In search of a biological constant: the maximum isometric stress of vertebrate skeletal muscle deduced from the flight performance of a Whooper Swan

C.J. Pennycuick

Written 2006: not published, but used in Chapter 7 of *Modelling the Flying Bird*, and for calculating rate of climb in the *Flight* program

Abstract

A bird that can maintain level flight without resorting to soaring must be able to supply sufficient mechanical power from its flight muscles to equal or exceed the aerodynamic power required to fly at the minimum-power speed. The power available from unit mass of muscle (specific power) can be found by multiplying together the stress and strain during shortening, and the wingbeat frequency. The stress for maximum power is a fixed proportion of the isometric stress, which is itself expected to be constant in all vertebrates, because of the uniformity at the molecular level of the contractile filaments, but this value is difficult to measure experimentally, and published estimates vary widely. The strain is better known, and a value of 0.26 for the muscle to deliver maximum power is derived from the classical literature. This value is considered to be constant for all vertebrates, while the wingbeat frequency in cruising flight can be estimated for individual birds from the mechanics of the beating wings (not from regressions). Because of scale effects, very large birds approach a limit of mass at which the minimum power required for level flight approaches the maximum available from the muscles. The minimum power required by a particular, very large Whooper Swan (*Cygnus cygnus*), was calculated from *Flight* 1.17, and found to exceed the maximum power available from its muscles, estimated from a value of the isometric stress (300 kN m^{-2}) that had previously been used for calculations of this kind. The isometric stress had to be raised to 560 kN m^{-2} to account for the swan's known capabilities. The discrepancy could alternatively be due to *Flight* over-estimating the minimum power required to fly, but this is considered unlikely as drastic and implausible adjustments to default values would be needed to resolve the discrepancy, and also because the existing defaults account satisfactorily for the known migration performance of two ultra-long distance migrants, the Great

Knot (*Calidris tenuirostris*) and the Alaskan Bar-tailed Godwit (*Limosa lapponica*). The value of 560 kN m^{-2} is above the range of values reported from measurements of the isometric stress of isolated muscles, but these suffer from difficulties in ensuring that the muscle is delivering its full performance, and also in measuring the cross-sectional area of the myofibrils, separately from that of other components of muscle cells. The new default value accounts satisfactorily for rate-of-climb observations on waders departing on migratory flights. *Flight* 1.17 also indicates that the giant pterosaur *Quetzalcoatlus northropi* might have been marginally able to maintain height in flapping flight, if the air density were increased to about 4 kg m^{-3}, a factor of 3.2 above the present sea-level value. This is conceivable as a transient effect of the massive volcanism that characterised the extreme end of the Cretaceous Period, when this huge pterosaur briefly occurred.

C.J. Pennycuick, School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, U.K. E-mail: c.pennycuick@bristol.ac.uk.

Key words: isometric stress, whooper swan, flight performance, pterosaur

Introduction

This paper is based on the assumption that the maximum specific power output available from the flight muscles of a particular bird is determined by the values of three quantities, two of which are effectively constant in all vertebrates, while the third is variable but can be estimated for a given bird in cruising flight. If the values of the two constants were known, then the maximum power available from the flight muscles could be easily calculated for any bird. The first of the constants is the isometric stress, i.e. the force per unit of cross-sectional area that the myofibrils are capable of exerting in an isometric contraction. The lower stress that prevails when the muscle is developing maximum power is a known proportion of the isometric stress. Values for the isometric stress have been obtained from experiments on isolated muscles, but are somewhat uncertain because of technical difficulties. The second constant, which is more accessible to accurate experimental measurement, is the active strain, meaning the change of length during shortening, divided by the length at which shortening begins. Between them the isometric stress and the active strain determine the specific work, that is the work done by unit mass of myofibrils in

each contraction. The third variable determining the power is the contraction frequency, which, in the case of bird flight muscles, is the same as the wingbeat frequency. This is not a constant, but is constrained by the mechanics and aerodynamics of the beating wings. A particular bird's wingbeat frequency in cruising flight can be predicted from the bird's body mass, wing span and wing area, provided that the strength of gravity and the air density are also known.

Most birds only require maximum power from their flight muscles during take-off or emergency manoeuvres, not in prolonged cruising flight. However, very large birds have little if any margin of the maximum power available from the muscles over the minimum aerodynamic requirements, because of a well-known scale effect whereby the minimum mechanical power required for cruising flight increases with increasing body mass, more steeply than the maximum power available from the muscles. One might suppose that larger birds would tend to have a larger flight muscle fraction (flight muscle mass divided by body mass) than smaller ones, but this has not been found in allometric studies. In the absence of any such trend, it follows that there must be an upper limit to the body mass, at which the maximum power available from the flight muscles is just sufficient to cover the minimum power required for sustained level flight, and it appears that the larger species of swans are near this limit. In that case, the observation that a particular swan is capable of migrating over a known migration route, without any known behaviour that would extract energy from the atmosphere (soaring), can be used to provide a minimum estimate for the power that can be continuously produced by the flight muscles, and this in turn can be used to estimate the isometric stress in the myofibrils, since good estimates are available for the other two variables involved, the active strain and the wingbeat frequency.

Constancy of muscle properties

The sliding filament mechanism

The classical theory of the molecular basis of muscle contraction was reviewed and explained by McMahon (1984) from both a morphological and a quantitative physiological point of view. As seen in longitudinal section (Fig. 1A) the repeating structural unit of striated (skeletal) muscle is the sarcomere, which consists of a parallel array of thick (myosin) filaments, with two arrays of thinner (actin) filaments

that slide in between the myosin filaments from either end. These *myofibrils* occur inside muscle cells together with other sub-cellular components such as nuclei and mitochondria. Neither the myosin nor the actin filaments themselves shorten when the muscle shortens. Instead, the two sets of actin filaments are attached to the Z-membranes, which mark the ends of the sarcomere, and move inwards towards the centre of the sarcomere when the muscle shortens, sliding past the myosin filaments. Tension is produced by cross-bridges that project from the myosin filaments, and connect to attachment sites on the actin filaments. Work is done by each cross-bridge as it repeatedly attaches to the actin filament and deflects, so walking along the actin filament and pulling it towards the centre of the sarcomere.

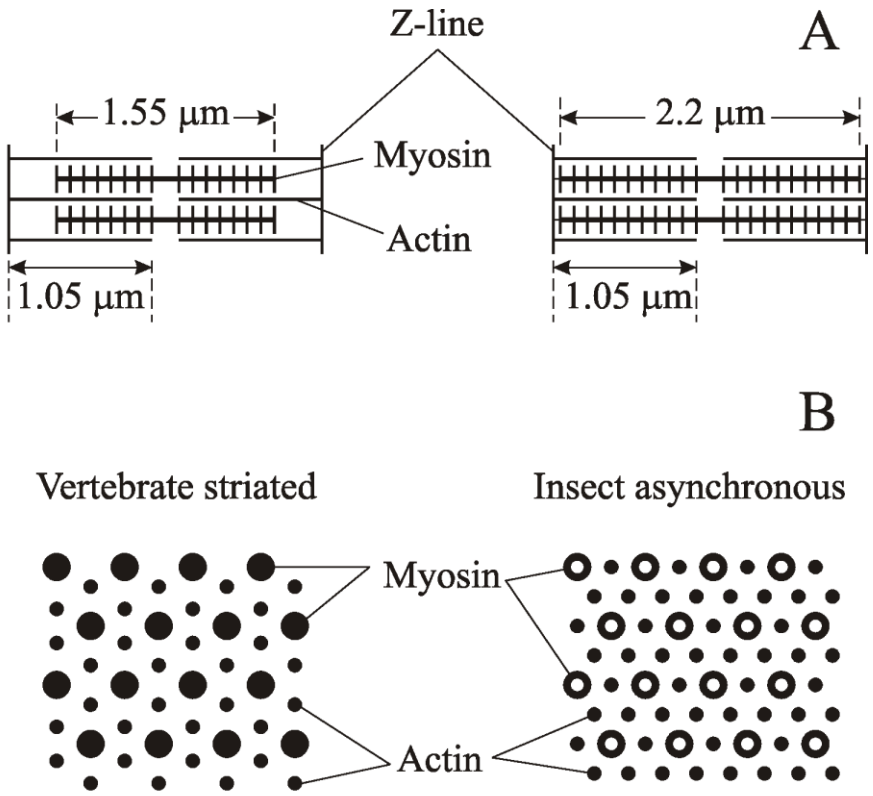


Fig. 1. A. Diagrammatic longitudinal section through a single sarcomere of a vertebrate striated muscle and an insect asynchronous muscle. The sarcomeres of each type have a standard morphology, which repeats end-to-end along the muscle fibre. The specific work is much lower in insect muscles, because the sarcomere can only shorten through about 2% of its extended length before the ends of the myosin filaments butt against the Z-membranes, as compared to 26% in vertebrate muscles. However, insect muscles achieve similar levels of specific power by operating at higher frequencies.
B. Cross-sectional views of the acto-myosin array. The ratio of thin (actin) to thick (myosin) filaments is 2:1 in vertebrates and 3:1 in the asynchronous flight muscles of insects. After White and Thorson (1975).

Constancy of isometric stress

According to Huxley (1985), the length of the myosin filaments is the same in the skeletal muscles of *all* vertebrates (1.55 μm), and their cross-sectional packing density is also constant at about 5.7 x 10^{14} per square metre (Fig 1). If the maximum isometric force that each myosin filament can exert were also constant, then this would be directly proportional to the isometric *stress* across the array (force per unit area). The maximum force that a myosin filament can exert depends on the number of cross-bridges that can be attached at the same time, and one might suppose that this could be increased by lengthening the filament to accommodate more cross-bridges. However, this would require the middle portion of the filament to be thicker, as it carries the tension developed by the cross-bridges at both ends, pulling outwards against one another. There must be an upper limit to the thickness of the myosin filaments, before their bulk disrupts the cross-sectional geometry of the array, and Huxley's (1985) observations imply that the length of each myosin filament is limited by the cross-sectional geometry to 1.55 μm, and that this in turn constrains the maximum force per filament to a value which is the same for all vertebrates. The actual value is not easy to measure, however. While there are many measurements in the literature of the isometric *force* developed by muscles that have been removed from the animal, converting these into measurements of stress is difficult and uncertain. Alexander (1985) and Alexander and Bennet-Clark (1977) cite estimates that range from about 300 to 450 kN m^{-2}, which reflects the difficulty of discriminating the cross-sectional area of the actual contractile filaments from that of the muscle as a whole, and also of ensuring that an isolated muscle is generating the maximum force of which it would be capable in the intact animal. This paper proposes an alternative, indirect method of estimating the isometric stress, after which the revised value, being assumed constant for all vertebrates, can be used to predict the performance of any vertebrate.

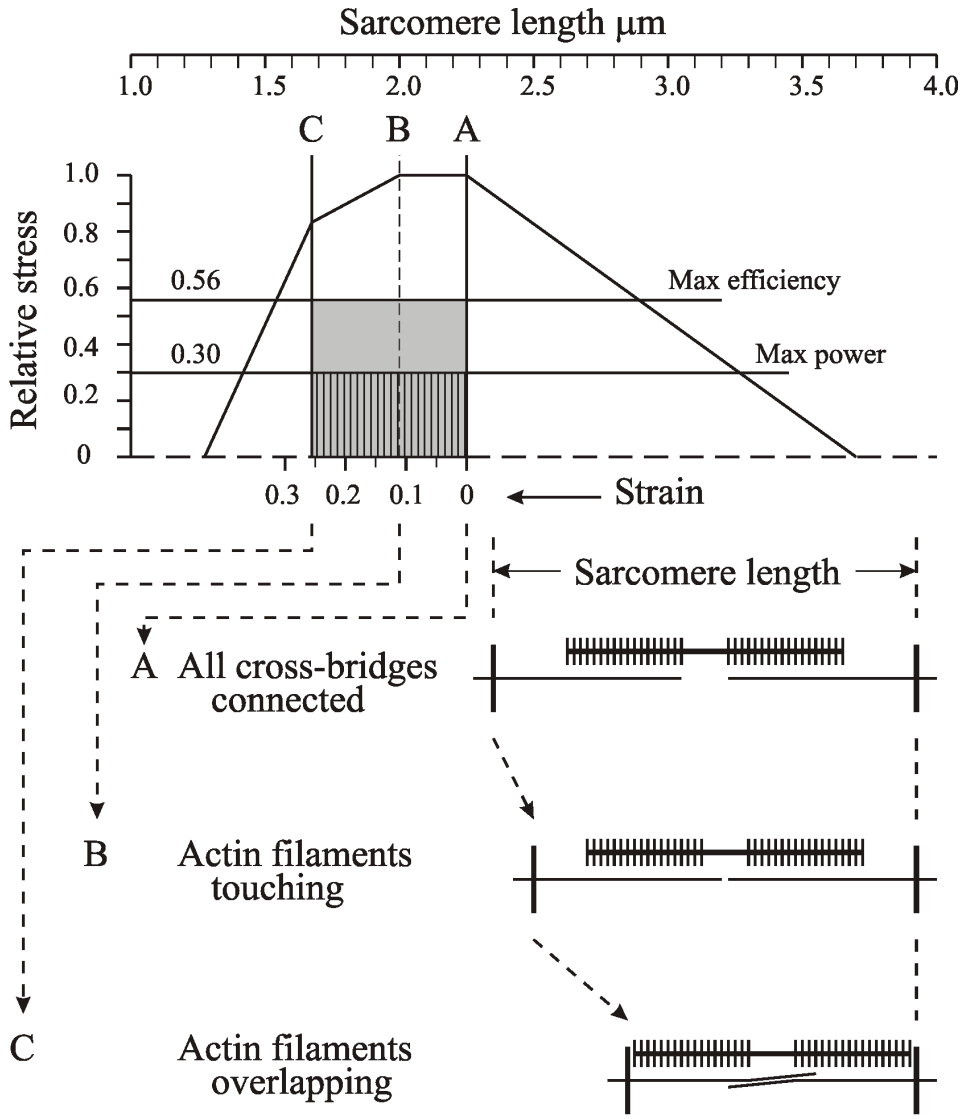


Fig. 2. Isometric stress developed by an isolated frog muscle over a length range of 1.25 - 3.70 μm. All cross-bridges are attached between 2.25 μm (A) and 1.67 μm (C) and this is presumed to be length range permitted by the skeleton, in muscles adapted for high power. The stress is reduced slightly between B and C, because the ends of the two sets of actin filaments, coming in from opposite ends, meet and overlap. Maximum power requires the stress to be 0.30 times the isometric stress, and the specific work is represented by the vertically hatched area. Maximum efficiency is obtained at a higher relative stress (0.56) and a lower strain rate (grey area). Based on Gordon et al. (1966).

Constancy of active strain

Gordon et al. (1966) measured the isometric force developed by an isolated frog muscle mounted in an apparatus with which they could impose length changes (Fig. 2). At the same time they observed the sarcomere length (Z-membrane to Z-membrane) through a microscope, and related this to the sliding filament configuration observed in electron micrographs. They found that the muscle could be extended to a sarcomere length of 3.7 μm, but that it exerts no force at this length,

because the tips of the actin and myosin filaments are then only just touching, with no overlap, and therefore no cross-bridges attached. As the muscle is allowed to shorten towards the normal range of length, more cross-bridges find attachment sites, and the tension increases. All the cross-bridges are attached when the sarcomere length is between 2.25 and 1.67 μm (points A and C in Fig. 2) and this is assumed here to be the range of length through which the muscle shortens, if maximum force (and power) is required. It corresponds to a shortening of 0.58 μm from a starting length of 2.25 μm, i.e. an active strain of 0.26. Obviously lesser strains are possible, and so are larger strains if the skeleton permits, at the cost of a diminution of stress, but this experiment supplies a value for the strain that delivers maximum specific work. The value is transferable to other vertebrates because of the morphological constancy of the sarcomere, but not to other taxa in which the cross-sectional geometry of the sliding filaments may be different (Fig. 1).

Power available from bird flight muscles

Stress, strain, work and power

The active stress (σ_{mf}) is defined as the force exerted per unit of cross-sectional area of myofibrils while the muscle is contracting. It has the dimensions of force divided by area, and if multiplied by the active strain (distance shortened divided by extended length), the result is the work done divided by the volume of the muscle, that is q_v, the volume-specific work.

$$q_v = \sigma_{mf} \lambda. \quad (1)$$

This is related to the mass-specific work (q_m) by the density of muscle (ρ_{musc}), which is usually taken to be constant at 1060 kg m^{-3}.

$$q_m = q_v / \rho_{musc} = \sigma_{mf} \lambda / \rho_{musc}. \quad (2)$$

If m_{mf} is the mass of myofibrils in a particular bird's flight muscles, then the cycle work (work done in each contraction) is $m_{mf} q_m$, and the mechanical power output of the muscles (P_{mech}) is

$$P_{mech} = m_{mf} \sigma_{mf} \lambda f / \rho_{musc}, \quad (3)$$

where f is the contraction frequency, which is the same as the wingbeat frequency. The subscript *mf* indicates that the muscle mass and active stress refer to the myofibrils, not necessarily to the muscle as a whole (below). In this paper an estimate

from aerodynamic considerations of the power required (P_{mech}) for a very large bird to fly level is used to get an estimate of σ_{mf} by inverting Equation 3:

$$\sigma_{mf} = P_{mech}\, \rho_{musc} / m_{mf}\, \lambda\, f. \qquad (4)$$

The values of all five variables on the right-hand side of Equation 4 can be estimated for an individual bird for which basic body measurements are available.

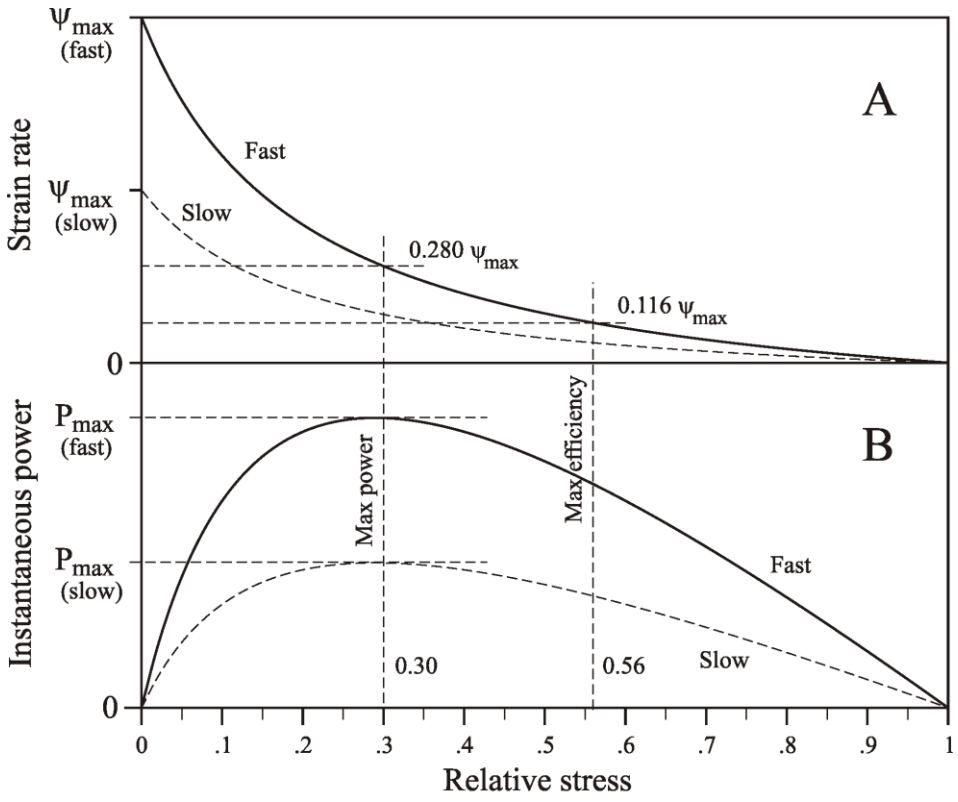


Fig. 3. A. Graph of Equation 5, the non-dimensional form of Hill's Equation, in which the abscissa (relative stress) is the ratio of the stress to the isometric stress, and the ordinate (strain rate) is the speed of shortening divided by the extended length. A "fast" muscle differs from a "slow" one in having a higher value of the maximum strain rate, corresponding to zero relative stress, but the isometric stress is the same for both.
B. Instantaneous specific power during shortening (as opposed to average power in serial contractions), found by multiplying the stress by the strain rate. Both fast and slow muscles deliver maximum power when the relative stress is 0.30 and the strain rate is 0.280 ψ_{max}, but the whole curve is higher for the fast muscle than for the slow one. Maximum efficiency is the same for a fast or a slow muscle, but is delivered at a higher relative stress (0.56) and a lower strain rate (0.116 ψ_{max}). After Pennycuick (1992).

Stress for maximum power output

If an active muscle is allowed to shorten, the *strain rate* (ψ) is related to the stress by Hill's Equation (Hill, 1938), of which the non-dimensional form is:

$$\psi = \beta\, (\sigma_{max} - \sigma_{mf}) / (\sigma_{mf} + \alpha). \qquad (5)$$

ψ is the speed of shortening divided by the extended length, and σ_{max} is the isometric stress, developed when the muscle is not allowed to shorten ($\psi = 0$). The constants α and β have the dimensions of stress and strain rate respectively. The graph of ψ from Equation 5 is shown in Fig. 3A for values of the stress from zero to σ_{max}. If the muscle

is allowed to shorten freely ($\sigma_{mf} = 0$), the muscle shortens at its maximum strain rate (ψ_{max}), where

$$\psi_{max} = \beta\, \sigma_{max} / \alpha. \qquad (6)$$

ψ_{max} is a property of the individual muscle, which distinguishes a "fast" muscle from a "slow" one. Its value has to be matched to the strain rate at which the muscle is constrained to shorten during locomotion by the load to which it is attached. This is done by adjustment of the rate constants that govern the detachment and reattachment of myosin cross-bridges (Pennycuick, 1991).

The instantaneous power developed during shortening is proportional to the product of the stress times the strain rate (Fig. 3B), and this peaks when the stress is 0.30 σ_{max}, falling to zero when the stress is zero, and also when the stress is equal to σ_{max} (because then the strain rate is zero). In a bird in cruising flight, the strain rate while the muscles are shortening is proportional to the wingbeat frequency (f) which can itself be predicted by the formula

$$f = m^{3/8}\, g^{1/2}\, b^{-23/24}\, S^{-1/3}\, \rho^{-3/8}, \qquad (7)$$

where m is the bird's all-up mass, g is the acceleration due to gravity, b is the wing span, S is the wing area and ρ (Greek rho) is the air density. This formula was derived from dimensional considerations (not from regressions) by Pennycuick (1990, 1996), and shown later to predict the wingbeat frequencies of species other than those in the original field study (Pennycuick, 2001). The five variables in Equation 7 are not under the direct control of the bird, except that small birds (passerines) manipulate gravity by bounding. Instead, a bird's wingbeat frequency is imposed upon it by the physics of flapping flight, and this in turn determines the strain rate in the flight muscles while they are shortening. From Equation 3, the maximum mechanical power (P_{max}) that the muscle is capable of delivering is

$$P_{max} = 0.30\, \sigma_{max}\, m_{mf}\, \lambda\, f / \rho_{musc}. \qquad (8)$$

This only applies if the muscle is matched to its load (by adjustment of ψ_{max}) in such a way that the stress is 0.30 σ_{max} during shortening. This is assumed to be the case in a bird that is adapted to operate continuously at near-maximum muscle power, but it is not, of course, the case in many experiments in the literature on birds operating under other circumstances, or on isolated muscles operating under arbitrary conditions imposed by the experimenter.

Mitochondria in aerobic muscle

The present argument is not concerned with the consumption of fuel energy or oxygen, but the observation that the bird can fly for prolonged periods means that its flight muscles are capable of operating aerobically, and this in turn means that the muscle cells must contain a sufficient volume of mitochondria to support the calculated mechanical power. The volume of mitochondria needs to be taken into account, because its presence means that the stress across the muscle as a whole is less than that across the myofibrils. Following Pennycuick and Rezende (1984), the total volume (v) of the muscle may be regarded as being made up of two components, the volume of myofibrils (v_{mf}) and the volume of mitochondria (v_{mt}). Neglecting other cell components,

$$v = v_{mf} + v_{mt}, \tag{9}$$

and the mitochondria fraction (ζ) is

$$\zeta = v_{mt} / v. \tag{10}$$

The volume of mitochondria needed for continuous flight is assumed to be proportional to the mechanical power output of the flight muscles:

$$v_{mt} = k P_{mech}, \tag{11}$$

where the constant k is the "inverse power density" of the mitochondria. It follows that if p_v is the specific power in the muscle as a whole, i.e.

$$p_v = P_{mech} / v, \tag{12}$$

then the mitochondria fraction required for continuous flight is

$$\zeta = p_v k. \tag{13}$$

k is a property of the mitochondria, and its value in bird flight muscles was estimated by Pennycuick and Rezende (1984) as 1.2×10^{-6} m^3 W^{-1}, meaning that 1.2 ml of mitochondria is assumed to be required to supply ATP for each watt of mechanical power produced by the muscle. If it is assumed that myofibrils and mitochondria have the same density, then ζ can be regarded as either the mass- or the volume-fraction of mitochondria.

Power required for level flight

Computed power curve

The mechanical power required to fly horizontally is a U-shaped function of speed, which can be synthesised for a particular bird by adding together the induced power

(needed to support the weight in air), the parasite power (to overcome the drag of the body) and the profile power (to overcome the profile drag of the wings). A theory that does this was adapted for birds from helicopter theory by (Pennycuick, 1969, 1975, 1989), and is implemented in the author's *Flight* program, available free from www.bio.bristol.ac.uk/people/pennycuick.htm. This generates the curve of mechanical power versus speed, and identifies the minimum power speed (V_{mp}), at which the power passes through a minimum. A bird with only marginally enough muscle power for level flight is confined to speeds very near V_{mp}.

The program also calculates the wingbeat frequency (f) for level flight at V_{mp} from Equation 7. The program accepts the flight muscle fraction (F_{musc}) as input, meaning the ratio of the total mass of the flight muscles (including mitochondria) to the all-up mass, and uses this to find the specific power in the whole muscle, and hence the mitochondria fraction (ζ), the mass of myofibrils (m_{mf}), and the specific work in the myofibrils (q_m). Thus estimates are available during the power-curve calculation for four out of the five variables (m_{mf}, λ, f and ρ_{musc}) needed to calculate the maximum available power (P_{max}) from Equation 8, if the fixed values noted above are assigned to the active strain (λ = 0.26) and the density of muscle (ρ_{musc} = 1060 kg m^{-3}). The remaining variable is the isometric stress (σ_{max}). The strategy of this paper is to find the minimum value of σ_{max} that will account for the power needed to maintain level flight, by a bird that is so large that near-maximum power is needed to do this. The actual calculation is done in terms of rate of climb, i.e. the maximum vertical component of velocity that the bird can achieve. This has to be zero or more for a bird that is able to maintain level flight.

Excess power and maximum rate of climb

From *Flight* Version 1.17 onwards, the power curve calculation includes estimates of the maximum rate of climb as a function of speed. This works by finding the excess power *available* (P_{ex}) as the difference between P_{max} and the power *required* to fly horizontally (P_{mech}) as calculated by the program.

$$P_{ex} = P_{max} - P_{mech}. \qquad (14)$$

The maximum rate of climb (V_c) is simply the excess power divided by the all-up weight (mg).

$$V_c = P_{ex} / m\,g. \qquad (15)$$

P_{ex} is maximal when the bird is flying at its minimum-power speed (V_{mp}) because the power required to fly horizontally is least at that speed. Finding the maximum rate of climb comes down to estimating P_{max}, which is assumed to be independent of speed, and determined by the mass and properties of flight muscle and the wingbeat frequency, and P_{mech}, which is estimated from aerodynamical considerations, and can be translated into conditions required in the muscle. The calculation is most economically expressed in terms of the specific work in the myofibrils, as this is directly related to the stress and strain (above). From Equation 2, the limiting specific work (q_{mlim}) is obtained when the muscle is shortening with a stress of 0.30 σ_{max}:

$$q_{mlim} = 0.30\ \sigma_{max}\ \lambda\ /\ \rho_{musc}, \qquad (16)$$

where λ is the active strain and ρ_{musc} is the density of muscle (above). Equation 8 for the maximum power *available* from the flight muscles can be expressed in terms of q_{mlim} as

$$P_{max} = m\ F_{musc}\ (1 - \zeta)\ q_{mlim}\ f, \qquad (17)$$

where m is the bird's all-up mass, and F_{musc} is the flight muscle *fraction*, that is the total mass of the flight muscles (including mitochondria) divided by the all-up mass. $m\ F_{musc}$ is the mass of the flight muscles, and this is multiplied by $(1 - \zeta)$ to get the mass of myofibrils, then by q_{mlim} to get the maximum possible cycle work, then by the wingbeat frequency (f) to get the power.

The power *required* for level flight is found by the *Flight* program's power curve calculation, and this can be expressed in terms of the specific work (q_m) required for level flight:

$$P_{mech} = m\ F_{musc}\ (1 - \zeta)\ q_m\ f. \qquad (18)$$

Substituting from Equations 17 and 18 in Equation 14 for the excess power gives the rate of climb from Equation 15 as

$$V_c = F_{musc}\ (1 - \zeta)\ (q_{mlim} - q_m)\ f\ /\ g. \qquad (19)$$

Dividing by the all-up weight to get the rate of climb eliminates the mass, so that Equation 19 for the rate of climb does not require either the mass of flight muscle or the all-up mass, but only the flight muscle fraction, which is the ratio of the one to the other. It also requires the mitochondria fraction (ζ), which is found from Equation 13 in the course of the power curve calculation, and the strength of gravity (g).

Application to a bird with marginal climb performance

Selection of subject bird

The first step towards estimating σ_{max} from flight performance is to identify a bird that has almost no margin of power available from the muscles over that required to fly, so that if it is seen flying at all, it must be exerting nearly the full power of which its flight muscles are capable (P_{max} in Equation 8). Very large birds are the best candidates, because of the different scaling relationships of the power required for level flight and power available from the muscles. In geometrically similar birds, the power required to fly level at V_{mp} increases with the seven-sixths power of the mass, because V_{mp} itself increases with the one-sixth power of the mass, whereas the power available from the flight muscles increases with only the five-sixths power of the mass, because the wingbeat frequency *decreases* with the one-sixth power of the mass (Pennycuick, 1989). This argument does not lead to an actual estimate of the maximum mass at which the power available can equal or exceed that required, but it does indicate that there must be a maximum mass above which sustained powered flight is not possible, allometric adjustments notwithstanding. It is no surprise that most very large birds, such as condors and albatrosses, are specialised for soaring, meaning flight behaviour that results in extracting work from the atmosphere, in place of that which would otherwise have to be supplied by the muscles. Swans, however, include some of the heaviest flying bird species, and they fly by continuous flapping. Some species migrate distances up to 3000 km or so, and if they soar at all (doubtful) they certainly do not rely on soaring, either when migrating or at other times.

The Whooper Swan (*Cygnus cygnus*) is one of the two largest Old World species, and unlike the other large species (the Mute Swan *Cygnus olor*) it is migratory. The western population breeds in Iceland, and mostly winters in the British Isles (Kirby et al., 1992). This migration was studied by Pennycuick et al. (1996a, 1999) by satellite-tracking swans travelling in both directions between their breeding areas in Iceland and the Wildfowl and Wetlands Trust's reserve at Caerlaverock in south-west Scotland, which involves a sea crossing of about 800 km between the Outer Hebrides and the south-east coast of Iceland. It became clear during this project that whoopers have very little reserve power, over that required to maintain height in level flight. When taking off from Caerlaverock, they require a run to take off from land or water, and once airborne, make detours around obstacles rather than

attempting to climb over them. Observed flying heights never reached 2000 m ASL, and the swans mostly flew close to the surface during the sea crossing, often stopping on the water. If the swans had had enough power to fly faster than V_{mp}, they would have been able to cover the distance for a lower expenditure of fuel, but the largest block of air speed observations (14) was between 20 and 22 m s^{-1}, compared with an estimated V_{mp} of 20.9 m s^{-1} for an average whooper. Only four out of 83 observations of average air speed between fixes exceeded 22 m s^{-1}, and none exceeded 27 m s^{-1}.

Whooper Swan JAP

The assumption behind the calculation in this paper is that if a particular swan is known to be able to fly, then the power available must cover the power required, as calculated from measurements taken *on that individual*, not from a statistical sample. Whoopers in general lack reserves of power, and the larger the individual, the more marginal it is likely to be, because of the scaling relationship outlined above. The chosen swan was a wild, adult male whooper known as JAP from the letters on his telescope-readable leg ring. I am indebted to Jenny Earle of the Wildfowl and Wetlands Trust for the information that JAP was a highly successful breeder, who migrated between the breeding grounds in Iceland and Caerlaverock, Scotland each year between 1983 and 2001, and brought 36 cygnets to Caerlaverock during that time. He was caught and weighed at Caerlaverock in most winters, along with most of the swans in the wintering flock, and was identifiable by eye as the largest swan in the flock. His highest recorded mass was 13.5 kg on 14 January 1993, and was the heaviest in the flock. His wing measurements were taken on the same occasion (Table 1), and his wing span (2.56 m) was also the largest in the flock, 4 cm more than that of the next largest individual. He was tracked by the Argos satellite system in 1995 on his spring migration to Iceland, during which he flew very low during the sea crossing, with prolonged stops on the water (Pennycuick et al 1996a).

Estimating flight muscle fraction

In addition to JAP's standard measurements in Table 1, which are required as input for *Flight*'s power curve calculation, an estimate is also needed for the flight muscle fraction, i.e. the ratio of the wet mass of the flight muscles to the all-up mass. This measurement can only be made on dead birds, and is the only one that was obtained from a statistical sample of other individuals, in this case four whoopers which were

dissected after fatal collisions with power wires. Although the flight muscle *mass* is highly variable from one individual to another, the flight muscle *fraction* varies much less, because birds consume protein from the flight muscles during migratory flights, and replace it, together with fat, when preparing to migrate or recovering afterwards (Lindström and Piersma, 1993). Under *Flight*'s default assumption that enough flight muscle is consumed to maintain the specific work in the myofibrils at its starting value, the flight muscle fraction changes only slightly during a migratory flight. This was both predicted and observed for a very long flight by Great Knots (*Calidris tenuirostris*), for which carcase analysis data were available from samples collected before departure and after arrival (Pennycuick and Battley, 2003). Since the flight muscle fraction remains nearly (not exactly) constant in spite of large changes in all-up mass, this fraction can be estimated by dissecting birds that were healthy when they died, without needing to take detailed account of their size or fat reserves.

Table 1. Whooper Swan JAP.

Standard measurements	
All-up mass	13.5 kg
Wing span	2.56 m
Wing area	0.756 m^2
Aspect ratio	8.67
Assumed values	
Air density (sea level)	1.23 kg m^{-3}
Flight muscle fraction (mean of 4)	0.131 (sd ±0.0086)
Fat fraction	0.200
Isometric stress	Trial values
Active strain	0.26
Body drag coefficient	0.10
Calculated performance for σ_{max} = 560 kN m^{-2}:	
Minimum power speed (V_{mp})	21.1 m s^{-1}
Maximum range speed (V_{mr})	33.3 m s^{-1}
Wingbeat frequency	3.44 Hz
Specific work in myofibrils at V_{mp}	40.2 J kg^{-1}
Effective lift:drag ratio at V_{mp}	11.9
Chemical power at V_{mp}	1.02 kW
Ratio chemical power to BMR at V_{mp}	48.1
Max air speed for level flight	24.6 m s^{-1}
Mitochondria fraction	0.149
Max rate of climb at V_{mp}	0.045 m s^{-1}
Max rate of climb at V_{mr}	-0.486 m s^{-1}

Calculated performance of Whooper JAP

Maximum rate of climb and assumed isometric stress

As noted above, all the information needed to calculate the maximum rate of climb as a function of speed is already available in *Flight*'s power curve calculation, except the maximum isometric stress of which the myofibrils are capable. The practical criterion for determining whether a bird can fly horizontally is that it is able to maintain height when flying at or near V_{mp}, i.e. that its maximum rate of climb is zero or above. Fig. 4 shows curves of maximum rate of climb *versus* true air speed, calculated from JAP's data in Table 1, flying at sea level, with different trial values for the isometric stress (σ_{max}). In the bottom left corner is the curve for the value σ_{max} = 300 kN m^{-2}, which was suggested for the isometric stress from earlier literature by Pennycuick (1992). This indicates that the maximum rate of climb would be -0.757 m s^{-1}, i.e. the best the swan could do by flying at V_{mp} (21.1 m s^{-1}) and exerting maximum power, would be to sink at 0.757 m s^{-1}. There are two possible ways in which this discrepancy might be resolved, since the rate of climb is derived from the difference between the power available calculated from the assumed value of σ_{max}, and the estimated power required to fly level at V_{mp} (Equations 16 and 17).

Resolution by upward revision of the isometric stress

Higher up Fig. 4 are three curves showing the maximum rate of climb as a function of speed, using the same calculation for the power required for level flight, but assuming higher values of σ_{max} from 540 to 560 kN m^{-2}. For σ_{max} = 540 kN m^{-2}, the swan is not able to maintain height at any speed, but if σ_{max} is raised to 550 kN m^{-2}, it can achieve a marginal rate of climb of 0.011 m s^{-1} when flying at V_{mp}, and can maintain height ($V_c \geq 0$) up to 22.8 m s^{-1}. An assumed isometric stress of 560 kN m^{-2} leads to a more practical maximum climb of 0.045 m s^{-1}, and level flight up to 24.6 m s^{-1}. This performance is hardly spectacular, and there is no suggestion that the swan could fly level at a speed anywhere near its maximum range speed (33.3 m s^{-1}), but it allows a small margin of power for takeoff, and for transient emergencies such as avoiding obstacles in flight, consistent with JAP's known capabilities. If the density in cross-section of myosin filaments is 5.7 x 10^{14} m^{-2} (White and Thorson 1975) then a stress of 560 kN m^{-2} would correspond to an isometric tension *force* of 980 pN at the centre

of each myosin filament, i.e. just under 1 nN. It may be possible to determine whether this estimate is reconcilable with the tensile strength at the centre of the myosin filament, but that is beyond the scope of this paper. A.F. Huxley's (1957) sliding filament model does not yield an estimate for the absolute value of the force exerted by an individual myosin filament, because it handles the force exerted and the work done by cross-bridges in a non-dimensional form (McMahon, 1984).

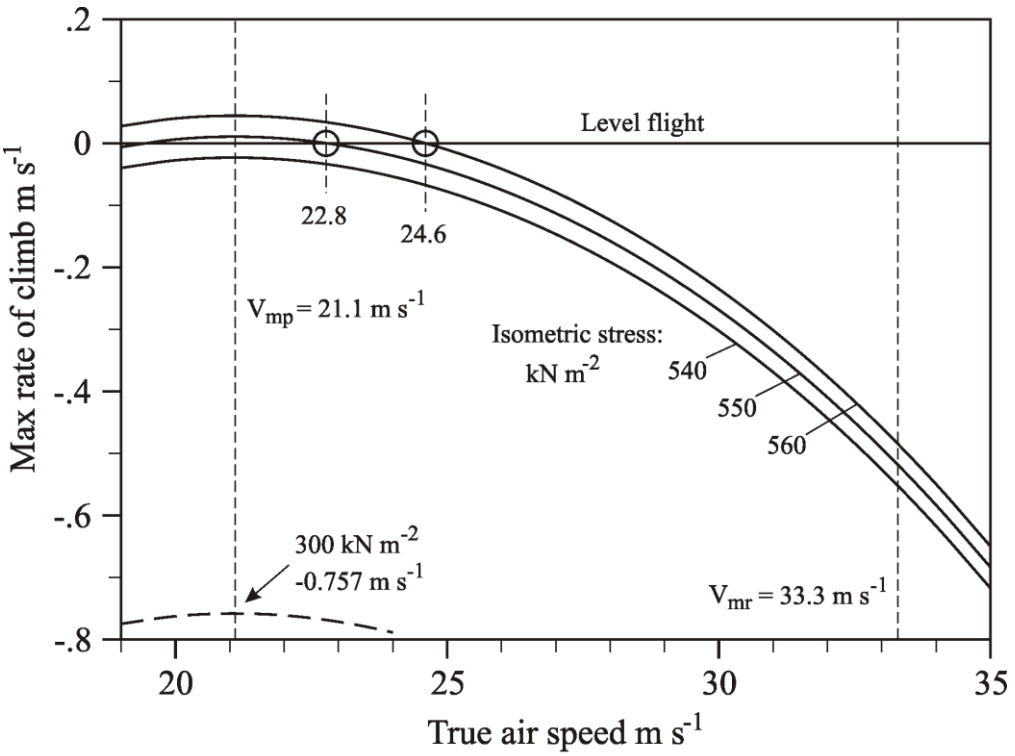


Fig. 4. Maximum rate of climb for Whooper Swan JAP, which was known to be capable of prolonged level flight, computed by *Flight* 1.17 from the data in Table 1, and plotted as a function of air speed. The computed speeds for minimum power (V_{mp}) and maximum range (V_{mr}) are shown. This swan would be unable to maintain height if the isometric stress were 300 kN m^{-2} (bottom left), but could do so with a small margin if the isometric stress were raised to 560 kN m^{-2}. Resolution of the discrepancy by adjusting other variables, so as to lower the power required to fly level, conflicts with other evidence (see text).

Resolution by downward revision of the power required

The discrepancy shown in Fig. 4 might alternatively be due to the *Flight* program over-estimating the power required for level flight. Resolution would require downward revision of the induced power, the parasite power or the profile power, or some combination of these. The calculated induced power could be reduced slightly by reducing the induced power factor from its default value of 1.2 to the theoretical minimum of 1.0, but this would have only a very small effect on the outcome. The parasite power was biased upwards in the earlier calculations of Whooper Swan performance by Pennycuick et al. (1996a), as unduly high values (above 0.25) were

then used for the body drag coefficient, from experiments on frozen bird bodies, in which there was massive separation of the boundary layer. This error was recognised in a later wind tunnel study on living birds (Pennycuick et al. 1996b), which led to the default body drag coefficient for *Flight* being reduced to 0.10. Following this adjustment, range calculations for two ultra long-distance migrants (Pennycuick, and Battley, 2003) indicated that both would arrive at their known destinations with fuel reserves far more generous than are required for airline operations. The field evidence, such as it is, does not suggest that *Flight*'s power estimates are too high.

That said, it remains true that the method of calculating profile power is an approximation that is not easily checked by experiment or observation. The estimate consists of multiplying the minimum value of the sum of induced and parasite powers (when flying at V_{mp}) by a factor which is itself found by dividing a "profile power constant" (C_{pro}) by the aspect ratio. The default value of C_{pro} is 8.4, and to resolve the discrepancy of Fig. 4, it would have to reduced to about 1. There is no supporting evidence for such a drastic downward revision of the profile power, and the conclusion is that the most likely explanation for the discrepancy of Fig. 4 is that the isometric stress is higher than has been previously assumed.

Climb performance in smaller birds

A default value for the isometric stress was not needed in *Flight* before the introduction of the rate of climb estimates in Version 1.17, but has now been introduced, and set at 560 kN m^{-2}. This results in initial maximum rates of climb (at sea level) for heavily laden waders such as the Great Knot of between 2 and 3 m s^{-1}, which is consistent with field observations of the rates of climb of waders presumed to be departing on long migratory stages by Hedenström and Alerstam (1992). The limiting value of the specific work from Equation 16 is q_{mlim} = 41.2 J kg^{-1} when the muscle is delivering maximum power, if the other variables take their default values λ = 0.26 and ρ_{musc} = 1060 kg m^{-3} as above.

Implications for the flight of giant pterosaurs

According to Wellnhofer (1991) the giant pterosaur *Quetzalcoatlus northropi* was not only by far the largest known pterosaur, but also the most recent, making a brief appearance in the fossil record right at the end of the Cretaceous period. Its discoverer

(Lawson, 1975) described partial remains of three specimens, and estimated the wing span of the largest by extrapolation from those parts that were preserved. Various methods gave results from 11 - 21 m, and Lawson favoured 15.5 m as a best guess. Subsequent authors have revised this estimate downwards, for example Chatterjee and Templin (2004) proposed 10.4 m for the span and 70 k g for the mass. However, there is no dispute that this animal was far larger and heavier than any extant flying bird.

Table 2. Data for *Quetzalcoatlus northropi*

Morphological estimates from Chatterjee and Templin (2004):	
Mass (kg)	70
Wing span (m)	10.4
Wing area (m^2)	9.55
Aspect ratio	11.3
Additional assumptions:	
Flight muscle fraction	0.14
Air density	Trial values
Other variables set to default values, including:	
Acceleration due to gravity ($m\ s^{-2}$)	9.81
Body drag coefficient	0.10
Max isometric stress ($kN\ m^{-2}$)	560
Active strain	0.26

Most commentators, including the present author, agree that *Q. northropi* was too big to have been capable of level flapping flight, if it is assumed that the environmental conditions at the end of the Cretaceous were similar to those prevailing today. On the other hand, the air density may have been higher then than it is now, possibly as a transient episode, that lasted only long enough for a giant form to evolve from one of the large pterodactyls that occurred throughout the Cretaceous. The effects of air density on flight performance are familiar to every pilot, and can readily be extrapolated by the *Flight* program to densities higher than are found in today's atmosphere. Fig. 5 shows some of the output from nine runs of the power curve calculation, all with the same data for *Q. northropi* (Table 2) from Chatterjee and Templin (2004), but with trial values of the air density from 1 to 5 $kg\ m^{-3}$. The vertical dashed line at the left side of the figure shows the sea-level air density in the International Standard Atmosphere (1.23 $kg\ m^{-3}$), which is essentially a representative value for the present atmosphere.

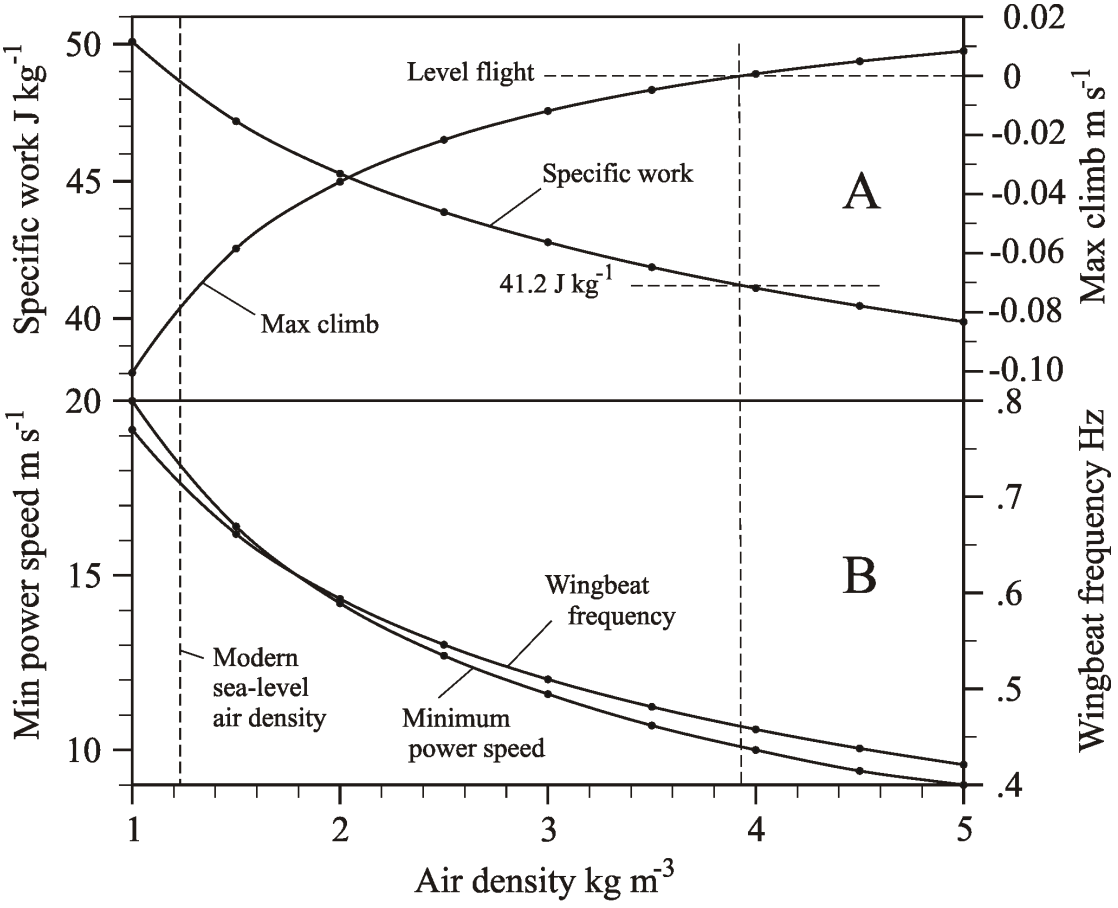


Fig. 5. A. Results of a similar calculation to that shown in Fig. 4 for the giant pterosaur *Quetzalcoatlus northropi*, using data (Table 2) from Chatterjee and Templin (2004). In this case the isometric stress was held constant at the new default value of 560 kN m^{-2} from Fig. 4, and the air density was adjusted upwards until the animal can maintain height, which requires a value about 3.2 times the modern sea-level air density. The specific work required to fly level falls from a value near 50 J kg^{-1} at an air density of 1 kg m^{-3}, passing the limiting value of 41.2 J kg^{-1} at the point where the animal can just maintain height, just below 4 kg m^{-3}.
B. The minimum power speed declines a little more strongly than the wingbeat frequency as the air density increases, which results in the increasing power margin reflected in the maximum rate of climb (above).

The lower graph (B) shows how both the minimum power speed and the wingbeat frequency come down as the air density increases. The power available from the flight muscles comes down because of the decreasing wingbeat frequency, but not so steeply as the power required. The specific work required from the flight muscles (A) starts at around 50 J kg^{-1}, which is far above the limiting value for vertebrate muscles (41.2 J kg^{-1} above), but drops with increasing air density, passing downwards through the limiting specific work when the air density is just below 4 kg m^{-3}. This is also the point where the maximum rate of climb rises above zero, meaning that the animal can maintain height when flying at V_{mp}. An increase in air density to 3.2 times

the modern sea-level value would make level flight a practical possibility for *Q. northropi*.

The chemical identity of the gas causing the increased density is immaterial, so long as it does not kill the animal, but oxygen is the only likely candidate for such a short-term effect, being the only gas that combines a large mass in the atmosphere with relatively high rates of formation and removal. According to Budyko et al. (1987), the present rate of oxygen formation due to photosynthesis is sufficient to generate the present mass of oxygen in the atmosphere in only 6000 years. An episode of increased carbon dioxide concentration due to outgassing is not unlikely at the end of the Cretaceous, as this was the time when vast lava eruptions created the Deccan Traps of India (Officer and Drake, 1985). Although added carbon dioxide would not in itself have an appreciable effect on the sea-level air density, it might have produced such an effect indirectly, by increasing the rate of oxygen production due to photosynthesis, especially if other effects of the outgassing were somehow to inhibit oxygen removal due to the oxidation of dead organic matter. It seems likely from Budyko et al.'s (1987) account of the evolution of the atmosphere that the mass of oxygen in the atmosphere, and hence the sea-level air density, was higher throughout the Mesozoic than it is now, which helps to account for the occurrence of large pterodactyls (but not giant forms) throughout the Cretaceous (Wellnhofer, 1991). A relatively short episode of strongly enhanced air density due to volcanism might account for *Q. northropi*'s brief appearance, just before the end.

Acknowledgements ─ Whooper JAP was the star of this study. It was a privilege to know this impressive swan in his prime, and to have a hand in documenting a few of his exploits. I am grateful to all those in the Wildfowl and Wetlands Trust, and others in the UK and Iceland who made the field study possible, especially Myrfin Owen, John Docherty, Eileen Rees, Richard Hesketh, Ólafur Einarsson, Tom Bradbury, Martin Brown, Sverrir Thorstensen and Þórey Ketilsdóttir.

References

Alexander, R.McN. 1985. The maximum forces exerted by animals. ─ J. Exp. Biol. 115: 231-238.

Alexander, R. McN., Bennet-Clark, H.C. 1977. Storage of elastic strain energy in muscle and other tissues. ─ Nature London 265: 114-117.

Budyko, M.I., Ronov, A.B., Yanshin, A.L. 1987. History of the Earth's atmosphere. ─ Springer, Berlin.

Chatterjee, S., Templin, R.J. 2004. Posture, locomotion and paleoecology of pterosaurs. ─ Geological Society of America Special Paper 376: 1-64.

Gordon, A.M., Huxley, A.F., Julian, F.J. 1966. The variation in isometric tension with sarcomere length in vertebrate muscle fibres. ─ J. Physiol. 184: 170-192.

Hedenström, A., Alerstam, T. 1992. Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. ─ J. Exp. Biol. 164: 19-38.

Hill, A.V. 1938. The heat of shortening and the dynamic constants of muscle. ─ Proc. R. Soc. London B 126: 136-195.

Huxley, A.F. 1957. Muscle structure and theories of contraction. ─ Progr. Biophys. and Biophys. Chem. 7: 255-318.

Huxley, H.E. 1985. The crossbridge mechanism of muscular contraction and its implications. ─ J. Exp. Biol. 115: 17-30.

Kirby, J.S., Rees. E.C., Merne, O.J., Garðarsson, A. 1992. International census of Whooper Swans *Cygnus cygnus* in Britain, Ireland and Iceland: January 1991. ─ Wildfowl 43: 20-26.

Lawson, D.A. 1975. Pterosaur from the latest Cretaceous of West Texas: discovery of the largest flying creature. ─ Science 187: 947-948.

Lindström, Å., Piersma, T. 1993. Mass changes in migrating birds: the evidence for fat and protein storage re-examined. ─ Ibis 135: 70-78.

McMahon, T.A. 1984. Muscles reflexes and locomotion. ─ Princeton University Press, Princeton.

Officer, C.B., Drake, C.L. 1985.Terminal Cretaceous environmental events. ─ Science 227: 1161-1167.

Pennycuick, C.J. 1969. The mechanics of bird migration. ─ Ibis 111: 525-556.

Pennycuick, C.J. 1975. Mechanics of flight. ─ In: Farner, D.S. and King, J.R. (eds.). Avian Biology Vol. 5. Academic Press, New York, pp. 1-75.

Pennycuick, C.J. 1989. Bird flight performance: a practical calculation manual. ─ Oxford University Press, Oxford.

Pennycuick, C.J. 1992. Newton rules biology: a physical approach to biological

problems. ─ Oxford University Press, Oxford.

Pennycuick, C.J. 1990. Predicting wingbeat frequency and wavelength of birds. ─ J. Exp. Biol. 150: 171-185.

Pennycuick, C.J. 1991. Adapting skeletal muscle to be efficient. ─ In: Blake, R.W. (ed). Efficiency and economy in animal physiology. Cambridge University Press, Cambridge, pp. 33-42.

Pennycuick, C.J. 1996. Wingbeat frequency of birds in steady cruising flight: new data and improved predictions. ─ J. Exp. Biol. 199: 1613-1618.

Pennycuick, C.J. 2001. Speeds and wingbeat frequencies of migrating birds compared with calculated benchmarks. ─ J.Exp. Biol. 204: 3283-3294.

Pennycuick, C.J., Einarsson, O., Bradbury, T.A.M., Owen, M. 1996a. Migrating whooper swans (*Cygnus cygnus*): satellite tracks and flight performance calculations. ─ J. Avian Biol. 27: 118-134.

Pennycuick, C.J., Klaassen, M., Kvist, A., Lindström, Å. 1996b. Wingbeat frequency and the body drag anomaly: wind tunnel observations on a Thrush Nightingale (*Luscinia luscinia*) and a Teal (*Anas crecca*). ─ J. Exp. Biol. 199: 2757-2765.

Pennycuick, C.J., Bradbury, T.A.M., Einarsson, Ó., Owen, M. 1999. Response to weather and light conditions of migrating Whooper Swans *Cygnus cygnus* and flying height profiles, observed with the Argos satellite system. ─ Ibis 141: 434-443.

Pennycuick, C.J., Battley, P.F. 2003. Burning the engine: a time-marching computation of fat and protein consumption in a 5420-km flight by Great Knots (*Calidris tenuirostris*). ─ Oikos 103: 323-332.

Pennycuick, C.J., Rezende, M.A. 1984. The specific power output of aerobic muscle, related to the power density of mitochondria. ─ J. Exp. Biol. 108: 377-392.

Wellnhofer, P. 1991. The illustrated encyclopedia of pterosaurs. Salamander, London.

White, D.C.S., Thorson, J. 1975. The kinetics of muscle contraction. ─ Pergamon, Oxford.