

LIMITATIONS ON ANIMAL FLIGHT PERFORMANCE

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Summary

Flight performance seems to change systematically with body size: small animals can hover and fly over a wide range of speeds, but large birds taxi for take-off and then fly over a narrow speed range. The traditional explanation for this is that the mass-specific power required for flight varies with speed according to a U-shaped curve, and it also scales between m^0 and $m^{1/6}$, where m is body mass. The mass-specific power available from the flight muscles is assumed to scale as $m^{-1/3}$. As available power decreases with increasing body size, the range of attainable flight speeds becomes progressively reduced until the largest animals can only fly in the trough of the U-shaped curve. Above a particular size, the available power is insufficient and flapping flight is not possible.

The underlying assumptions of this argument are examined in this review. Metabolic measurements are more consistent with a J-shaped curve, with little change in power from hovering to intermediate flight speeds, than with a U-shaped curve. Scaling of the mass-specific power required to fly agrees with predictions. The mass-specific power available from the muscles, estimated from maximal loading studies, varies as $m^{0.13}$. This scaling cannot be distinguished from that of the power required to fly, refuting the argument that power imposes an intrinsic scaling on flight performance. It is suggested instead that limitations on low-speed performance result from an adverse scaling of lift production with increasing body size.

Introduction

Large birds have to taxi before take-off or swoop down from a prominence, gradually acquiring enough speed for flight. Once in the air they cruise over a very restricted range of speeds until landing, which is a seemingly dangerous, high-speed event. Smaller birds have a more versatile and manoeuvrable flight performance: they launch into flight immediately, and they can land with pin-point accuracy. While in the air, they can fly over a wide range of speeds, and hover for brief moments. Tiny hummingbirds are even more impressive because they can hover for sustained periods while they feed on the wing, dart between flowers faster than the eye can follow, but still migrate over long distances. At still smaller sizes we find the most successful and versatile group of flying animals – the insects – whose mastery of the air is unchallenged.

Key words: animal flight, flight performance, muscle power.

What limits flight performance in such a manner that larger animals have more restricted capabilities? The traditional answer to this question is *power*. The mass-specific *power required* for flight is virtually independent of body size, but varies with flight speed according to a U-shaped curve with a minimum at some intermediate speed. If the mass-specific *power available* from the muscles is low, flight is only possible over a small range of speeds close to this minimum. As the power available increases so does the range of attainable speeds, and at some level hovering flight becomes possible. The mass-specific power available supposedly increases for smaller animals, and this is believed to be responsible for the observed scaling of flight performance with body mass.

This explanation was first proposed by Pennycuik (1968), and it has since become firmly entrenched in the literature on animal flight. There are very good reasons for its widespread acceptance: it is an elegantly simple answer that seems to work! However, recent investigations have questioned the shape of the U-shaped curve, and the assumed scaling of available muscle power can now be tested against experimental measurements. In this review I shall examine our conventional wisdom about animal flight performance in the light of these studies, and conclude that a major revision of our thinking might be required.

Power and flight performance

Our current understanding of flight performance stems from a combination of several points. A critique of each one as it is presented would be disruptive, so I shall instead develop the conventional argument and then return to each point for further examination.

Power required for flight

The energetic cost of animal flight is of great interest to those who study aerodynamics, biomechanics, foraging behaviour, ecology and migration. The cost is most readily discussed in terms of the *mechanical power* required to move the animal through the air, which can be predicted using various aerodynamic theories (e.g. Pennycuik, 1968, 1969, 1975, 1989; Tucker, 1973; Rayner, 1979, 1986). The power is traditionally divided into three components, as shown in Fig. 1. The *induced power* P_{ind} represents the kinetic energy per unit time imparted to the air in giving it downwards momentum; this downwash is simply the reaction to the lift force supporting the animal's weight. Induced power is inversely related to flight speed, and it is the major power requirement at low speeds. *Parasite power* P_{par} is required to overcome the drag force on the body, and it increases as the speed cubed to a first approximation. Similarly, *profile power* P_{pro} is needed to overcome drag on the wings. It should be estimated from a detailed analysis of the wing motion, but simplifying assumptions are commonly employed; Pennycuik, for example, argues that it is relatively constant except at low speeds. When added, these three components require a total power output P_{total} which changes with flight speed according to the familiar U-shaped curve: the

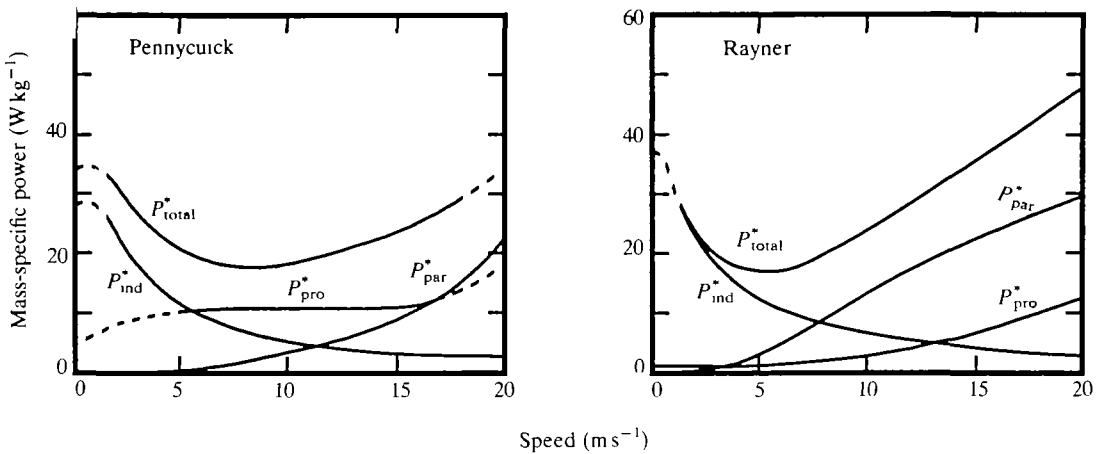


Fig. 1. U-shaped mechanical power curves for a 333 g pigeon according to the theories of Pennycuik (1975) and Rayner (1979). Power has been divided by body mass to give mass-specific power P^* . P_{total}^* , total power; P_{par}^* , parasite power; P_{pro}^* , profile power; P_{ind}^* , induced power. Adapted from Norberg (1990).

power is large in hovering and at high flight speeds, and is least at some intermediate speed. The exact shape of the curve varies between theories (Fig. 1), but the pronounced U-shape is a common feature. The theories predict unique speeds for minimum power and for minimum cost of transport, which are especially relevant to foraging and migration studies.

Apart from its dependence on speed, the *mass-specific* power requirement is thought to be almost independent of body size (Pennycuik, 1968, 1969, 1975, 1989). Flying animals, taken as a whole, show isometric scaling of body dimensions (Greenewalt, 1962). The characteristic speed V of any flying machine is proportional to the square root of its wing loading (weight divided by wing area), and thus $V \propto m^{1/6}$ for flying animals in general, where m is body mass. The total drag on the animal is likely to be a constant fraction of its weight, and so the power required for flight (speed multiplied by drag) is proportional to $m^{7/6}$. The mass-specific power, or power per unit body mass, therefore increases with size as $m^{1/6}$. This scaling is probably offset by a small reduction in drag for larger animals due to lower skin friction coefficients at higher Reynolds numbers. The extent of this reduction is not known in detail, but it seems reasonable to assume that the mass-specific power requirement scales somewhere between m^0 and $m^{1/6}$, showing a slight increase, if at all, with body size. To a first approximation, at least, all flying animals should therefore have a mass-specific power curve similar to those in Fig. 1: the same number of watts per kilogram should be required for small and large animals.

Power available for flight

The power available from the flight muscles has been considered by Pennycuik

(1968, 1969) and Pennycuick and Rezende (1984). If the available power is less than that required for flapping flight at a particular speed, then flight is simply not possible. If it exceeds the power required, then the excess power can be used for other demanding tasks such as manoeuvring or climbing flight.

Derivation of the mean power output of a muscle performing cyclic contractions is very straightforward (e.g. Pennycuick and Rezende, 1984). Let the muscle exert a force F over its cross-sectional area A while contracting through a length ΔL . The stress σ is defined as F/A , and the strain ϵ as $\Delta L/L$, where L is the initial length of the muscle. The work ($F\Delta L$) 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 and Keys, 1960). If the frequency of contractions is f , the mean power output per unit mass of muscle P_m^* is:

$$P_m^* = \sigma\epsilon f / \rho.$$

This expression is correct provided that a suitably weighted value is chosen for stress, which varies as a function of time. The choice of a weighting factor, however, is not important to the general argument.

It is assumed that the flight muscles operate at values of stress and strain that do not vary much with body size. The isometric stress of muscles is a strongly conserved trait (e.g. Close, 1972; Alexander, 1985), and it seems reasonable to postulate that the muscles work at some fraction of the isometric stress that maximizes their efficiency. It also seems likely that muscles operate over a similar region of the tension-length curve, and thus strain values would be similar. The *muscle* mass-specific work done in a contraction is therefore size-independent, and the *muscle* mass-specific power is simply proportional to frequency. The flight muscles constitute a relatively constant fraction of the body mass (Greenewalt, 1962, 1975), and so the *body* mass-specific power output available from the muscles will also be proportional to frequency.

Larger animals flap their wings more slowly than smaller ones, and the general trend is for frequency to scale as $m^{-1/3}$ (Greenewalt, 1975). The mass-specific power available for flight should thus scale as $m^{-1/3}$, meaning that smaller animals have relatively more power available. Pennycuick (1975) points out that $f \propto m^{-1/6}$ might be more appropriate for some groups of fliers; this keeps the flapping velocity of the wings at a constant fraction of the characteristic flight speed, and therefore ensures aerodynamic similarity for cruising flight. The mass-specific power available for flight would then scale as $m^{-1/6}$.

The argument is complicated somewhat by the heterogeneity of fibre types in vertebrate flight muscle. The reasoning is valid for all fibre types, and thus their scaling exponents should be the same. Nevertheless, the faster types are typically more powerful, so intra- and interspecific differences in the fibre proportions might cause variation about the general allometric trend for available power.

Power limitations on flight performance

The preceding section shows that the mass-specific power available scales

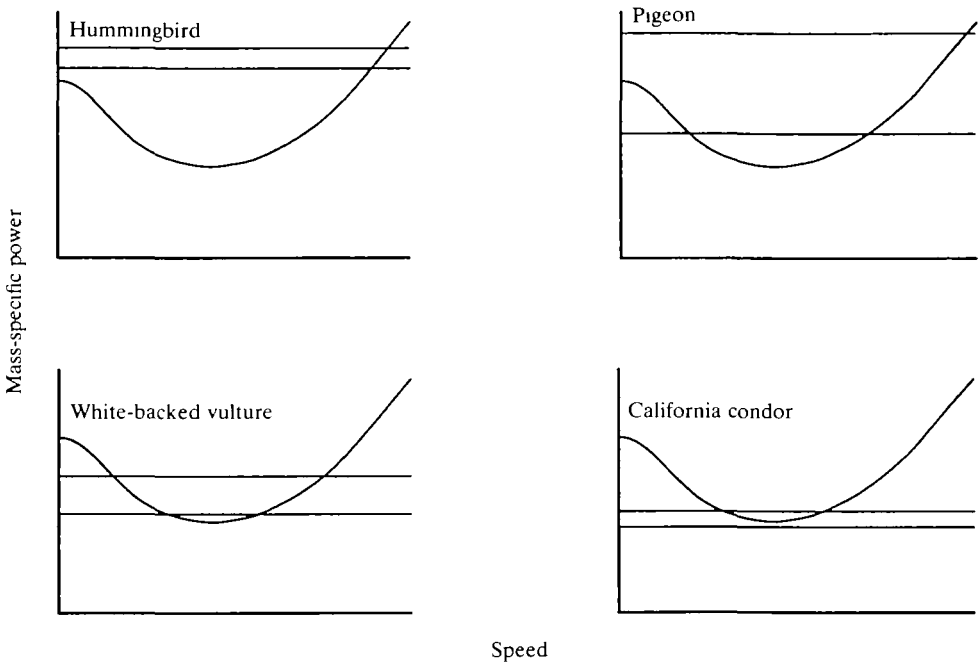


Fig. 2. Available power levels drawn against the power required for flight for four birds. The lower horizontal lines represent the maximum sustained power (aerobic), and the upper lines indicate the maximum power (aerobic plus anaerobic) available for short periods. From Pennycuik (1968).

adversely with body size; the maximum power output for larger animals is relatively lower. This relationship is very different from the mass-specific power required for flight; as already noted, the U-shaped curve of the latter is virtually independent of size. The limit imposed by the power available can therefore be represented by a horizontal line drawn across the U-shaped curve, and this line moves downwards with increasing body size but the U-shaped curve remains in the same position. For small animals, the power available exceeds that required except at the highest speeds. For intermediate-sized animals, the range of possible flight speeds is more restricted; they cannot hover or fly at very low speeds, and their maximum speeds are also reduced. Large animals would be capable of flight only near the trough of the U-shaped curve, and their performance is severely restricted.

This scaling of flight performance is illustrated in Fig. 2, from Pennycuik (1968). For hummingbirds (2–20 g) maximum aerobic power is well developed, as shown by the lower horizontal line, and it is sufficient for sustained hovering and for flight at high speeds. The anaerobic capacity of hummingbirds is presumably restricted and adds little to the maximum power available (upper horizontal line). The aerobic power of the largest hummingbird, *Patagonia gigas* (20 g), probably just matches that required for hovering flight. For a bird the size of a pigeon

(400 g), the available aerobic power has dropped to a level that is inadequate for flight at low speeds and hovering. A generous anaerobic capacity enables brief flights at these speeds for take-off, landing and climbing flight, and it greatly extends the maximum possible flight speed. The white-backed vulture is large enough (5–7 kg) that even anaerobic power is insufficient for slow and hovering flight; animals of this size must taxi for take-off, or launch from an elevated position to pick up flight speed. Their aerobic power is enough for sustained flight only over a narrow speed range. As size increases further there must be a point where the power available is insufficient for flight at any speed, and this imposes an upper limit to the size of animals that use flapping flight. The California condor (12 kg) may be close to this limit; it relies on soaring for sustained flight and flaps its wings only on take-off or in emergencies. There are three other birds from different orders that are of a similar size (Kori bustard, white pelican and mute swan), and the maximum size for flapping flight is often taken as 12–16 kg. Rayner (1988) and Pennycuik (1989) point out the existence of larger fossil birds, however, so extant birds may not be against the upper size limit.

A test of underlying assumptions

Fig. 2 is a splendid illustration of the power limitations on animal flight performance. However, the available power lines are drawn from *prior* knowledge of the flight performance; the figures do not actually represent *predictions* of performance. Can the conventional wisdom be tested? Two underlying assumptions must be verified in order to prove the argument: (1) mass-specific power required follows a pronounced U-shaped curve, and it is nearly independent of or increases slightly with body size; (2) mass-specific power available scales adversely with increasing size.

There are now enough data in the flight literature to test these assumptions. How do they bear up under scrutiny?

Power required

A direct measurement of the mechanical power required for flight is possible, but it has only just been accomplished. Biewener *et al.* (1992) obtained *in vivo* force records of the pectoralis muscle of European starlings during level flight in a wind tunnel at a single speed. Force was determined from calibrated bone strain recordings at the muscle's attachment site on the humerus. The mean mass-specific power output of the muscle was 104 W kg^{-1} muscle for a flight speed of 14 m s^{-1} . These measurements represent a remarkable technological advance and, when repeated over a range of speeds, will offer the first direct test of the U-shaped mechanical power curve predicted by aerodynamic theory.

At present, however, we must resort to an indirect method for evaluating the U-shaped curve: measurement of the *metabolic power* used in flight. Metabolic power is used by all physiological processes, but consumption by the flight muscles must necessarily dominate during flight. The metabolic power of the muscles

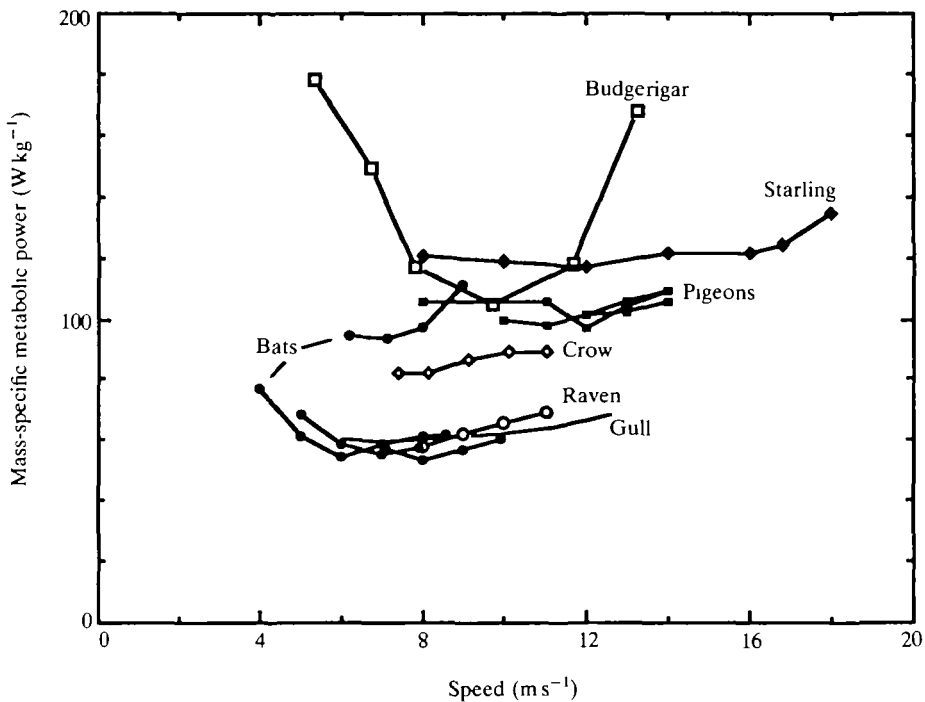


Fig. 3. Mass-specific metabolic power plotted against speed for birds and bats flown in wind tunnels.

related to the power output by the overall muscle efficiency. If that efficiency is assumed to be constant over different airspeeds, then the metabolic power will vary according to the same U-shaped function as the mechanical power. This assumption is implicitly made in all studies that compare the metabolic costs of flight with predictions from the mechanical power models.

The metabolic power during flight in a wind tunnel has been measured for several species of birds and bats (Fig. 3), typically by analysing the oxygen content of respiratory gases withdrawn from a mask, or by monitoring the decline in oxygen levels in a closed-circuit wind tunnel during prolonged flights. The metabolic power follows a distinctly U-shaped curve in a few species, but quantitative agreement with theoretical predictions is nevertheless unsatisfactory (Tucker, 1968; Thomas, 1975; Carpenter, 1975, 1985). In other species, either the curve is much flattened or the power shows no significant change with flight speed (Tucker, 1972; Bernstein *et al.* 1973; Torre-Bueno and Larochelle, 1978; Hudson and Bernstein, 1983). In the case of one pigeon the agreement between theory and experiment is remarkable over the limited speed range under test (Rothe *et al.* 1987; Pennycuik, 1989), but there is a discrepancy in the shapes of the two curves that would lead to large differences outside that speed range.

These studies provide only a limited test of the U-shaped curve because they do

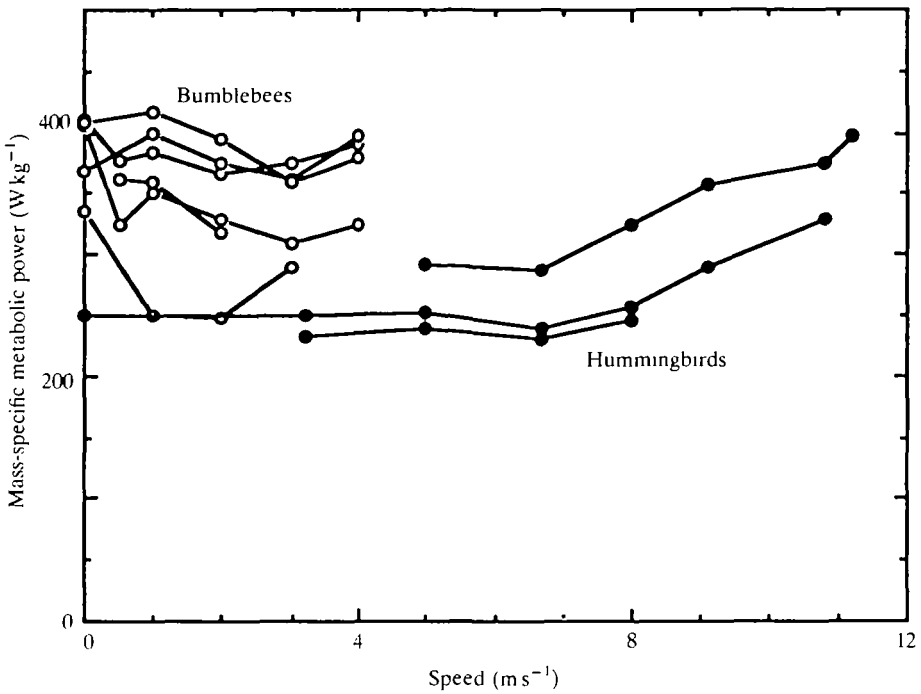


Fig. 4. Mass-specific metabolic power plotted against speed for hummingbirds and bumblebees, extending down to hovering flight.

not extend to hovering and very slow flight, where the predicted costs increase sharply. Given the inevitable scatter in the measurements, any number of curves of different shapes could be drawn through a collection of data points restricted to the trough of a U-shaped curve. However, these birds and bats are simply not capable of very slow flight, so the results cannot be extended. Hummingbirds are, in fact, the only vertebrates suitable for a complete test of the theories, because they are the only ones that can fly over the entire speed range. Berger (1985) measured their oxygen consumption, and found no significant difference in flight metabolism over speeds from hovering up to 7 m s^{-1} ; at even higher speeds the metabolic rate increases, presumably due to the increased power needed to overcome body drag (Fig. 4). When added to the results for other birds and bats, we see that there is not a single example from the vertebrate studies where metabolic power measurements agree closely with the *shape* of the mechanical power curve predicted by theories.

Insects are also ideal candidates for a test of the theories because most are capable of flight over a wide speed range, including hovering. However, the metabolic rate of insects in free forward flight has not been reported until recently; a few values have been published for tethered insects at one or two flight speeds (Kammer and Heinrich, 1978), but the relevance of these results to free-flight performance is questionable. Measurement of the oxygen consumption of insects

Free forward flight presents severe technical difficulties. For vertebrates, a small mask is normally used to collect expired gases for analysis, but the mask required for the spiracle system of insects would be too large and cumbersome. The alternative approach of measuring the decline in oxygen levels in a closed-circuit wind tunnel is beyond the capabilities of unmodified commercial instruments. Recently, Ellington *et al.* (1990) were able to improve the resolution and accuracy of the Ametek S3A/II analyser to this extent, and they reported the oxygen consumption of bumblebees in free forward flight. The metabolic power is generally independent of speed from hovering up to 4 m s^{-1} (Fig. 4), which is close to the maximum recorded flight speed (5 m s^{-1}) for bumblebees (Demoll, 1918). A shallow U-shaped curve is suggested by some of the results, but this small curvature is within the experimental errors and is certainly much less than that predicted by the usual aerodynamic theories. Thus, as with the vertebrate studies, these results offer little support for the conventional U-shaped curve.

The discrepancy between metabolic power measurements and mechanical power estimates has existed for almost two decades and is still unresolved. Participants in the debate generally fall into two camps: those who believe in theory, and those who trust only what they can measure. It is not surprising, therefore, that possible explanations of the discrepancy range from an oversimplified theoretical analysis to difficulties in identifying the fraction of the total metabolic power that is actually used by the flight muscles. It has even been suggested that both theory and measurement are correct, and that a speed-dependent change in muscle efficiency accounts for the difference. However, this diplomatic explanation must be untenable; if the metabolic power curve is flatter than the mechanical power curve, as most results would suggest, then the muscle efficiency would be lowest at the cruising speeds typically used by the animal!

The dispute can only be settled by more experimental work, combining metabolic measurements with recording of the wingbeat kinematics. A detailed aerodynamic analysis can be performed from such kinematic data, providing a check for oversimplifications in the conventional theories. This has been done for bumblebees by Dudley and Ellington (1990*a,b*), who found a much flatter mechanical power curve that closely resembles the metabolic power measurements. A similar comparison of the theories with detailed aerodynamic analyses and metabolic data is sorely needed for vertebrate flight.

Some preliminary results on bumblebees by A. J. Cooper in our laboratory are particularly relevant to this discussion. She has been measuring maximum flight speeds and has found that *some* bumblebee queens are capable of speeds over 7 m s^{-1} . Extrapolation of the mechanical power curve to such high speeds leads to a steep increase in power, very akin to the metabolic results for hummingbirds. Dudley and DeVries (1990) have also constructed mechanical power curves for a migrating moth, showing a similar pattern. Finally, it is worth noting that Pennycuik's (1968) original, detailed mechanical power estimates for pigeons and hummingbirds do not show such a pronounced rise in power at low speeds as is predicted from his simplified theory, which he warned would 'lead to noticeable

errors at low speeds, but should be adequate in the medium speed region which is of most interest in connection with migration' (Pennycuick, 1969). Indeed, his original hummingbird calculations using data from the literature provide quite an acceptable match to Berger's metabolic results. I will not be surprised, therefore, if future research forces us to redraw our image of the U-shaped curve into a J-shaped curve with little variation in mechanical power from hovering to intermediate flight speeds, and then a sharp increase at higher speeds.

A J-shaped curve is consistent with an upper limit to flight speeds imposed by the available power, because of the steep increase in the power requirement. However, the flattened curve at low speeds is poorly suited to the hypothesis that minimum flight speeds are limited by power.

The remaining question about the mass-specific power requirement is how it scales with body size. Rayner (1979) reported that the minimum mass-specific power for flight scaled between $m^{0.05}$ and $m^{0.16}$ for different groups of birds, and Norberg and Rayner (1987) found $m^{0.19}$ for bats. Additionally, there have been two broad surveys of hovering animals, and a systemic variation of mass-specific power with body size was not evident (Weis-Fogh, 1973; Ellington, 1984c). Casey and Ellington (1989) have also examined the power requirements of hovering euglossine bees over a 15-fold range in body mass and found no significant scaling. Thus, the assumption that the mass-specific power required for flight scales between m^0 and $m^{1/6}$ is supported by the available data.

Power available

We now turn to the power available for flight: does the maximum mass-specific power output of the muscle scale adversely with increasing body size? Are the muscles of larger animals relatively weaker? This is a difficult question to answer, and three approaches have been employed in recent years.

Pennycuick and Rezende (1984) presented an elegantly simple model of maximum power output in which the power depends on stress, strain and contraction frequency. Their model is, in many respects, a much simplified version of that by Weis-Fogh and Alexander (1977); it is interesting to note that Weis-Fogh (1977) regarded the maximum mass-specific power output of muscle to be size-independent. Pennycuick and Rezende assumed that muscle strain and myofibrillar stress are relatively constant muscle properties, leaving frequency as the primary determinant of power. They further assumed that the rate of ATP production per unit volume of mitochondria is constant, and that the mitochondrial volume fraction is just sufficient to balance the maximum power output of the myofibrils. Thus, a frequency increase allows a greater power output, but this requires a greater mitochondrial fraction to fuel the myofibrils; the myofibrillar fraction must consequently 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 with mitochondria. In practice,

The mitochondrial fraction never reaches such absurd proportions, so the power of real muscles should increase almost linearly with frequency. Because frequency scales as $m^{-1/3}$ for flying animals as a whole, their model therefore offers support for the inverse relationship between mass-specific power and body size.

Ellington (1985) used their theoretical framework to estimate the maximum power available from insect flight muscle. Revised parameter values were used in the equations, leading to a predicted maximum power output of 80 W kg^{-1} for the synchronous muscle of locusts. The value agrees very well with two independent measures: Jensen's (1956) aerodynamic analysis predicted $67\text{--}100 \text{ W kg}^{-1}$, 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. Power output for the asynchronous flight muscle of the giant waterbug *Lethocerus* was estimated to be 113 W kg^{-1} : the only comparable data for intact asynchronous muscle are 29 W kg^{-1} for the coconut beetle *Oryctes rhinoceros* and 88 W kg^{-1} for the bumblebee *Bombus terrestris* (Machin and Pringle, 1959). The data required for such calculations are extremely scarce, and it was something of a triumph to obtain estimates for even those two examples. The scaling of power output with frequency for synchronous and asynchronous flight muscle clearly should not be extrapolated from these two estimates! Many more data on the operating stress and strain of muscles from a wide range of animals are required before the model, even with revision, can be used with confidence.

Josephson's (1985a) pioneering study then appeared and heralded the second approach to maximum power output. He adapted the work-loop technique used by Machin and Pringle (1959) on asynchronous muscle to the synchronous flight muscle of tettigoniids. In this technique, the muscle is forced into sinusoidal length oscillations while the tension is recorded. The net work is the area of the work loop formed when force is plotted against length; the power is simply frequency multiplied by the net work per cycle. The experimental technique permits variation of several parameters (e.g. strain, frequency, stimulus phase and temperature) in the search for conditions that maximise power output. A number of studies have since followed Josephson's lead, and Johnston (1991) provides an excellent review in this volume. For our purposes, we shall simply note the maximum power values that have been obtained: 76 W kg^{-1} for tettigoniid flight muscle (Josephson, 1985a); 33 W kg^{-1} for tettigoniid flight and singing muscle (Josephson, 1985b); 78 W kg^{-1} for locust flight muscle (Mizisin and Josephson, 1987); and 90 W kg^{-1} for the hawkmoth *Manduca sexta* flight muscle (Stevenson and Josephson, 1990). These values are reassuringly close to the theoretical estimate of 80 W kg^{-1} for locust flight muscle at similar frequencies. Stevenson and Josephson (1990) also point out that the thermal sensitivity of *Manduca* flight muscle is similar to that of muscles from other taxa, suggesting that maximum power output may simply reflect the operating temperature of the muscle. Given the complex nature of insect thermoregulation (e.g. Casey, 1988), this could be a very interesting observation indeed. Josephson's technique probably gives the best independent measure of maximum power output, but it will be many years before

enough data exist for a comprehensive test of the scaling of power output with body size. The tettigonids, locusts and hawkmoths all have similar maximum values, but they are of similar body sizes and wingbeat frequencies.

The third approach to maximum power output is to study the maximum flight performance of animals. Marden (1987) used a convenient experimental method in which power is manipulated simply by changing the weight of the animal; lead weights were attached until the animals could no longer take off from the ground and fly. Maximum load-lifting capabilities were determined for 147 insects, 10 birds and 3 bats. Marden (1990) added Pennycuick *et al.*'s (1989) data on the load-lifting ability of Harris' hawks to his earlier study, giving a set of results ranging from 19 mg damselflies to the 920 g Harris' hawk. If a scaling of maximum power exists, it should be evident in this work!

Marden found that the total flight muscle mass was the best predictor of lifting ability, and that all of the animals could lift about six times their muscle mass – a remarkably consistent result given the physiological differences between birds, bats and insects. From this, Marden (1987) concluded that mass-specific power did not change with body mass, but the link between lifting ability and power output was not properly established. Marden (1990) then estimated induced power under the conditions of maximum load, using the equation for hovering flight: at maximum loads the take-off speeds would certainly be low enough to be classified as 'hovering'. The maximum mass-specific induced power increased only slightly with increasing size, proportional to $m^{0.08}$.

Is maximum induced power an accurate reflection of the maximum power output of the muscles? They might have to provide inertial power to oscillate the wings. This could be a large power component for insects because of their high wingbeat frequencies, but it is thought that elastic structures in the flight motor maintain the oscillation at negligible cost (e.g. Weis-Fogh, 1973; Alexander and Bennet-Clark, 1977; Ellington, 1984c). For vertebrates, even if there is no elastic storage, the inertial power is a very small proportion of the total power requirement (Norberg, 1990). Marden's data are insufficient for calculations of profile power, the second largest power component in hovering, but its magnitude can still be estimated. For flying animals in general, as body size increases the mass-specific induced power will increase and the mass-specific profile power will decrease (Weis-Fogh, 1977). Induced power is therefore likely to dominate the total power output for larger animals. The calculations of Pennycuick (1968) for hovering pigeons and hummingbirds show that it is 73 % and 66 % of the total power, respectively, and a more recent detailed analysis of hummingbirds gives values between 75 % and 83 % (Wells, 1990). For large animals that are maximally loaded the induced power will necessarily be an even higher percentage, because more lift must be generated. The maximum power output of the muscles is thus perhaps some 25 % greater than the maximum induced power for birds. In the size range of insects, induced power is typically about half of the total power during unloaded hovering flight (Weis-Fogh, 1973; Ellington, 1984c). We have recently completed loading studies on bumblebees *Bombus lucorum* and hover flies

Cristalis tenax, and the results suggest that maximum power output is about 30 % greater than maximum induced power.

Marden's values for induced power are probably underestimates in themselves because of his aerodynamic analysis. Ellington (1984b) suggested that the 'actuator disc' area for induced power calculations should equal the area actually swept by the beating wings, and not the area of a circle with radius equal to the wing length, as is commonly used. Marden used the latter definition, and this is likely to underestimate induced power by about 20 % for typical wingbeat amplitudes of 120°. Amplitudes were not recorded, however, so the values cannot be corrected. Furthermore, some of his animals apparently flew in close proximity to the ground where the induced power is reduced by the 'ground effect'. His estimates could be about 10–30 % too high if the animals were between 2 and 1 winglengths above the ground (Bramwell, 1976), but adjustments cannot be made without knowing their height. Errors arising from the ground effect and the actuator disc area largely cancel out, fortunately, so the maximum power output is probably some 25–30 % higher than his maximum induced power estimates due to profile power. This correction pales into insignificance compared with the 36-fold change in available power over the mass range of 19 mg to 920 g if the assumed scaling of $m^{-1/3}$ is true.

Marden's results therefore provide an excellent opportunity for evaluating the scaling of available muscle power under maximal conditions. I have estimated *muscle* mass-specific induced powers from his data, instead of *body* mass-specific values, and the results are most interesting (Fig. 5). Regression of the pooled log-transformed estimates reveals that the maximum *muscle* mass-specific induced power scales with body mass according to an exponent of 0.13 ± 0.02 (± 95 % confidence limits, as used for tests of significance). Given that the maximum power output is probably 25–30 % higher, and that the correction varies little with body size, we should expect maximum available power to scale with a very similar exponent.

To test for taxonomic bias in this result, I have also analysed separate groups within Marden's data (Table 1). The largest animals in the study were birds, which should have an additional contribution of anaerobic power to maximally loaded take-offs. This enhanced power at large masses could bias the pooled scaling exponent upwards, but neither the slope nor the y-intercept of the log-transformed regression for birds are significantly different from the pooled results. Indeed, only the Zygoptera (damselflies) and Hymenoptera (bees) have y-intercepts that differ significantly from the pooled value of 1.84: a low value of 1.39 and a slightly high value of 1.93, respectively. The Zygoptera are doubly curious in that they have a negative slope of -0.23 in contrast to the pooled result of 0.13. The other sub-order of the Odonata, the Anisoptera (dragonflies), are the only other group with a significantly different slope (0.27) from the pooled value.

Over the restricted size range of each group, changes in power with mass are comparable with the unexplained variance of the data (r^2 values are typically between 0.2 and 0.8), so it is also useful to discuss mean values for each group.

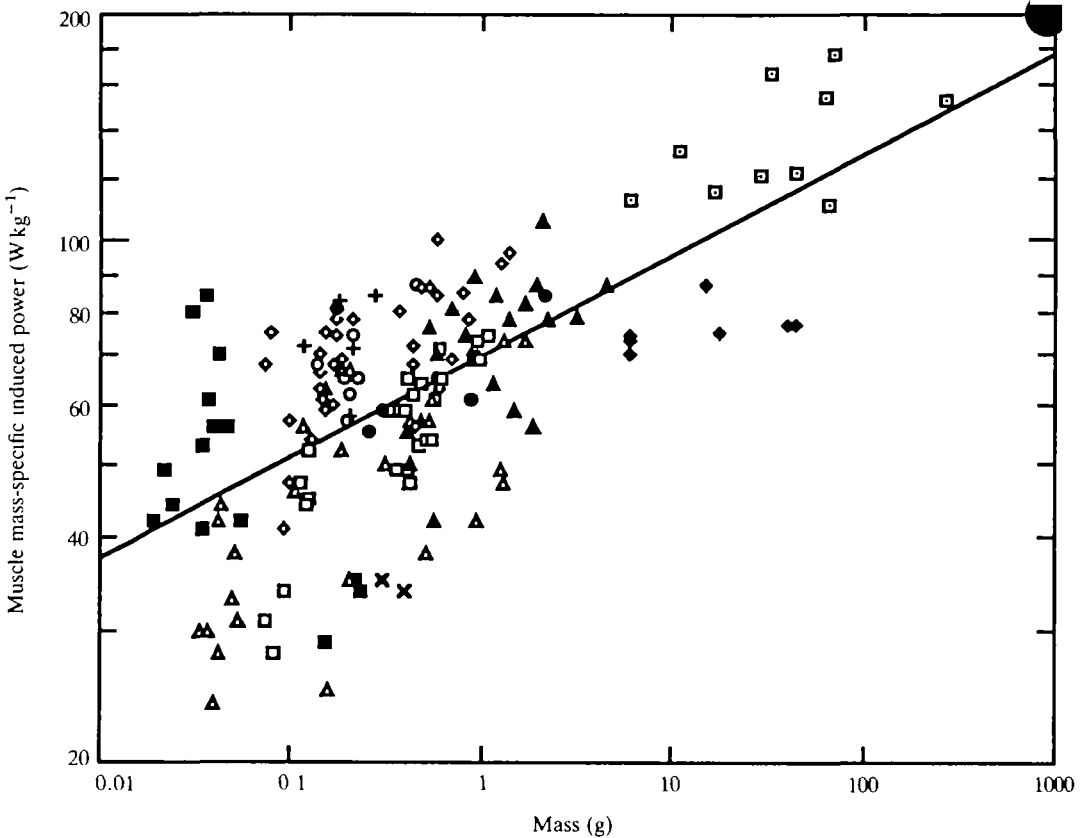


Fig. 5. Induced power per unit muscle mass plotted against body mass for maximally loaded animals. Power values are calculated from data in Marden (1987, 1990). Symbols for different groups are as follows: \square birds, \blacklozenge bats, \triangle Lepidoptera that use a clap-and-fling, \blacktriangle Lepidoptera - sphingids, \square Anisoptera (Odonata), \blacksquare Zygoptera (Odonata), \diamond Hymenoptera, \bullet Coleoptera, \circ Hemiptera, $+$ Diptera, \times Orthoptera.

Indeed, the slopes for four groups (birds, bats, Hemiptera and Diptera) are not significantly different either from zero or from the pooled result, so the possibility of size-independence within some groups cannot be excluded. Values for birds range from 111 to 177 W kg^{-1} muscle with a mean of 137 W kg^{-1} . Some of the variance may reflect differences in muscle fibre composition; a hummingbird had one of the lowest values (113 W kg^{-1}), and this would be consistent with a reduced anaerobic capacity. Allowing an additional 25 % for profile power, the maximum power output is 171 W kg^{-1} on average for bird flight muscle, including both aerobic and anaerobic contributions.

Six taxonomic groups had values clustered between 65 and 76 W kg^{-1} muscle: bats, sphingid hawkmoths, Hymenoptera, Coleoptera, Hemiptera and Diptera. Insect flight muscle has virtually no anaerobic capacity (Beenakkers *et al.* 1984), so those values might represent the maximum possible under strictly aerobic muscle.

Table 1. Group regressions of log-transformed data in Fig. 5

Group	N	y-intercept	Slope
Birds	10	2.00 (0.18)	0.08 (0.11)
Bats	7	1.84 (0.10)	0.03 (0.08)
Insects			
Lepidoptera			
Clap-and-fling	28	1.76 (0.07)	0.16 (0.08)
Sphingids	21	1.84 (0.04)	0.18 (0.13)
Odonata			
Anisoptera	29	1.86 (0.03)	0.27 (0.06)
Zygoptera	15	1.39 (0.26)	-0.23 (0.19)
Hymenoptera	33	1.93 (0.04)	0.15 (0.07)
Coleoptera	5	1.84 (0.06)	0.17 (0.15)
Hemiptera	8	1.98 (0.25)	0.21 (0.37)
Diptera	6	1.93 (0.51)	0.08 (0.69)
Pooled	164	1.84 (0.02)	0.13 (0.02)

N is the number of individuals in each group.

Linear regressions were performed on $\log(\text{muscle mass-specific induced power})$ versus $\log(\text{body mass})$. Values of y-intercept and slope are followed by $\pm 95\%$ confidence limits in parentheses.

operation. Bats have a fibre composition that is almost as variable as that of birds (Norberg, 1990), but their maximum induced power is clearly lower than that of birds of the same size. If the values are increased by 25 % for bats and 30 % for insects, to allow for profile power, maximum power outputs of $85\text{--}98\text{ W kg}^{-1}$ muscle are obtained: a nicely rounded figure of 100 W kg^{-1} would not be far off. The agreement with Stevenson and Josephson's value of 90 W kg^{-1} for intact muscle from the sphinx moth *Manduca sexta* is reassuring. It is remarkable that the values are so similar for three different types of muscle: vertebrate striated, insect synchronous and insect asynchronous.

A third group had maximum mass-specific induced powers between 47 and 56 W kg^{-1} muscle for their synchronous flight muscle: the Odonata, and those butterflies and moths that augment their lift generation with the fling mechanism (Weis-Fogh, 1973; Ellington, 1984a). Within the Odonata, the Zygoptera use a fling and the Anisoptera do not, but their values do not differ by much. It is not clear why power values for this group are substantially lower than those for the insects of comparable size above, but it is worth noting that they are not strong fliers in general.

The fourth group consists of only two mantids (Orthoptera), which are very weak fliers and have a low maximum mass-specific induced power of 35 W kg^{-1} of muscle. It is a pity that other Orthoptera were not investigated, allowing a comparison with Josephson's results for synchronous locust and tettigoniid flight muscle.

The results of this section confirm Marden's (1987) rather premature conclusion that available mass-specific muscle power does not scale as $m^{-1/3}$; the assumption that the muscles of larger animals are relatively weaker is flatly contradicted by experimental results showing that they are, if anything, relatively stronger. The general trend is for total mass-specific power to scale as $m^{0.13}$. The results for most groups show a similar scaling, but mass-specific power might be nearly size-independent in some groups.

Given the trend for frequency to scale as $m^{-1/3}$, these results also imply that the muscle mass-specific work W_m^* per cycle of contraction ($=P_m^*/f$) is proportional to $m^{0.46}$. This strong increase with increasing body size is at the heart of the discrepancy with the available power argument, which assumes that W_m^* is size-independent. The mass-specific work can be written as (e.g. Pennycuick and Rezende, 1984):

$$W_m^* = \sigma \epsilon / \rho,$$

where ϵ ($=\Delta L/L$) is the strain and ρ is the mass density of muscle. The stress σ ($=F/A$) during contraction is more properly defined as the weighted stress *difference* between shortening and lengthening, to allow for non-zero stresses during the relaxation phase. For W_m^* to increase with increasing body size, then stress and/or strain cannot be constant as assumed.

The intrinsic speeds of muscles are likely to impose limits on possible values of strain ϵ at higher frequencies (Weis-Fogh and Alexander, 1977); indeed, Ellington (1985) and Josephson (1985*b*) criticised the model of Pennycuick and Rezende (1984) for neglecting this. The strain rate during contraction is proportional to ϵf , and it cannot exceed the intrinsic speed. For strain to be constant the intrinsic speed must scale in proportion to frequency, but the muscles of smaller animals seem to have reached an upper limit on intrinsic speed. The strain must therefore decrease for smaller animals because of this restriction on strain rate; the muscles will necessarily contract through shorter distances at higher frequencies. The range of body sizes corresponding to this restriction is not known, but a decrease of strain between the smaller vertebrates and the larger insects is apparent: strains for the flight muscles of the budgerigar and zebra finch have been estimated as 20% (Cutts, 1986), while those giving maximum power for synchronous insect flight muscle are typically about 5–8% (Josephson, 1985*a,b*; Mizisin and Josephson, 1987; Stevenson and Josephson, 1990). The strains for asynchronous insect flight muscle, which operates up to much higher frequencies, might be expected to decrease even further. However, they are not much smaller (e.g. Ellington, 1985), perhaps because strains of less than about 3% would come within the elastic range of cross-bridge deformations (Huxley and Simmons, 1971; Rack and Westbury, 1974; Ford *et al.* 1977; Flitney and Hirst, 1978). Constant strain and a decrease of stress with decreasing body size have instead been reported for some asynchronous muscles (Casey and Ellington, 1989). Many more data are clearly required on the stress and strain of locomotor muscles before we can understand the scaling of mass-specific work, but it would be unwise to assume that they are constant.

What actually limits flight performance?

The conventional wisdom that flight performance is limited by the intrinsic scaling of available and required power is beginning to look decidedly suspect. The key reason for this conclusion is the finding that the mass-specific power available scales as $m^{0.13}$ in general rather than the assumed $m^{-1/3}$. This empirical exponent, and those for individual groups, overlaps with the scaling exponents for the mass-specific power required to fly. Without much more extensive data, I do not think we can distinguish between the scaling of available and required powers. One consequence of this conclusion is that, to a first approximation, all flying animals should have the same fraction of available power left for energetically demanding manoeuvres and climbing flight. Another is that we cannot predict a maximum body size for flapping flight: the scaling of power required is too similar to that of power available for an accurate prediction of the intersection of the two relationships. Large fossil birds, if they were still alive, might be relieved to learn that they could fly after all!

Are maximum flight speeds limited by power? The steep increase in power requirements with speed on the right-hand side of the U-shaped curve has not been questioned, and its intersection with available power would provide a clear-cut limit. Given the similar scaling of available and required powers, this limit would be size-independent to a first approximation. It seems very reasonable to suspect that the limit exists, but reliable measures of maximum airspeeds are far too few to test their scaling. Typical flight speeds of many insects are some 2–4 times slower than those of birds (Hocking, 1953; Rayner, 1985), and it is likely that their maximum speeds differ by a similar amount. Is this due to a scaling of power with body mass? A factor of two or four is within the scatter of the allometric trends and could easily be explained by other considerations, such as the deterioration of aerodynamic performance at the low Reynolds numbers characteristic of insect flight. Indeed, if power does not provide a significant intrinsic scaling of flight performance, then departures from the general isometry of flying animals become of prime interest.

Marden (1987) identified perhaps a major parameter to understanding flight performance: the flight muscle ratio (flight muscle mass/unladen body mass). Although muscle mass scales isometrically for all flying animals, there are significant departures which correlate with the flying ability of different groups. He defined the 'marginal flight muscle ratio' as the ratio of flight muscle mass to total mass (body mass plus attached weights) when take-off ability was marginal: remarkably consistent values between 0.16 and 0.18 were found for birds, bats and insects that use a conventional wingbeat (i.e. without the lift-enhancing clap-and-fling mechanism). This illustrates the lack of an intrinsic scaling of flight performance most effectively: all animals, from damselflies to birds, would just be capable of a standing take-off if 16–18 % of their unladen mass were flight muscle. A size-independent improvement in performance was shown by shallow take-off angles at a ratio of 0.20, and by higher angles with larger ratios.

In a literature survey of 425 bird species, Marden found that unladen flight

muscle ratios for birds ranged from 0.12 to 0.44. The lowest ratios were found in aquatic and semi-aquatic birds that are weak fliers and generally must taxi for take-off, and in reclusive, mostly neotropical birds whose flight behaviour is little known. At the other extreme, high ratios can be found in birds that make rapid bursts or steep take-offs: pigeons, larks, sandpipers, bustards, Old World finches, trogons and grouse (Rayner, 1988). Thus, the flight muscle ratio, and not size *per se*, is the best available predictor of flight ability. Marden points out the obvious disadvantages of an unnecessarily high ratio in reducing load-carrying capacity, and suggests that a high ratio should occur in animals that frequently need high power for lifting loads, capturing prey, avoiding predators or competing aerially for territories and mates.

Does power limit the minimum speed for birds that are incapable of low-speed flight and hovering? If the low-speed end of the required power curve is a pronounced U-shape rather than a more flattened J-shape, then the power available from the flight muscle ratio might determine low-speed performance. In his literature survey, Marden found that only 3 % of bird species had ratios less than the marginal value of 0.16. All of the birds in his experiments had ratios greater than 0.2, but unless his empirical results suddenly break down for small ratios then 97 % of bird species should be capable of a standing take-off; this includes the 12 kg Kori bustard, which was chosen by Pennycuick (1969) to illustrate the marginal power available for the largest birds. Even the most casual observer cannot accept this conclusion, suggesting that it is not power that limits low-speed performance. Unfortunately, this means that the question of U-shaped and J-shaped curves cannot be resolved from these data.

For an alternative explanation of flight performance, maybe aerodynamics can help. How the wings generate enough lift for the animal to stay aloft is, of course, a fundamental aspect of flight. The production of lift is not usually thought to be a limiting factor in the scaling of flight performance, but perhaps it should be re-examined. At present, there is some uncertainty about the aerodynamic mechanisms involved in hovering and low-speed flight: the weight of modern evidence is clearly against a conventional aerodynamic mechanism (Cloupeau *et al.* 1979; Ellington, 1984c; Ennos, 1989; Dudley and Ellington, 1990b; Wells, 1990; Wilkin, 1990; Dudley, 1991), but we are undecided about the alternative unsteady mechanisms. Nevertheless, progress can still be made. The lift force on wings can be expressed as the lift coefficient C_L , a dimensionless form that can be defined for conventional or unsteady mechanisms. A maximum C_L must exist for any aerodynamic mechanism, representing the maximum lift force that can be generated. Does the lift coefficient required for flight change with speed, or scale with body size? If so, then the maximum possible C_L might impose limitations on flight performance.

The lift coefficient required for flight drops sharply from hovering to intermediate flight speeds (Pennycuick, 1968; Dudley and DeVries, 1990; Dudley and Ellington, 1990b; Dudley, 1991). As speed increases the velocity of the wing relative to the air also increases, and this explains why it becomes easier

Generate the required lift. If flying animals are close to the maximum lift coefficient, as many seem to be, then flight at low speeds and hovering might not be possible. The lift coefficient for hovering flight increases as the $1/3$ power of body mass for isometric animals with wingbeat frequency proportional to $m^{-1/3}$, as is generally found (Greenewalt, 1975). This strong scaling is true for both conventional and unsteady mechanisms (Weis-Fogh, 1977; equations in Ellington, 1984c), and it would certainly impose an upper size limit for hovering and slow flight. Some of the morphological and kinematic adaptations which depart from isometry in many groups probably represent an attempt to circumvent this scaling over restricted size ranges. The general trend must triumph eventually, however, and this might explain why larger birds cannot hover or fly at low speeds.

I thank Alison Cooper for use of her preliminary results and the Science and Engineering Research Council for financial support.

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