

POWER AND EFFICIENCY OF INSECT FLIGHT MUSCLE

By C. P. ELLINGTON

*Department of Zoology, University of Cambridge, Downing Street, Cambridge
CB2 3EJ, England*

SUMMARY

The efficiency and mechanical power output of insect flight muscle have been estimated from a study of hovering flight. The maximum power output, calculated from the muscle properties, is adequate for the aerodynamic power requirements. However, the power output is insufficient to oscillate the wing mass as well unless there is good elastic storage of the inertial energy, and this is consistent with reports of elastic components in the flight system. A comparison of the mechanical power output with the metabolic power input to the flight muscles suggests that the muscle efficiency is quite low: less than 10%.

INTRODUCTION

In recent years the mechanical analysis of animal locomotion has become increasingly sophisticated, resulting in accurate estimates of the sustained, aerobic mechanical power output required of the locomotor muscles. These estimates have been compared with the metabolic power input, as measured by the rate of oxygen consumption, to determine the muscle efficiency. Two major studies, one on running birds and mammals (Heglund, Fedak, Taylor & Cavagna, 1982) and the other on hovering insects (Ellington, 1984), have both concluded that the muscle efficiency can be much lower than the commonly expected 20–30%. The results for terrestrial locomotion are discussed elsewhere in this volume (Heglund, 1985), and I shall review the power and efficiency of insect flight muscle during hovering, a type of flight so energetically demanding that only hummingbirds and insects can sustain it aerobically.

MECHANICAL ANALYSIS OF HOVERING FLIGHT

We begin with the estimates of the mechanical power output required of the flight muscles. My estimates were obtained in a study that extended Weis-Fogh's (1972, 1973) pioneering work on hovering flight. This study involved determining the wing motion from high-speed ciné films of a variety of insects in free hovering flight, and combining this data with morphological measurements in a new aerodynamic analysis. The oxygen consumption during hovering has been measured for only three

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of these insects, so I shall just present the results for them: a bumblebee, *Bombus* sp., a honey-bee, *Apis mellifera*, and a drone-fly, *Eristalis tenax*. For these insects, the *aerodynamic power* required to move the wings through the air ranged between 167 and 186 W kg⁻¹ (muscle mass): all mass-specific powers will refer to the power per unit muscle mass.

Inertial power is needed to oscillate the wing mass during each wingbeat, but its net value will depend on the amount of elastic storage that is present. Perfect elastic storage will require no inertial power from the muscles, and the *total* mechanical power output will just be the mean aerodynamic power over the cycle: 167–186 W kg⁻¹. If there is no elastic storage, then the inertial power requirement raises the total power output to 441–568 W kg⁻¹. Elastic storage, and hence the muscle power output, will lie somewhere between these two extreme cases.

These power outputs can be compared with the metabolic power input for hovering insects to determine the overall mechanochemical muscle efficiency. The oxygen consumption of hovering insects has been reported many times in the last decade, and the metabolic power input can be estimated using a standard conversion factor: 20 J of chemical energy per ml O₂ consumed. From the published data, the metabolic power for my three insects is 3.2 kW kg⁻¹ for *Bombus* (Heinrich, 1975), 3.7 kW kg⁻¹ for *Apis* (Withers, 1981) and 2.0 kW kg⁻¹ for *Eristalis* (Gilbert, 1983).

The metabolic rates during insect flight are often 50–100 times the resting level, and it is commonly assumed that the metabolic cost of physiological support systems is negligible in flight. Despite Casey's (1981a) warning that the cost of ventilation may be significant, it is customary to assume that virtually all of the O₂ uptake is used by the flight muscles for mechanical (i.e. aerodynamic plus inertial) work. Dividing this mechanical power output by the metabolic power input gives the following efficiencies for the flight muscles: 5–8% assuming perfect elastic storage, and 12–29% assuming no elastic storage. These values are in close agreement with measurements of the metabolic power input and estimates of the mechanical power output presented by Casey (1981b) for hovering sphinx moths: his data yield mean efficiencies of 6% and 17% for perfect and zero elastic storage, respectively (Ellington, 1984).

We are thus left with an unpleasant choice. If there is good elastic storage then the muscle efficiency is much lower than the common expectation of 20–30%, based on measurements from vertebrate striated muscle. To obtain more palatable values of efficiency we must stipulate negligible elastic storage, but this grates against an optimistic belief that locomotor systems are sensibly designed. It also denies the existence of three elastic elements that have previously been discovered in the insect flight system (Buchthal & Weis-Fogh, 1956; Machin & Pringle, 1959; Weis-Fogh, 1959, 1972; Jensen & Weis-Fogh, 1962; Alexander & Bennet-Clark, 1977): (i) the hard skeletal cuticle, (ii) elastomers such as the protein resilin, and (iii) an elastic component present in the flight muscle.

The evidence for elastic storage makes it likely that the muscle efficiency is indeed low. This tentative conclusion is also supported by Weis-Fogh's & Alexander's (1977) estimate of the maximum power output from striated muscle (about 250 W kg⁻¹ for

insect non-fibrillar and vertebrate striated muscle) and there seems little reason to suspect that the value for insect fibrillar muscle should be any greater. If their estimate is correct, the insects mentioned above would be unable to hover unless they had very good elastic storage; otherwise, the power output required from the muscles would be about twice the maximum available.

Pennycuik & Rezende (1984) have just published new estimates of the power output of muscle, based on a simplified form of the model of Weis-Fogh & Alexander (1977). They suggest that the power output asymptotically approaches a limit of 860 W kg^{-1} as wingbeat frequency increases; for the frequencies of my three insects mentioned above the value would be $340\text{--}400 \text{ W kg}^{-1}$. If their estimates are true, then only a moderate amount of elastic storage would be required, and the muscle efficiency could increase to 11–17%. These values are more acceptable than the earlier estimates of 5–8%, but would still conflict with the experimental evidence for good elastic storage. In this paper I shall look at the characteristics of insect flight muscle to obtain new estimates of the power output, and show that the conclusion of low muscle efficiency is probably still with us.

POWER OUTPUT OF THE MUSCLES

Pennycuik & Rezende (1984) use a very simple expression for the mean power output of a muscle performing cyclic contractions. Let the muscle exert a force F over its cross-sectional area A while contracting through a length ΔL . We define the stress, σ , as F/A and the strain ϵ as $\Delta L/L$, where L is the initial length of the muscle. The work done per unit mass of muscle is then $\sigma\epsilon/\rho$, where the mass density of muscle ρ is about 1060 kg m^{-3} (Méndez & Keys, 1960). If the frequency of contractions is f , the mean power output per unit mass of muscle \overline{P}_m^* is just

$$\overline{P}_m^* = \sigma\epsilon f/\rho.$$

For a given skeletal lever system, the product of strain and frequency determines the flapping velocity of the wings. Aerodynamic requirements fix the flapping velocity within narrow limits for any particular flying insect, so the estimation of mean power output depends only on the choice of a suitable value for the muscle stress.

In choosing a value for stress, we must distinguish between two quite different types of insect flight muscle. In many respects, the main power-producing flight muscles of all insects are similar to vertebrate striated muscle. There is a comparable pattern of cross-striation from the actin- and myosin-containing filaments, the sarcoplasmic reticulum mediates calcium activation of the myofibrillar ATPase, and vesicles of the sarcoplasmic reticulum are closely associated with the transverse, or T, system that is formed by invaginations of the plasma membrane. Indeed, the only anomaly readily apparent under the light microscope is the tracheal system with its terminal tracheoles that supply the muscles with oxygen.

In the more primitive *synchronous* insect flight muscles there is direct nervous stimulation of each muscle contraction. Limitations on the speed of muscle relaxation

are believed to impose an upper frequency limit of about 100 Hz on these muscles (Pringle, 1981). Insects achieved even higher wingbeat frequencies with the evolution of a special type of flight muscle, called *asynchronous* flight muscle. This name arises from the physiological peculiarity that muscle contractions proceed at a rate which is not coupled to the rate of nervous stimulation. General reviews of both types of flight muscle are plentiful (e.g. Pringle, 1967, 1972, 1981; Elder, 1975; Cullen, 1974; Usherwood, 1975; Tregear, 1977); I shall discuss only those aspects directly concerned with force and power production.

Synchronous muscle

Synchronous flight muscle occurs in relatively primitive insects like the Odonata (dragonflies and damselflies), Orthoptera (grasshoppers and locusts) and Lepidoptera (butterflies and moths). Many of the structural characteristics of synchronous muscle suggest high rates of contraction and high rates of energy utilization. The sarcoplasmic reticulum (SR) is well developed, and forms a fenestrated curtain around the fibrils. The distance from the SR to the myofibrils is generally less than $0.5 \mu\text{m}$, facilitating rapid movement of Ca^{2+} , and this extensive SR system occupies 5–20% of the fibre volume. Large and numerous mitochondria fill some 30–40% of the fibre, a proportion that is found in only the most aerobically active vertebrate muscles. Oxygen is supplied by tracheoles which, for most synchronous muscle, indent the plasma membrane and ramify throughout the fibres, reducing diffusion distances to the mitochondria to about $5 \mu\text{m}$.

We now turn to the flight muscle of the locust, which is the only synchronous muscle that has been studied extensively. It is a typical twitch muscle that is stimulated once per wingbeat in normal flight, and twice in more strenuous flight (Wilson & Weis-Fogh, 1962). Its intrinsic speed is not very impressive, $6\text{--}9 \text{ s}^{-1}$ at 30°C (Buchthal, Weis-Fogh & Rosenfalck, 1957), so the strain during contraction is only about 5% (Weis-Fogh, 1956a) at the wingbeat frequency of 17 Hz (Weis-Fogh, 1956b). This strain is much less than that characteristic of vertebrate muscle and, as in all insects, the movement must be greatly amplified by the lever-like articulation of the wing base to produce the required wing motion. The mitochondria and SR occupy about 30% and 20% of the fibre volume, respectively, (Bücher, 1965; Elder, 1975), leaving only half of the volume for myofibrils. The fibres constitute about 80% of the muscle volume, with haemolymph and the tracheal system filling the rest (Buchthal & Weis-Fogh, 1956).

The maximum isometric stress σ_0 exerted by the muscle is 160 kN m^{-2} at 11°C (Weis-Fogh, 1956a). From his isotonic experiments Weis-Fogh suggested that σ_0 might be 400 kN m^{-2} at 35°C , which is close to the thoracic temperature during flight, but this would require a stress of 1000 kN m^{-2} (myofibril), more than twice the values for vertebrate striated muscle (Close, 1972; Weis-Fogh & Alexander, 1977). Buchthal *et al.* (1957) measured a maximum isometric twitch stress of 196 kN m^{-2} at 30°C , which would give a more reasonable myofibrillar stress of 490 kN m^{-2} (myofibril). We may also note that σ_0 for the flight muscle of a katydid, *Neoconocephalus robustus*, is

137 kN m⁻² at 35 °C; the myofibrils of this muscle occupy 57 % of the fibres, and the intrinsic speed is about 11 s⁻¹ (Josephson, 1984). Taking all of these values into account, I would thus be surprised if σ_0 for the locust muscle was much greater than about 200 kN m⁻² at flight temperatures.

Isotonic contractions of synchronous muscle exhibit a typical force-velocity curve, so the operating stress must be considerably less than σ_0 . Pennycuick & Rezende (1984) suggest that a stress of 0.5 σ_0 might be appropriate, assuming that the muscle is working near maximum efficiency. From the force-velocity curves of the locust (Buchthal *et al.* 1957) and the katydid (Josephson, 1984), a strain of 5 % at the respective wingbeat frequencies would indeed correspond to stresses close to 0.5 σ_0 . Taking an operating stress of 100 kN m⁻², the maximum power output would then be 80 W kg⁻¹ for the locust, and 94 W kg⁻¹ for the katydid. The value for the locust agrees very well with two independent measures: Jensen's (1956) aerodynamic analysis predicted 67–100 W kg⁻¹, depending on assumptions about elastic storage and negative work, and Buchthal *et al.* (1957) measured a maximum of 81 W kg⁻¹ for isotonic twitch contractions.

Why is my estimate of 80 W kg⁻¹ so much less than the 250 W kg⁻¹ predicted by Weis-Fogh & Alexander (1977) and the 284 W kg⁻¹ for the locust from Pennycuick & Rezende (1984)? Both previous studies ignored the relatively large volume occupied by the SR, and hence overestimated the myofibrillar content. Furthermore, Pennycuick & Rezende assumed that the locust muscle contracts 15 % of its length instead of the observed 5 %, and this factor of 3 largely accounts for the difference between our estimates. The estimate of maximum power output by Weis-Fogh & Alexander is based on an intrinsic speed of 25 s⁻¹ and an optimum strain rate derived from Hill's equation and the isometric tension-length curve. For an intrinsic speed of 9 s⁻¹ and the observed strain rate, their model would, in fact, predict a power output close to 80 W kg⁻¹. Weis-Fogh & Alexander also quote a value of 170 W kg⁻¹ for the maximum power output that has been determined experimentally for the locust, which is about twice the value predicted here. However, that value results from a measured metabolic power input (Weis-Fogh, 1964) multiplied by an assumed muscle efficiency of 20 %; since we are presently questioning the efficiency of flight muscle, that estimate should be regarded as dubious, if not misleading. Indeed, Weis-Fogh (1976) derived the efficiency of locust flight muscle as only 11 %, which would reduce the estimate to 94 W kg⁻¹.

In general, a maximum power output of about 80 W kg⁻¹ agrees fairly well with the scanty experimental data for the locust, and the discrepancies with other estimates are readily explained. It is quite likely that the maximum power output scales with wingbeat frequency, so estimates for all other synchronous fliers will have to be extrapolated from this one value pieced together for the locust! These estimates are discussed in the section on scaling.

Asynchronous muscle

Asynchronous flight muscle is found in the Diptera (flies), Coleoptera (beetles), Hymenoptera (bees), Thysanoptera (thrips), Psocoptera (booklice) and Hemiptera

(true bugs). Much of the research has concentrated on a glycerol-extracted flight muscle preparation from the giant waterbug *Lethocerus*, and Tregear (1977) provides a convenient review of this work.

Even though asynchronous muscle evolved independently many times from synchronous muscle (Cullen, 1974), it always shows the same basic structure. The myofibrils tend to have large diameters, and so it is often known as *fibrillar* flight muscle; synchronous muscle is then referred to as *non-fibrillar* muscle, but this classification is not very reliable (Josephson & Young, 1981). In asynchronous muscle, large mitochondria occupy 30–40% of the fibre volume, and the T-system is well developed, although the location of the transverse tubules differs from that in synchronous muscle. The SR is greatly reduced, consisting of little more than isolated vesicles in association with the T-system. Such a degenerate system is incapable of releasing and sequestering Ca^{2+} during each contraction, and indeed these muscles contract rhythmically under constant Ca^{2+} concentrations. The muscles contract through strains of less than 5%, and this near isometric specialization is reflected in an almost complete overlap of the thick and thin filaments.

The most interesting feature of asynchronous muscle is that its contractile activity is maintained by a self-oscillatory mechanism that is under *mechanical*, not nervous, control. This is shown in Fig. 1 by the loop in the stress/strain diagram for the intact flight muscle of a coconut beetle *Oryctes rhinoceros*. Machin & Pringle (1959) replaced the natural load on that muscle with an artificial inertia, stiffness and damping. They discovered that the muscle would not contract rhythmically if it was highly damped or if an inertial load was absent; under those conditions the muscle simply exhibited a high stiffness, even when unstimulated. This stiffness is considerably greater than locust synchronous flight muscle (Buchthal *et al.* 1957), which in turn is much higher than vertebrate striated muscle (Pringle, 1977). All insect flight muscle is extremely stiff; even at the small operating strains it can store elastically much, if not all, of the inertial energy of the oscillating wings (Weis-Fogh, 1959; Alexander & Bennet-Clark, 1977; Ellington, 1984).

For oscillatory operation the asynchronous muscle must be under static tension, and it must also be stretched dynamically by an inertial load (the lower half of the loop in Fig. 1) before it will contract (the upper half). To produce rhythmic contractions, all that is required is a mechanism which will produce a delayed tension after the muscle is stretched. Wray (1979) has proposed a plausible answer, which involves a periodic matching of myosin heads with the preferred attachment sites on the actin filaments. Oscillatory contraction and/or delayed tension after stretch is also widespread in vertebrate muscle (Goodall, 1956; Lorand & Moos, 1956; Armstrong, Huxley & Julian, 1966; Rüegg, Steiger & Schädler, 1970; Steiger, 1977; Kawai & Brandt, 1980), and can even be found in the anterior byssus retractor muscle of the mussel *Mytilus edulis* (Gagelmann, Göth & Rüegg, 1984), although the underlying mechanism has not been established for these examples.

We now return to the main problem: what is the power output of asynchronous flight muscle? Hill's relation is clearly not applicable to this muscle and cannot be used

to estimate the operating stress. From Fig. 1 it is evident that the net work per cycle is equal to the loop area, and it is substantially smaller than the inertial energy absorbed and returned each cycle (the shaded area). The effective operating stress can therefore be defined as the maximum difference between the stress during the shortening and lengthening half-loops (Pennycuick & Rezende, 1984). When multiplied by the operating strain, this stress will somewhat overestimate the work done since the average stress difference must be less than the maximum.

The maximum stress difference that has been measured is 200 kN m^{-2} (myofibril) for glycerol-extracted *Lethocerus* muscle oscillating at a strain of 7.8% at 2 Hz at 20°C (Pringle & Tregear, 1969); this agrees with the maximum delayed stress developed in response to a stretch (Schädler, Steiger & Rüegg, 1971). Allowing for mitochondria and extracellular spaces, the operating muscle stress would be close to 100 kN m^{-2} , the same as the locust. If the same stress could be achieved at the normal wingbeat frequency of 30 Hz and strain of 4%, the power would be 113 W kg^{-1} . For the maximum power output of intact asynchronous muscle we must go back to Machin & Pringle (1959), who measured 29 W kg^{-1} for *Oryctes* and 88 W kg^{-1} for the bumblebee *Bombus terrestris*. These values are less than the power output of *Lethocerus* extrapolated to 30 Hz, but Machin & Pringle pointed out that their values

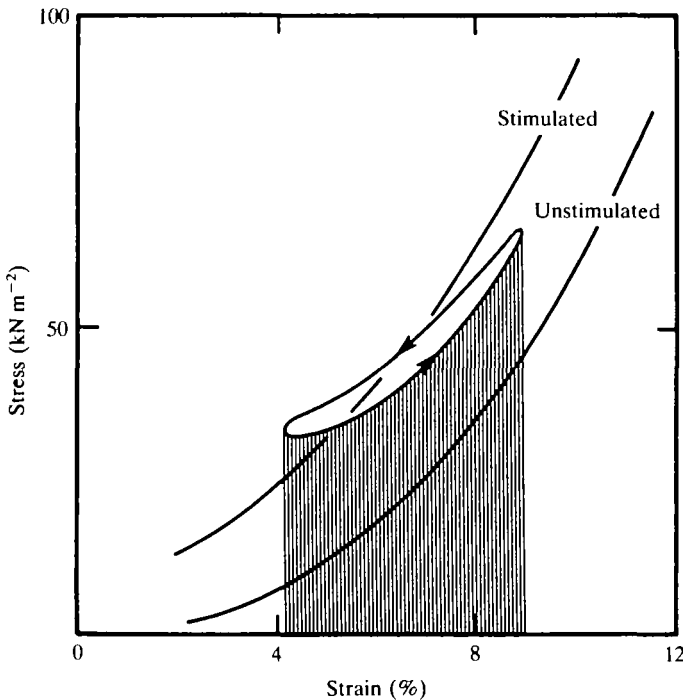


Fig. 1. Typical stress/strain curve for intact asynchronous flight muscle of *Oryctes rhinoceros* under non-oscillatory (stimulated and unstimulated) and oscillatory (the loop) conditions. Adapted from Machin & Pringle (1959).

were probably lower than those achieved during flight because they could not mimic the special loading conditions produced by the natural wing articulation.

SCALING OF POWER OUTPUT

The data required to estimate the maximum aerobic power output of insect flight muscle are extremely scarce. In the preceding sections we obtained (with difficulty) estimates for just two cases, synchronous locust muscle and asynchronous *Lethocerus* muscle. Do these values apply to all synchronous and asynchronous insects, or does the power output scale with body size? Perhaps it would be more appropriate to ask whether power scales with wingbeat frequency, since the power equation (page 295) suggests a linear dependence on f . The frequency increases for smaller insects, so the power equation may indicate that their power outputs are greater than the two relatively large insects considered so far.

Pennycuik & Rezende (1984) have investigated the effect of frequency on power output in an elegantly simple model. They assume that the muscle strain and myofibrillar stress are relatively constant muscle properties, leaving the contraction frequency as the primary determinant of power. They further assume that the rate of ATP production per unit volume of mitochondria is a constant, and that the mitochondrial fraction is just sufficient to balance the maximum power of the myofibrils. Thus a frequency increase allows a greater power output, but this requires a greater mitochondrial fraction; the myofibrillar fraction must therefore be reduced, decreasing the muscle stress and yielding a lower power output than predicted by the linear dependence on frequency alone. The net result is that the power increases with frequency, but at a progressively lower rate as the mitochondria occupy more of the fibres, and eventually a limit is reached when the muscle is almost entirely filled by mitochondria.

Fig. 2 shows the results of Pennycuik & Rezende for insect synchronous and vertebrate striated muscle (curve A) and for asynchronous muscle (curve B). However, their results for synchronous muscle are marred by incorrect data for the locust, as described above; at 17 Hz the power should be 80 W kg^{-1} , as indicated by the square, which is less than one-third the value from their curve A. I have not drawn a corrected curve for synchronous muscle in Fig. 2, even though one is desirable, because of a failing of the Pennycuik & Rezende model: they neglect the relatively large volume fraction of the SR, and without knowing how this fraction scales with frequency it cannot be corrected for. We can consider two extreme cases, though: (i) the fraction remains a constant 20% and (ii) the fraction increases in proportion to the mitochondrial fraction. The power output at the 100 Hz upper limit for synchronous muscle would then be 168 and 137 W kg^{-1} for these two assumptions, respectively, as shown by the circles in Fig. 2. Thus the curve for synchronous muscle should be below Pennycuik's & Rezende's curve B for asynchronous muscle, but the exact shape of the curve cannot be established without more information. These power estimates are of the right magnitude to account for the aerodynamic power expended

by synchronous fliers (Casey, 1981*b*; Ellington, 1984), but little would be left over for inertial power, indicating that elastic storage would have to be quite effective.

Pennycuick's & Rezende's results for vertebrate striated muscle (curve A) indicate that it is more powerful than synchronous insect muscle, based on our new estimates. The myofibrillar stress of both muscle types is similar, suggesting that the lower power of synchronous muscle is attributable mainly to its smaller operating strains. Why should the strain be lower? Perhaps because it is limited by the maximum strain rate. Josephson (1984) noted that the twitch rise time (6–7 ms) and duration (6 ms) of the katydid are comparable with the fastest known vertebrate muscles, even though the intrinsic speeds of katydid and locust muscles are not very impressive. If the intrinsic speeds of synchronous muscles are seriously limited, then a small operating strain would necessarily result from the high contraction frequencies.

Pennycuick's & Rezende's model is much more appropriate for asynchronous muscle (Fig. 2, curve B), where the myofibrils and mitochondria do account for nearly all of the fibre volume. Their analysis predicts a power output of 340–400 W kg⁻¹ for the three insects I studied, but they did not allow for the extracellular volume of the muscles, which would reduce the power to about 300 W kg⁻¹. Furthermore, their power must be overestimated because the *maximum* stress difference of 200 kN m⁻² (myofibril) was used instead of an *average* difference, so the power output is probably very close to Weis-Fogh's & Alexander's (1977) value of 250 W kg⁻¹.

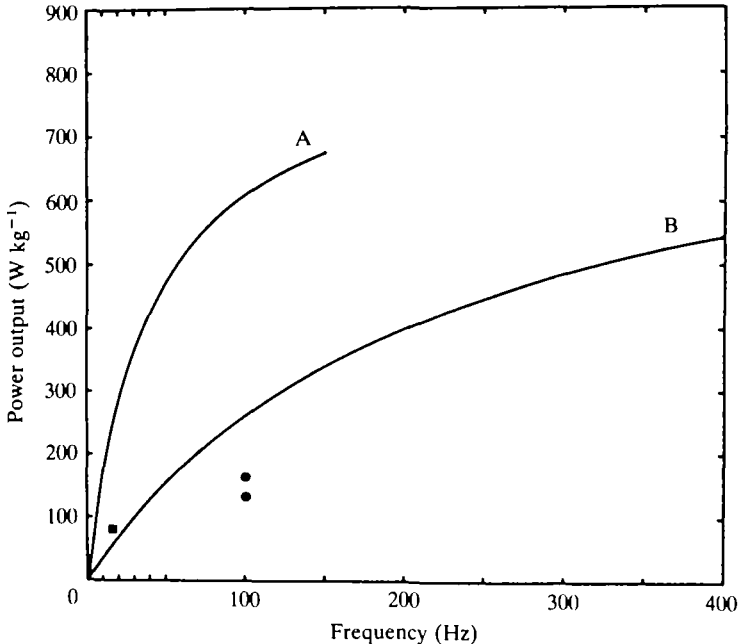


Fig. 2. The mass-specific power output, predicted by Pennycuick & Rezende, as a function of contraction frequency for (A) insect synchronous and vertebrate striated muscle, and (B) asynchronous muscle. Symbols explained in text. Adapted from Pennycuick & Rezende (1984).

CONCLUSION

This evaluation of Pennycuick's & Rezende's analysis of asynchronous muscle confirms that the maximum power output for my three insects is sufficient for aerodynamic requirements, but that little power is available for inertial work. Extensive elastic storage is therefore implied, which is consistent with other results, and we are led to the conclusion that the efficiency of asynchronous flight muscle is indeed low – less than 10%. The maximum power output of synchronous muscle is even smaller, and again it is just adequate for aerodynamic needs, indicating good elastic storage and similarly low efficiencies. This evidence for the low efficiency of insect flight muscles is persuasive but indirect, and future research must aim for more conclusive results and a rigorous examination of the scaling of maximum power output.

It is a pleasure to thank Dr K. E. Machin for stimulating discussions and comments on the manuscript.

NOTE ADDED IN PROOF

I have recently learned of a very relevant paper in press by R. K. Josephson (*J. exp. Biol.* 114). He measured the mechanical power output of a flight muscle of the katydid *Neoconocephalus triops* while it was subjected to sinusoidal length oscillations and stimulated at selected phases of the cycle. The experiments deliberately searched for the conditions giving maximum power output, and were performed at normal flight frequency (25 Hz) and temperature (30 °C). A maximum power output of 76 W kg⁻¹ was obtained with a strain of 6.0% and three stimuli per cycle. Using that strain and frequency with the data from the closely related *N. robustus* on maximum isometric stress (137 kN m⁻² at 35 °C), the power equation (page 295) would predict a maximum power output of 97 W kg⁻¹. The agreement between prediction and observation is satisfactory given the limitations on both, and it provides support for the conclusions above.

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