

Review

Muscle designed for maximum short-term power output: quail flight muscle

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Accepted 13 May 2002

Summary

Take-off in birds at high speeds and steep angles of elevation requires a high burst power output. The mean power output of the pectoralis muscle of blue-breasted quail (*Coturnix chinensis*) during take-off is approximately 400 W kg⁻¹ muscle, as determined using two independent methods. This burst power output is much higher than has been measured in any other cyclically contracting muscle. The power output of muscle is determined by the interactions between the physiological properties of the muscle, the stimulation regime imposed by the central nervous system and the details of the strain cycle, which are determined by the reciprocal interaction between the muscle properties and the environmental load. The physiological adaptations that enable a high power output to be achieved are those that allow the muscle to develop high stresses whilst shortening rapidly. These characteristics include a high myofibrillar density, rapid twitch contraction kinetics and a high maximum intrinsic velocity of shortening. In addition, several features of the strain cycle increase the power output of the quail pectoralis muscle. First, the

muscle operates at a mean length shorter than the plateau of the length/force relationship. Second, the muscle length trajectory is asymmetrical, with 70% of the cycle spent shortening. The asymmetrical cycle is expected to increase the power output substantially. Third, subtle deviations in the velocity profile improve power output compared with a simple asymmetrical cycle with constant lengthening and shortening rates. The high burst power outputs found in the flight muscles of quail and similar birds are limited to very brief efforts before fatigue occurs. This strong but short flight performance is well-suited to the rapid-response anti-predation strategy of these birds that involves a short flight coupled with a subsequent sustained escape by running. These considerations serve as a reminder that the maximum power-producing capacities of muscles need to be considered in the context of the *in vivo* situation within which the muscles operate.

Key words: blue-breasted quail, *Coturnix chinensis*, muscle, mechanics, power output, take-off, flight.

Introduction

For many species of bird, being able to take off at high speed and at a steep angle is an important survival strategy (Rayner and Swaddle, 2000). Rapid take-off is particularly important for birds that spend most of their time on the ground because these species are vulnerable to terrestrial and aerial predation. Some of these species show morphological adaptations that favour take-off at high speed. For example, members of the pheasant family (Phasianidae) have short wings (low aspect ratio) with a high wing loading, adaptations that favour fast flight and take-off from the cluttered environment in which they live. Take-off is one of the most energetically demanding modes of flight in birds (Swaddle et al., 1999), requiring energy to overcome the drag on the wings and body and to impart momentum to the air in order to gain altitude and accelerate the body. The power requirements increase at steeper take-off

angles (Fig. 1), and the low-aspect-ratio/high-wing-loading morphology results in a low aerodynamic efficiency and increases the induced power requirements. Most of the power required for flight is provided by the large pectoralis muscles, which makes up as much as 15–26% of the body mass in species that have a rapid take-off ability such as grouse and partridges (order Galliformes) and tinamous (order Tinamiformes) (Magnan, 1922; Hartman, 1961; Thomas, 1985; Rayner, 1988; Tobalske and Dial, 2000; Liukkonen-Anttila et al., 2000).

In this paper, we review the power produced during the explosive take-off flight of blue-breasted quail (*Coturnix chinensis*) and examine some of the physiological properties of the pectoralis muscle that enable these remarkable performances to be achieved.

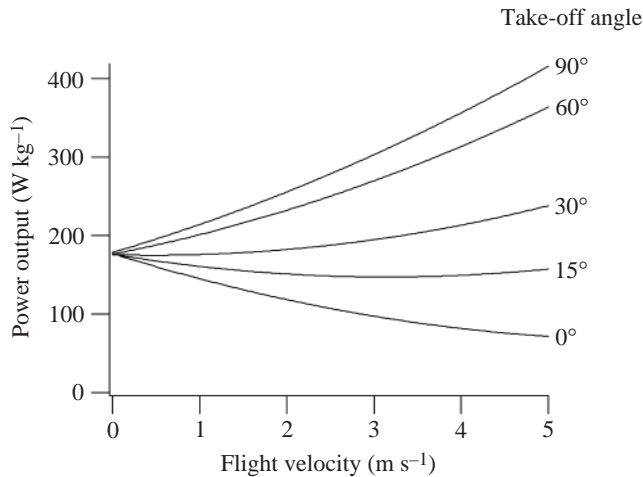


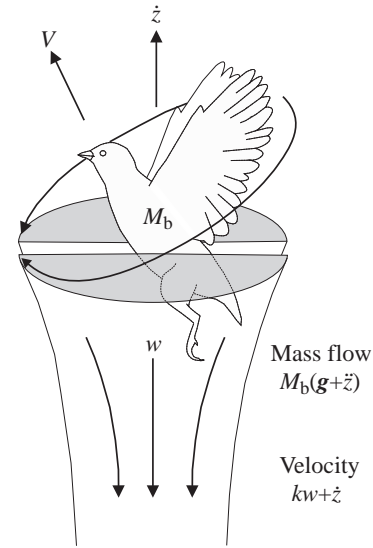
Fig. 1. Effects of take-off angle on power output calculated for blue-breasted quail for a range of flight velocities using the techniques presented in Askew et al. (2001). For all conditions, the bird was assumed to travel at a constant velocity.

Power output of the pectoralis muscle during take-off

Estimates from body and wing kinematics and an aerodynamic analysis

Askew et al. (2001) estimated the power required from the pectoralis muscles of blue-breasted quail during take-off using a kinematic and aerodynamic analysis. To provide a vertical force, the wings must impart a downward momentum to the air to balance the weight and any vertical acceleration of the bird. The induced power output is equal to the sum of the rate of increase in potential and kinetic energy and the product of the induced velocity and vertical force (Fig. 2; Askew et al., 2001). By tracking the movement of the centre of mass of the bird in three dimensions, the power required to increase the potential and kinetic energy of the bird was calculated. Detailed wing kinematics obtained from high-speed video recordings were used to calculate the remaining component of induced power and the profile power output required to overcome the pressure and friction drag on the wings. The total aerodynamic power output was 390 W kg^{-1} of pectoralis muscle and was dominated by the power required to gain altitude (Askew et al., 2001).

In arriving at this estimate of muscle-mass-specific power output, we assumed that all the aerodynamic power was provided by the pectoralis muscle. In fact, this must be the case unless (i) significant aerodynamic power is provided during the upstroke, or (i) the kinetic energy of the wing during the upstroke is stored elastically in the pectoralis tendon and recovered during the downstroke. With regard to the first possibility, we saw no evidence of a wing-tip reversal during the upstroke that would allow aerodynamic power to be produced. We consider it unlikely that the second possibility significantly reduces the power produced by the pectoralis muscles for the following reasons. First, the detailed kinematics of the wings reported by Askew et al. (2001) shows that the decrease in kinetic energy of the wing



$$P_{\text{ind}} = M_b(\mathbf{g} + \ddot{z})(kw + \dot{z}) = M_bkw(\mathbf{g} + \dot{z}) + M_b\dot{\mathbf{g}}z + M_b\ddot{z}z$$

$$P_{\text{pro}} = 2\Sigma(\frac{1}{2}\rho V_{R,i}^3 S_i C_{D,\text{pro}})$$

$$P_{\text{par}} = \frac{1}{2}\rho S_b C_{D,\text{par}} v^3$$

$$P_{\text{aero}} = P_{\text{ind}} + P_{\text{pro}} + P_{\text{par}}$$

Fig. 2. Illustration of the technique for estimating the mechanical power output of the muscles of blue-breasted quail during take-off. To provide a vertical force, the wings must impart a downward momentum to the air to balance the weight and any vertical acceleration of the bird. The actuator disc represents the area over which the wings interact with the air to give it a downward impulse, and it generates a vertical force equal to the weight and acceleration force $M_b(\mathbf{g} + \ddot{z})$ by imparting an induced velocity kw to air entering the disc with vertical velocity \dot{z} . The rate at which work is done by the disc is the induced power, P_{ind} , and is equal to this force multiplied by the total air velocity. The second and third terms of the induced power equation are the rate of increase of potential energy of the body ($M_b\dot{\mathbf{g}}z$) and the rate of increase of kinetic energy ($M_b\ddot{z}z$). Both these quantities were calculated from the movement of the centre of mass. The profile power (P_{pro}) required to overcome the pressure and friction drag acting on the wing was calculated from the resultant velocity and area of the wing using blade-element analysis. The parasite power (P_{par}) required to overcome drag on the body was calculated from the velocity and frontal area of the bird. The total aerodynamic power (P_{aero}) is equal to the sum of the induced power, profile power and parasite power. See Askew et al. (2001) for further details of the calculations. M_b is body mass, \mathbf{g} is acceleration due to gravity, \dot{z} is vertical velocity, \ddot{z} is vertical acceleration, k is the induced power factor, w is induced velocity, v is the velocity of the bird, ρ is air density, S_i is wing strip area, $V_{R,i}$ is the velocity of the wing strip, S_b is body frontal area, $C_{D,\text{pro}}$ is the profile drag coefficient and $C_{D,\text{par}}$ is the parasite drag coefficient.

during the upstroke approximately coincides with the start of shortening of the pectoralis muscle. Second, the pectoralis has an internal aponeurosis, but no free tendon, and thus appears to have limited ability for elastic energy storage. Third, during the upstroke, the work required to provide the kinetic energy to the wing would require the major upstroke

muscle, the supracoracoideus, to produce more than 300 W kg^{-1} , and additional power is required for profile power during the upstroke. This level of power output from a muscle that shortens for only 30% of the cycle period is extraordinarily high (Askew et al., 2001). Thus, it seems more likely that transfer of energy is required at the end of the downstroke to provide energy to accelerate the wing during the upstroke. The very long tendon of the supracoracoideus provides a ready structure that could store this energy, and the decrease in kinetic energy of the wing at the end of the downstroke begins before the proximal wing reverses direction. Any transfer of energy at the end of the downstroke would require even higher power output from the pectoralis than we have estimated.

Work loop measurements using *in vivo* strain and activity patterns

Askew and Marsh (2001) used sonomicrometry and electromyography to determine the *in vivo* strain and activity patterns (Fig. 3A,B). Bundles of fibres dissected from the pectoralis were subjected *in vitro* to these *in vivo* operating conditions, using the work loop technique (Josephson, 1985a). The mean power output of the pectoralis muscle during shortening (equivalent to the downstroke) averaged over the whole wingbeat cycle was approximately 350 W kg^{-1} , with a maximum recorded value of 433 W kg^{-1} .

These two independent methods yield pectoralis muscle power outputs of approximately 400 W kg^{-1} . This power output far exceeds that measured in other cyclically contracting non-avian fast vertebrate muscles in which a high power output has been of selective advantage. For example, the adductor muscle of swimming scallops generates approximately 30 W kg^{-1} (Marsh and Olson, 1994), the external oblique muscles of hylid tree frogs generate $50\text{--}60 \text{ W kg}^{-1}$ (Girgenrath and Marsh, 1999) and the white muscle of fish during fast-starts produces 143 W kg^{-1} (Wakeling and Johnston, 1998). In the following sections, we consider the physiological adaptations that enable the pectoralis muscle of the quail to generate these high powers during take-off.

Adaptations that facilitate the generation of a high power output

To maximise power output, the muscle should be able to shorten rapidly while developing high stresses. The most rapid cyclical contractions for vertebrate skeletal muscle are of the order 90–200 Hz in the rattlesnake shaker muscle and toadfish swimbladder muscle, respectively (Rome et al., 1996). These frequencies are greater than the wingbeat frequency of the blue-breasted quail (23 Hz; Askew and Marsh, 2001). However, the relatively large strain in the pectoralis muscle of blue-breasted quail (0.23) results in mean shortening rates that are the highest yet determined for any vertebrate muscle ($7.8Ls^{-1}$, where L is muscle length; Table 1). Shortening strain rates in synchronous insect muscles are also lower (Table 1), and only in asynchronous flight muscle from a

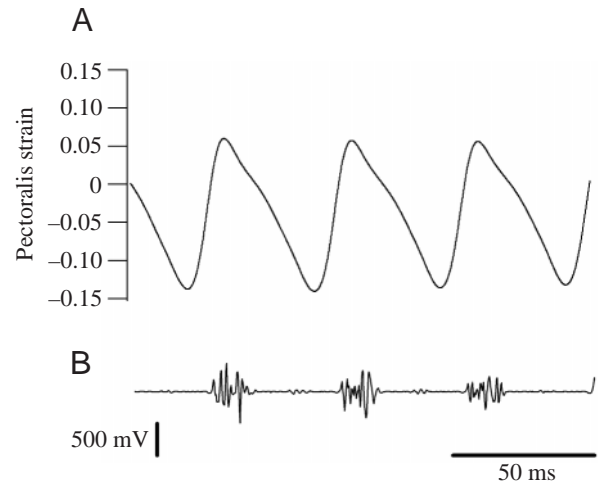


Fig. 3. *In vivo* sonomicrometry (A) and corresponding electromyography (B) recordings from the pectoralis muscle during take-off in blue-breasted quail (*Coturnix chinensis*).

beetle (*Cotinus mutabilis*) have higher mean strain rates been found to be optimal for power generation (Josephson et al., 2000).

The mean muscle stress during a cyclical contraction can be calculated as follows (illustrated for blue-breasted quail pectoralis muscle):

Mean muscle stress =

$$\frac{\text{Net muscle-mass-specific power} \times \text{density}}{\text{Frequency} \times \text{strain}}, \quad (1)$$

$$= \frac{390 \times 1060}{23.2 \times 0.234 \times 1000}$$

$$= 76 \text{ kN m}^{-2} \text{ for quail pectoralis muscle.}$$

Note that the mean muscle stress calculated in this way is the difference between the mean shortening stress and the mean lengthening stress.

The mean muscle stress developed by quail pectoralis muscle is similar to that generated by many other power-generating muscles, including examples from several vertebrates and invertebrates (Table 1) whose muscles operate over a wide range of cycle frequencies. Thus, the high shortening strain rates in blue-breasted quail pectoralis muscle are not at the expense of the muscle's ability to develop high stresses during cycling. This enables quail pectoralis muscle to generate much higher power outputs compared with other muscles. The physiological properties that allow these stresses to be developed at such high strain rates include the density of myofibrils in the muscle, the force/velocity characteristics and the kinetics. In addition, a number of properties of the strain cycle contribute to the high performance, including the point on the length/force relationship at which the muscle operates, the asymmetry of the strain cycle and changes in velocity during shortening. Each of these properties will be reviewed in the subsequent sections.

Table 1. *Performance characteristics of some power-generating muscles*

Species	Muscle	Cycle frequency (Hz)	Strain	Mean muscle stress (kN m ⁻²)	Mean strain rate (L s ⁻¹)	Net power output (W kg ⁻¹)
Vertebrate striated muscle						
Blue-breasted quail (<i>Coturnix chinensis</i>) ¹	Pectoralis	23.2	0.234	76	7.8	390
Mallard (<i>Anas platyrhynchos</i>) ²	Pectoralis	9	0.36	57	4.8	175
Gray tree frog (<i>Hyla chrysoscelis</i>) ³	External oblique	44	0.08	16	5.9	54
Gray tree frog (<i>Hyla versicolor</i>) ³	External oblique	21	0.12	24	3.4	58
Rattlesnake (<i>Crotalus atrox</i>) ⁴	Tail shaker	100	0.02	?	4.0	?
Scorpion fish (<i>Scorpaena notata</i>) ⁵	White	10.9	0.14	99	5.1	143
Invertebrate striated and synchronous muscle						
Scallop (<i>Argopecten irradians</i>) ⁶	Adductor	1.8	0.23	75	0.7	29
Locust (<i>Schistocerca gregaria</i>) ⁷	Metathoracic Tcx2	20	0.04	50	1.6	75
Tettigoniid (<i>Neoconocephalus triops</i>) ⁸	Mesothoracic Tcx1	25	0.06	23	3.1	33
Tettigoniid (<i>N. triops</i>) ⁸	Mesothoracic Tcx1	100	0.02	8.3	4.6	18
Invertebrate asynchronous muscle						
Beetle (<i>Cotinus mutabilis</i>) ⁹	Metathoracic basalar	94	0.05	45	9.4	198

¹Askew et al. (2001), ²Williamson et al. (2001), ³Girgenrath and Marsh (1999), ⁴Conley and Lindstedt (2000), ⁵Wakeling and Johnston (1998), ⁶Marsh and Olson (1994), ⁷Mizisin and Josephson (1987), ⁸Josephson (1985b), ⁹Josephson et al. (2000).

L, muscle length.

Physiological properties

Myofibrillar density

The myofibrils comprise the contractile portion of the muscle, so maximising the relative myofibrillar cross-sectional area gives the highest force output per unit cross-sectional area of muscle. Mitochondria, sarcoplasmic reticulum, capillaries and other non-contractile components of the muscle reduce the stress developed by the muscle. In vertebrates, fast fibres with low oxidative capacity have the highest relative myofibrillar volume. The pectoralis muscle of many members of the family Phasianidae consists primarily of large low-oxidative-capacity fibres, which make up approximately 85 % of the fibre volume (based on estimates for five members of the Phasianidae; Kaiser and George, 1973; Kiessling, 1977; Pyörnilä et al., 1998). The remaining fibres are smaller and have a higher oxidative capacity (Pyörnilä et al., 1998). Reliance on anaerobic metabolic pathways is also reflected in the low concentrations of myoglobin (Nishida et al., 1997; Saunders and Fedde, 1994), the low numbers and small size of mitochondria (Rosser et al., 1987) and the low concentrations of enzymes associated with the oxidative pathways (Kiessling, 1977; Saunders and Fedde, 1994). An exception to this predominantly fast low-oxidative-capacity fibre composition among the phasianids occurs in migratory quail species, such as the European quail *Coturnix coturnix*. The pectoralis muscles in these species contain a higher proportion of fast oxidative fibres (approximately 60 % of the fibre volume; Kaiser and George, 1973; Kiessling, 1977). The blue-breasted quail (*Coturnix chinensis*) is a non-migratory species, and most of the fibre volume in the pectoralis muscle is likely to be fast non-oxidative fibres, approximately 70 %, calculated from relative fibre numbers (Boesiger, 1992) by assuming similar-

sized fibres to those found in the Japanese quail *Coturnix japonica* (Rosser et al., 1987).

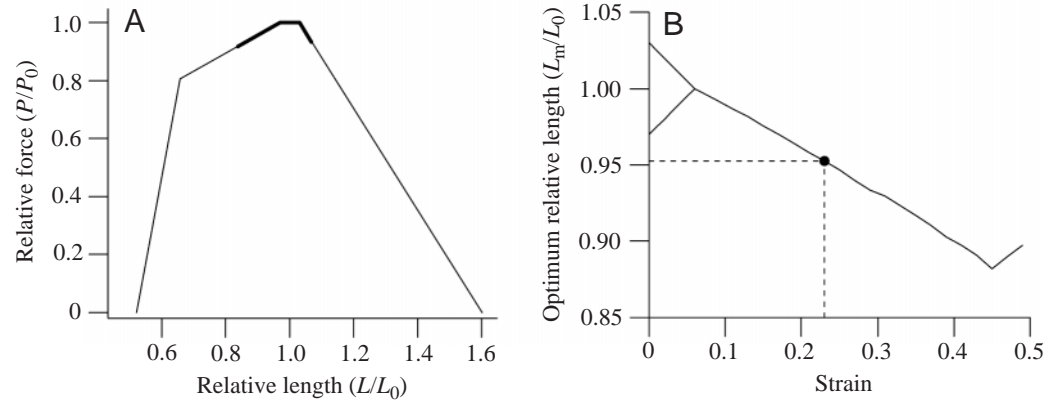
The effect of myofibrillar density can be seen in muscles that produce power continuously as opposed to the burst power required in the quail. The sound-producing muscles of hylid frogs have a reduced mean stress (Table 1) at least in part because of a low myofibrillar volume, although other effects are evident in these high-frequency muscles (Marsh, 1999a; Girgenrath and Marsh, 1999). Also, hummingbirds, which have high sustained power capacities (Chai and Dudley, 1995), have lower muscle-mass-specific burst power capacities than quail (Chai and Millard, 1997; Chai et al., 1997).

The high myofibrillar volumes in the pectoralis muscle of blue-breasted quail give these muscles the potential for generating large forces. Whether this potential translates into high power outputs depends on the performance of the muscle during dynamic contractions. The generation of large forces at high cycling rates requires that the muscle can activate and deactivate rapidly and requires the muscle to have force/velocity characteristics that allow large forces to be developed at rapid shortening velocities.

Twitch characteristics

To allow operation at high wingbeat frequencies, the pectoralis muscle must have rapid rates of activation and deactivation. Although twitch kinetics is affected by the rate at which the muscle lengthens or shortens (Askew and Marsh, 1997, 1998), isometric twitch times can be used as a comparative measure of deactivation rates. The twitch times measured for cyclic power-producing muscles are proportional to the operating frequency of the muscle (Askew and Marsh, 2001). Blue-breasted quail pectoralis muscle has rapid twitch

Fig. 4. (A) Length/force relationship based on data for rat muscle (Woledge et al., 1985). The bold line shows the relative length range over which a muscle should operate to maximise work and power output for a strain of 0.23. (B) Optimum relative length (L_m/L_0) about which a muscle should operate to maximise work and power for a range of strains. An optimum L_m/L_0 of 0.95 should be used for a strain of 0.23. Note that the divergence of the line at strains shorter than 0.06 represents the range of relative optimum lengths (L_m ; see text) over which the muscle can still operate on the plateau of the length/force relationship.



kinetics with a twitch rise-time of 10.8 ms and a half-twitch relaxation time of 8.8 ms (Askew and Marsh, 2001). These twitch parameters are similar to those of muscles that operate at similar cycle frequencies, such as the calling muscles of hylid tree frogs (McLister et al., 1995; Girgenrath and Marsh, 1999), zebra finch pectoralis muscle (Hagiwara et al., 1968) and a locust flight muscle (Josephson and Stevenson, 1991).

Force/velocity relationship

The instantaneous isotonic power output is obtained by multiplying force by velocity during contractions against a constant load and depends on the maximum velocity of shortening at zero load and the shape of the force/velocity curve. Although muscles do not operate isotonically *in vivo*, the isotonic speed clearly limits power output, and maximising power output requires a high maximum intrinsic shortening velocity. Preliminary measurements during afterloaded isotonic contractions indicate a high maximum shortening velocity for quail pectoralis muscle. Maximum power output is also affected by the curvature of the force/velocity curve. The force/velocity curve of the pectoralis in the blue-breasted quail has a low curvature (G. N. Askew and R. L. Marsh, unpublished observations). Relatively flat force/velocity curves have been measured for the external oblique muscles of tree frogs (Girgenrath and Marsh, 1999; Marsh, 1999a). Flattening of the force/velocity curve increases the maximum instantaneous power output and the optimal relative shortening velocity at which it is attained.

Muscle length trajectory

The potential power output of a muscle depends on its physiological properties, but the actual level of performance during natural movements is a function of the pattern of lengthening and shortening with respect to time (strain or velocity trajectory) and of the timing and rates of activation and deactivation (Askew and Marsh, 1997, 1998; Girgenrath and Marsh, 1999). The strain trajectory of the muscle is determined by the reciprocal interaction between the

physiological and architectural properties of the muscle and the load against which it contracts (Marsh, 1999b). During take-off, the aerodynamic and inertial torque about the shoulder joint and the muscle's moment arm largely determine the load against which the pectoralis muscle must contract.

Length/force relationship

The active force that can be developed by an isometrically contracting muscle is a non-linear function of its length (Fig. 4A) and is determined by the amount of overlap between the thick and thin filaments (Gordon et al., 1966) and, hence, the number of crossbridges that can be formed. On the basis of the length/force relationship, we have calculated the optimum relative length (L_m/L_0) about which a muscle should oscillate to maximise work (Fig. 4B; L_m is the length at the midpoint of the length cycle and L_0 is the length at the midpoint of the plateau of the length/force relationship). Optimum L_m/L_0 was calculated by maximising the integral of force with respect to relative muscle length change (dL) over a sinusoidal length change for a range of starting length (force/velocity effects and time for activation and deactivation have not been included). For strains equal to 0.06, the muscle should clearly operate on the plateau, and for strains less than this there is a range of values of L_m/L_0 that allows the muscle to operate entirely on the plateau (the diverging lines at relative lengths below 0.06 represents the extremes of the range of optimum lengths over which the muscle can perform whilst still operating on the plateau of the length/force relationship). Strains greater than 0.06 require that part of the length excursion should occur at lengths not on the plateau. For these strains, optimal L_m/L_0 is less than 1 because, for a given change in dL , the decline in relative force is greater on the descending limb than on the first part of the ascending limb of the length/force relationship.

The strain in the pectoralis muscle in blue-breasted quail is 0.23 (Askew and Marsh, 2001). From Fig. 4B, an optimum L_m/L_0 of 0.95 is predicted, giving a maximum length excursion of $0.04L_0$ above the plateau and a minimum length excursion of $0.13L_0$ below the plateau. For strains of 0.36, as have been observed in mallards during take-off (Williamson et al., 2001),

the predicted optimum relative length is 9% below L_0 . The length/force relationship has not been systematically measured for these bird flight muscles in relation to the lengths about which the muscles oscillate *in vivo*. However, Askew and Marsh (2001) noted that the peak stress during work loops exceeded by 7% that measured under isometric conditions at the mean *in vivo* resting length about which the muscle was oscillated. They suggested that this indicated that the mean *in vivo* resting length was shorter than the plateau of the length/force relationship. It should be noted, however, that the length/force relationship for whole muscle does not have the distinct regions illustrated in Fig. 4A (see Askew and Marsh, 1998) because of inhomogeneities among the sarcomeres and possibly as a result of inhomogeneities in the lengths of the thick and thin filaments in individual sarcomeres (Edman and Reggiani, 1987; Josephson, 1999).

Other reasons may also exist for operating predominantly on the ascending limb of the length/force relationship. The effects of the strain trajectory on activation and deactivation events may vary with length. In addition, the ascending limb is an inherently stable part of the length/force curve on which to operate compared with the descending limb, where sarcomeres can become unstable during lengthening (Morgan, 1990). At long muscle lengths, sarcomere inhomogeneity may result in longer, weaker sarcomeres being 'popped' by shorter, stronger ones. However, such effects could presumably be avoided by having a muscle with a high passive tension, which is determined by the content of the protein titin (Rief et al., 1997).

Cycle asymmetry

In vitro experiments have shown that the proportion of the cycle time spent shortening is an important determinant of power output. In experiments in which mouse limb muscles were subjected to sawtooth cycles in which the proportion of the cycle spent shortening was varied, Askew and Marsh (1997) showed that net power output increased as the proportion of the cycle spent shortening increased. Net power output during asymmetrical sawtooth cycles in which 75% of the cycle was spent shortening was approximately 40% greater than during symmetrical sawtooth cycles and was 50–60% of the maximum instantaneous power output that can be generated during after-loaded isotonic contractions (Askew and Marsh, 1997). The increase in power is attributable to more complete activation of the muscle as a result of the longer stimulation duration, to a more rapid rise in force resulting from increased stretch velocity and to an increase in the optimal strain amplitude.

During flight, the downstroke (the main power-generating stroke) is often longer in duration than the upstroke. For example, in osprey and Rüpell's griffon vulture, the downstroke represents 63% and 70% of the wing stroke, respectively (Scholey, 1983; G. N. Askew, personal observation). The precise phase of the length changes in the pectoralis muscles cannot be determined from these observations because of the lack of synchrony between wing tip movements and the movements of the humerus to which the pectoralis is attached (Askew et al., 2001).

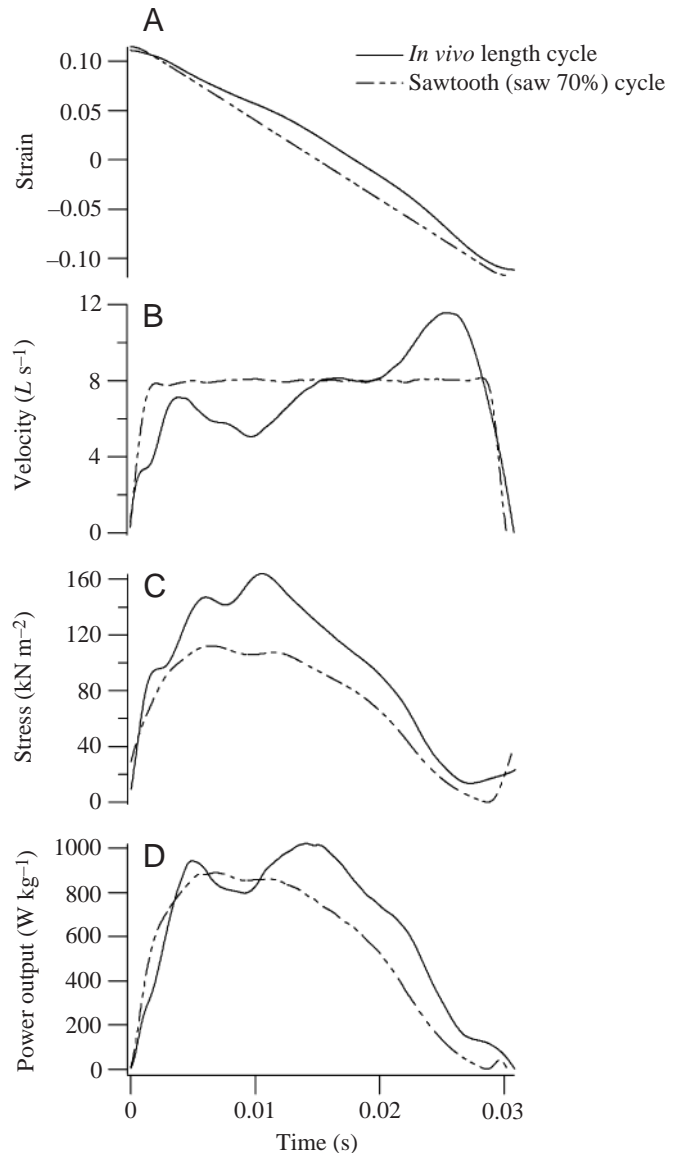


Fig. 5. Comparison of the strain (A) and shortening velocity (B) for the simulation and sawtooth cycles and the stress (C) and instantaneous power output (D) developed. The stress was higher during the simulation (*in vivo* length cycle) cycle than during the sawtooth cycle throughout most of shortening; however, the instantaneous power output was only greater during the later part of shortening. L is muscle length, and saw 70% cycle refers to a sawtooth length cycle in which 70% of the total cycle duration is spent shortening.

Sonomicrometry recordings from the pectoralis muscle in various species of bird during take-off reveal that the length trajectory of these muscles is definitely asymmetrical. For example, during take-off, pectoralis muscle shortening represents 63% of the total wing stroke duration in pigeons (Biewener et al., 1998), 68% in mallards (Williamson et al., 2001) and 56–70% in some members of the Phasianidae (Fig. 3A; Tobalske and Dial, 2000; Askew and Marsh, 2001).

The strain measured in the avian pectoralis muscle during take-off is high in comparison with optimal strains observed in many *in vitro* work loop experiments using symmetrical cycles. The strain in blue-breasted quail pectoralis muscle is 23 % of the muscle's resting length, which is comparable with that measured in the ring-necked pheasant, although not as high as in the pigeon and mallard (32 and 36 %, respectively; Biewener et al., 1998; Williamson et al., 2001). The optimum strain occurs at an optimal relative shortening velocity that is dependent on the length/force relationship, the force/velocity relationship and the state of activation of the muscle (Askew and Marsh, 1998). However, for a given cycle frequency, as the proportion of the cycle spent shortening increases, the optimal strain also increases to maintain an optimal relative shortening velocity. This has the effect of increasing the work generated and, hence, the power output of the muscle.

Velocity profile

In addition to enhancing power by prolonging the shortening phase of the contraction, Askew and Marsh (2001) have shown that during take-off flights in quail there may be improvements in power output due to subtle changes in the velocity profile. They compared the power output during simulated natural length trajectories with that during sawtooth cycles that had the same proportion of the cycle spent shortening as the natural cycles (Fig. 5). The timing and duration of stimulation and the total strain were identical in both sets of cycles. The power output was 16 % higher during the natural cycles than during the sawtooth cycles. The higher peak lengthening velocity during the natural cycles appeared to result in greater activation and led to higher instantaneous power outputs towards the end of shortening compared with the sawtooth cycles (Askew and Marsh, 1998, 2001). The rate at which force rises during activation increases with higher velocities of stretch during cyclical length changes (Askew and Marsh, 1997, 1998) and when the stretch is imposed during a tetanic contraction (Edman et al., 1978; Lombardi and Piazzesi, 1990; Takarada et al., 1997). Reducing the time required to activate the muscle means that the muscle is more completely activated during shortening.

Furthermore, during the second half of the downstroke, the rate of shortening increases (see Fig. 3), which further enhances deactivation of the muscle (Askew and Marsh, 1998; Askew et al., 2001). Shortening of a partially activated muscle reduces its ability to develop force, with the magnitude of the reduction being positively correlated with the shortening velocity (Gordon and Ridgway, 1987; Caputo et al., 1994; Askew and Marsh, 1997, 1998). Rapid deactivation at the end of shortening ensures that there is little residual force during re-lengthening of the pectoralis on the upstroke, which would increase the power required from the supracoracoideus muscle. However, even during this relaxation period, the instantaneous power output is greater during the *in vivo* simulation than during the sawtooth trajectory because of the higher stress and higher shortening velocity (Fig. 5).

Concluding remarks

The characteristics of the pectoralis muscles of blue-breasted quail are well suited to generating high stress whilst cycling at rapid rates. These characteristics provide the quail with very high burst power outputs. The reliance on burst power output is feasible because the duration of effort needed by the birds is short. Typical flight behaviour in quail and similar birds involves an explosive take-off followed by brief intermittent flap-gliding flight. The birds then land and escape by running. The non-sustainable nature of their flights is illustrated by the fact that they rapidly become exhausted and after several flushes and are rendered incapable of flight (Marden, 1994). Power outputs in animals that function aerobically will inevitably be lower because of the greater proportion of the muscle occupied by mitochondria and oxygen delivery systems. However, some animals that function largely aerobically, e.g. hummingbirds, also have reserves of power that can be used in a burst mode (Chai and Millard, 1997; Chai et al., 1997). These considerations are an important reminder that muscle performance must be examined in the context of *in vivo* function. Comparisons of the power produced *in vivo* should include a consideration of the sustainability of the effort.

This work was funded by a Wellcome Research Travel Grant (to G.N.A.) and by the NIH (grant AR39318 to R.L.M.).

References

- Askew, G. N., Ellington, C. P. and Marsh, R. L. (2001). The mechanical power of the flight muscles of blue-breasted quail (*Coturnix chinensis*) during take-off. *J. Exp. Biol.* **201**, 3601–3619.
- Askew, G. N. and Marsh, R. L. (1997). The effects of length trajectory on the mechanical power output of mouse skeletal muscles. *J. Exp. Biol.* **200**, 3119–3131.
- Askew, G. N. and Marsh, R. L. (1998). Optimal shortening velocity (V/V_{\max}) of skeletal muscle during cyclical contractions: length–force effects and velocity-dependent activation and deactivation. *J. Exp. Biol.* **201**, 1527–1540.
- Askew, G. N. and Marsh, R. L. (2001). The mechanical power output of the pectoralis muscle of blue-breasted quail (*Coturnix chinensis*): the *in vivo* length cycle and its implications for muscle performance. *J. Exp. Biol.* **204**, 3587–3600.
- Biewener, A. A., Corning, W. R. and Tobalske, B. W. (1998). *In vivo* pectoralis muscle force–length behavior during level flight in pigeons (*Columba livia*). *J. Exp. Biol.* **201**, 3293–3307.
- Boesiger, B. (1992). Histologie, immunocytologie, histochemie et innervation des fibres musculaires du muscle pectoralis major et du muscle supracoracoideus de *Excalfactoria chinensis chinensis* (L.). *Acta Anat.* **145**, 35–43.
- Caputo, C., Edman, K. A. P., Lou, F. and Sun, Y.-B. (1994). Variation in myoplasmic Ca^{2+} concentration during contraction and relaxation studied by the indicator fluo-3 in frog muscle fibres. *J. Physiol., Lond.* **478**, 137–148.
- Chai, P., Chen, J. S. C. and Dudley, R. (1997). Transient hovering performance of hummingbirds under conditions of maximal loading. *J. Exp. Biol.* **200**, 921–929.
- Chai, P. and Dudley, R. (1995). Limits to vertebrate locomotor energetics suggested by hummingbirds hovering in heliox. *Nature* **377**, 722–725.
- Chai, P. and Millard, D. (1997). Flight and size constraints: hovering performance of large hummingbirds under maximal loading. *J. Exp. Biol.* **200**, 2757–2763.
- Conley, K. E. and Lindstedt, S. L. (2002). Energy-saving mechanisms in muscle: the minimization strategy. *J. Exp. Biol.* **205**, 2175–2181.

- Edman, K. A. P., Elzinga, G. and Noble, M. I. M.** (1978). Enhancement of mechanical performance by stretch during tetanic contractions of vertebrate skeletal muscle fibres. *J. Physiol., Lond.* **281**, 139–155.
- Edman, K. A. P. and Reggiani, C.** (1987). The sarcomere length–tension relation determined at short segments of intact muscle fibres of the frog. *J. Physiol., Lond.* **385**, 709–732.
- Girgenrath, M. and Marsh, R. L.** (1999). Power of sound-producing muscles in the gray tree frogs *Hyla versicolor* and *Hyla chrysoscelis*. *J. Exp. Biol.* **202**, 3225–3237.
- Gordon, A. M., Huxley, A. F. and Julian, F. J.** (1966). The variation in isometric tension with sarcomere length in vertebrate muscle fibres. *J. Physiol., Lond.* **184**, 170–192.
- Gordon, A. M. and Ridgway, E. B.** (1987). Extra calcium on shortening in barnacle muscle: Is the decrease in calcium binding related to decreased crossbridge attachment, force or length? *J. Gen. Physiol.* **90**, 321–340.
- Hagiwara, S., Chichibu, S. and Simpson, N.** (1968). Neuromuscular mechanisms of wing beat in hummingbirds. *Z. Vergl. Physiol.* **60**, 209–218.
- Hartman, F. A.** (1961). Locomotor mechanisms of birds. *Smithson. Misc. Collns.* **143**, 1–91.
- Josephson, R. K.** (1985a). Mechanical power output from striated muscle during cyclical contractions. *J. Exp. Biol.* **114**, 493–512.
- Josephson, R. K.** (1985b). The mechanical power output of a tettigoniid wing muscle during singing and flight. *J. Exp. Biol.* **117**, 357–368.
- Josephson, R. K.** (1999). Dissecting muscle power output. *J. Exp. Biol.* **202**, 3369–3375.
- Josephson, R. K., Malamud, J. G. and Stokes, D. R.** (2000). Power output by an asynchronous flight muscle from a beetle. *J. Exp. Biol.* **203**, 2667–2689.
- Josephson, R. K. and Stevenson, R. D.** (1991). The efficiency of a flight muscle from the locust *Schistocerca americana*. *J. Physiol., Lond.* **442**, 413–429.
- Kaiser, C. E. and George, J. C.** (1973). Interrelationship amongst the avian orders Galliformes, Columbiformes and Anseriformes as evidenced by the fibre types in their pectoralis muscle. *Can. J. Zool.* **51**, 887–892.
- Kiessling, K.-H.** (1977). Muscle structure and function in the goose, quail, pheasant, guinea hen and chicken. *Comp. Biochem. Physiol. B* **57**, 287–292.
- Liukkonen-Anttila, T., Saartoala, R. and Hissa, R.** (2000). Impact of hand-rearing on morphology and physiology of the capercaillie (*Tetrao urogallus*). *Comp. Biochem. Physiol.* **125A**, 211–221.
- Lombardi, V. and Piazzesi, G.** (1990). The contractile response during steady lengthening of stimulated frog muscle fibres. *J. Physiol., Lond.* **431**, 141–171.
- Magnan, A.** (1922). Les caractéristiques des oiseaux suivant le mode de vol. *Ann. Sci. Nat. Dixième Série* **5**, 125–334.
- Marden, J. H.** (1994). From damselflies to pterosaurs: how burst and sustainable flight performance scale with size. *Am. J. Physiol.* **266**, R1077–R1084.
- Marsh, R. L.** (1999a). Contractile properties of muscles used in sound production and locomotion in two species of gray tree frog. *J. Exp. Biol.* **202**, 3215–3223.
- Marsh, R. L.** (1999b). How muscles deal with real-world loads: the influence of length trajectory on muscle performance. *J. Exp. Biol.* **202**, 3377–3385.
- Marsh, R. L. and Olson, J. M.** (1994). Power output of scallop adductor muscle during contractions replicating the *in vivo* mechanical cycle. *J. Exp. Biol.* **193**, 139–156.
- McLister, J. D., Stevens, E. D. and Bogart, J. P.** (1995). Comparative contractile dynamics of calling and locomotor muscles in three hylid tree frogs. *J. Exp. Biol.* **198**, 1527–1538.
- Mizisin, A. P. and Josephson, R. K.** (1987). Mechanical power output of a locust flight muscle. *J. Comp. Physiol. A* **160**, 413–419.
- Morgan, D. L.** (1990). New insights into the behavior of muscle during active lengthening. *Biophys. J.* **57**, 209–221.
- Nishida, J., Machida, N. W., Tagome, M. and Kasugai, Y.** (1997). Existence of parvalbumin and biochemical characterization in quail and pigeon skeletal muscles with different fiber type compositions. *J. Exp. Zool.* **277**, 283–292.
- Pyörnilä, A. E. I., Putaala, A. P. and Hissa, R. K.** (1998). Fibre types in breast and leg muscles of hand-reared and wild grey partridge (*Perdix perdix*). *Can. J. Zool.* **76**, 236–242.
- Rayner, J. M. V.** (1988). Form and function in avian flight. In *Current Ornithology* vol. 5, chapter 1 (ed. R. F. Johnston), pp. 1–66. New York: Plenum Press.
- Rayner, J. M. V. and Swaddle, J. P.** (2000). Aerodynamics and behaviour of moult and take-off in birds. In *Biomechanics in Animal Behaviour* (ed. P. Domenici and R. W. Blake), pp. 125–157. Oxford: BIOS Scientific Publishers Ltd.
- Rief, M., Gautel, M., Oesterhelt, F., Fernandez, J. M. and Gaub, H. E.** (1997). Reversible unfolding of individual titin immunoglobulin domains by AFM. *Science* **276**, 1109–1112.
- Rome, L. C., Syme, D. A., Hollingworth, S., Lindstedt, S. L. and Baylor, S. M.** (1996). The whistle and the rattle: The design of sound producing muscles. *Proc. Natl. Acad. Sci. USA* **93**, 8095–8100.
- Rosser, B. W. C., George, J. C. and Frombach, S. K.** (1987). Architecture of the pectoralis muscle of the Japanese quail (*Coturnix japonica*): histochemical and ultrastructural characterization and distribution of muscle fiber types. *Can. J. Zool.* **65**, 63–71.
- Saunders, D. K. and Fedde, M. R.** (1994). Exercise performance of birds. *Adv. Vet. Sci. Comp. Med.* **38B**, 139–190.
- Scholey, K. D.** (1983). Developments in vertebrate flight: climbing and gliding in mammals and reptiles and the flapping flight of birds. PhD thesis, University of Bristol, UK.
- Swaddle, J. P., Williams, E. V. and Rayner, J. M. V.** (1999). The effect of simulated flight feather moult on escape take-off performance in starlings. *J. Avian Biol.* **30**, 351–358.
- Takarada, Y., Iwamoto, H., Sugi, H., Hirano, Y. and Ishii, N.** (1997). Stretch-induced enhancement of mechanical work production in frog single fibres and human muscle. *J. Appl. Physiol.* **83**, 1741–1748.
- Thomas, V. G.** (1985). Myoglobin levels and mATPase activity in pectoral muscles of spruce and ruffed grouse (Aves: Tetraoninae). *Comp. Biochem. Physiol.* **81A**, 181–184.
- Tobalske, B. W. and Dial, K. P.** (2000). Effects of body size on takeoff flight performance in the Phasianidae (Aves). *J. Exp. Biol.* **203**, 3319–3332.
- Wakeling, J. M. and Johnston, I. A.** (1998). Muscle power output limits fast-start performance in fish. *J. Exp. Biol.* **201**, 1505–1526.
- Williamson, M. R., Dial, K. P. and Biewener, A. A.** (2001). Pectoralis muscle performance during ascending and slow level flight in mallards (*Anas platyrhynchos*). *J. Exp. Biol.* **204**, 495–507.
- Woledge, R. C., Curtin, N. A. and Homsher, E.** (1985). *Energetic Aspects of Muscle Contraction*. London: Academic Press.