracy in calculation of one or more of the mechanical values, errors in the measurements of metabolic rates, or errors in the values assumed for muscle efficiency. For example, if muscle efficiency is assumed to be 0.15 rather than 0.20, differences in dynamic efficiency estimated by the two approaches (Fig. 6) largely disappear.

In the absence of metabolic data, flight metabolism may be estimated directly from calculations of aerodynamic power requirements (e.g. Pennycuik, 1969; Tucker, 1973). In the range of body size where inertial power represents a significant fraction of the total mechanical power requirements, flight cost should be estimated based on

calculations of aerodynamic plus inertial power (i.e. mechanical power output) since these parameters will scale differently (Figs. 2, 4), resulting in different E_T . This is particularly important when comparing individuals from diverse taxa, whose morphological characteristics do not conform to geometrical similarity. For example, Fig. 7 shows the mechanical power requirements for the sphingid, *Manduca sexta* and the hummingbird, *Amazillia fimbriata*. The sphingid has a lower mass-specific aerodynamic power requirement, as a result of its lower wing disc load, and the hummingbird has a lower mass-specific inertial power requirement. However, the total power requirement is similar for the two species. As would be predicted from this, the metabolic rates of these two species are similar (232 mW/g for *A. fimbriata* (Berger & Hart, 1972), and 237 mW/g for *M. sexta* (Casey, 1976a).

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REFERENCES

- BARTHOLOMEW, G. A. & CASEY, T. M. (1978). Oxygen consumption of moths during rest, pre-flight warm-up, and flight in relation to body size and wing morphology. *J. exp. Biol.* **76**, 11-25.
- BERGER, M. & HART, J. S. (1972). Die Atmung beim Kolibri *Amazillia fimbriata* während des Schwirfluges bei verschiedenen Umgebungstemperaturen. *J. comp. Physiol.* **81**, 363-380.
- CASEY, T. M. (1976a). Flight energetics of sphinx moths: power input during hovering flight. *J. exp. Biol.* **64**, 529-543.
- CASEY, T. M. (1976b). Flight energetics in sphinx moths: heat production and heat loss in *Hyles lineata* during free flight. *J. exp. Biol.* **64**, 545-560.
- ELLINGTON, C. P. (1977). Vortices and hovering flight. In *Proceedings of the Conference on Unsteady Effects of Oscillating Animal Wings* (ed. W. Nachtigall). Saarbrücken.
- ELLINGTON, C. P. (1978). The aerodynamics of normal hovering flight: three approaches. In *Comparative Physiology—Water, Ions and Fluid Mechanics* (ed. K. Schmidt-Nielsen, K. L. Bolis and S. P. H. Maddrell). Cambridge University Press.
- HEINRICH, B. (1970). Thoracic temperature stabilization by blood circulation in a free-flying moth. *Science, N.Y.* **168**, 580-581.
- HEINRICH, B. (1971). Temperature regulation of the sphinx moth, *Manduca sexta*. I. Flight energetics and body temperature during free and tethered flight. *J. exp. Biol.* **54**, 141-152.
- HEINRICH, B. & CASEY, T. M. (1973). Metabolic rate and endothermy in sphinx moths. *J. comp. Physiol.* **82**, 195-206.
- LIGHTHILL, J. (1974). Aerodynamic aspects of animal flight. In *Swimming and Flying in Nature*, vol. 2 (ed. T. Y. Wu, C. J. Brokaw and C. Brennan), pp. 423-491. New York: Plenum Press.
- PENNYCUICK, C. J. (1968). Power requirements for horizontal flight in the pigeon *Columba livia*. *J. exp. Biol.* **49**, 527-555.
- PENNYCUICK, C. J. (1969). The mechanics of bird migration. *Ibis* **111**, 525-556.
- RAYNER, J. M. V. (1979). A new approach to animal flight mechanics. *J. exp. Biol.* **80**, 17-54.
- SOTAVOLTA, O. (1947). The flight tone (wing stroke frequency) of insects. *Acta. Ent. Fenn.* **4**, 1-117.
- SOTAVOLTA, O. (1952). The essential factor regulating the wing stroke frequency of insects in wing mutilation and loading experiments at subatmospheric pressure. *Ann. Zool. Soc. 'Vanomom'* **15** (2), 1-67.
- TUCKER, V. A. (1973). Bird metabolism during flight, evaluation of a theory. *J. exp. Biol.* **58**, 689-709.
- WEIS-FOGH, T. (1961). Power in flapping flight. In *The Cell and the Organism* (ed. J. A. Ramsey and V. B. Wigglesworth), pp. 283-300. Cambridge University Press.
- WEIS-FOGH, T. (1965). Elasticity and wing movements in insects. *Proc. XII Int. Cong. Ent.* p. 868.
- WEIS-FOGH, T. (1967). Respiration and tracheal ventilation in locusts and other flying insects. *J. exp. Biol.* **47**, 561-587.

- WEIS-FOGH, T. (1972). Energetics of hovering flight in hummingbirds and *Drosophila*. *J. exp. Biol.* **56**, 79-104.
- WEIS-FOGH, T. (1973). Quick estimates of flight fitness in hovering animals, including novel mechanisms of lift generation. *J. exp. Biol.* **47**, 561-587.
- WEIS-FOGH, T. (1977). Dimensional analysis of hovering flight. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 405-420. New York: Academic Press.
- ZEBE, E. (1954). Über den Stoffwechsel der Lepidopteran. *Z. vergl. Physiol.* **36**, 290-317.

