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## Review

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# How important are skeletal muscle mechanics in setting limits on jumping performance?

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### Summary

Jumping is an important locomotor behaviour used by many animals. The power required to perform a jump is supplied by skeletal muscle. The mechanical properties of skeletal muscle, including the power it can produce, are determined by its composition, which in turn reflects trade-offs between the differing tasks performed by the muscle. Recent studies suggest that muscles used for jumping are relatively fast compared with other limb muscles. As animals get bigger absolute jump performance tends to increase, but recent evidence suggests that adult jump performance may be relatively independent of body size. As body size increases the relative shortening velocity of muscle decreases, whereas normalised power output remains relatively constant. However, the relative shortening velocity of the fastest muscle fibre types appears to remain relatively constant over a large body size range of species. It appears likely that in many species during jumping, other factors are compensating for, or allowing for, uncoupling of jumping performance from

size-related changes in the mechanical properties of muscle. In some species smaller absolute body size is compensated for by rapid development of locomotor morphology to attain high locomotor performance early in life. Smaller animal species also appear to rely more heavily on elastic storage mechanisms to amplify the power output available from skeletal muscle. Adaptations involving increased relative hindlimb length and relative mass of jumping muscles, and beneficial alteration of the origin and/or insertion of jumping muscles, have all been found to improve animal jump performance. However, further integrative studies are needed to provide conclusive evidence of which morphological and physiological adaptations are the most important in enhancing jump performance.

Key words: energy storage, jump, locomotion, morphology, muscular, scaling, temperature, trade-offs.

### Introduction

Jumping is a locomotor behaviour that is used by most groups of vertebrates and many invertebrates to move about in complex three-dimensional environments. Jumping provides a sudden, and largely unpredictable, form of locomotion to escape from predators, to capture prey or to provide the initial acceleration when taking off against gravity for subsequent flight. The term jumping often implies a jump from a standing start or a single running jump and is sometimes distinguished from hopping, which tends to involve multiple, often submaximal, ‘jumps’. Although most species of vertebrates can jump, some have become highly specialised and use jumping as their only means of locomotion (e.g. some species of frogs, kangaroos, bush babies, etc...). The

ecological importance of jump performance in many species is likely to be related to predator avoidance and/or prey capture success (Marsh, 1994). Key components of fitness in species that jump on a regular basis would probably include a higher behavioral tendency to jump, along with adaptations in morphological and physiological traits that lead to maximisation of jump performance. There has been much discussion as to which measure of jumping performance is most important as a potential correlate of fitness (Emerson, 1978; Watkins, 1996; Wilson et al., 2000); however, it is very unlikely that a single key variable is determinant across different systematic groups and in different ecological settings. Indeed, this key variable may change among species and during growth/development, depending on the natural

history of the species under consideration. Therefore, this review will concentrate on jump take-off velocity, with some consideration of other measures such as acceleration and unpredictability of jump direction.

The horizontal distance an animal can jump can be predicted using simple ballistic equations:

$$d = v^2 \sin 2\alpha / g, \quad (1)$$

where  $d$  is distance jumped (e.g. m),  $v$  is take-off velocity (e.g.  $\text{m s}^{-1}$ ),  $\alpha$  is take-off angle and  $g$  is the acceleration due to gravity (approximately  $9.8 \text{ m s}^{-2}$ ). Eqn 1 suggests that jump distance is largely dependent on take-off velocity and take-off angle. Eqn 1 involves the assumptions that air resistance is negligible, force and acceleration are constant during take-off and that the height of the centre of gravity is similar at take-off and landing. However, force platform records of animals such as frogs demonstrate that force and acceleration are not constant during take-off, causing peak force and peak acceleration to be higher than predicted (Calow and Alexander, 1973; Emerson, 1985). Some jumping animals have a difference in the position of the centre of their body mass between take-off and landing. This change in jumping kinematics results in jumping performance being relatively insensitive to take-off angle, and take-off angle to be lower than predicted from equations, but causes take-off height as well as take-off velocity to be important (Marsh, 1994). The take-off angle selected during jumping may be relatively invariant across species, representing a compromise among maximising jump distance, minimising flight time and, in some cases, minimising jump height (Toro et al., 2004).

Eqn 1 can be further modified (Marsh, 1994) to indicate some of the physiological and morphological factors that affect jump distance:

$$d = (\bar{W} \times L / M_b)^{\frac{2}{3}} \times (\sin 2\alpha / g), \quad (2)$$

where  $\bar{W}$  is total average power required for the jump (e.g. W),  $L$  is the distance from the centre of mass to the most distal part of the limb (e.g. m) and  $M_b$  is body mass of the animal (e.g. kg). This equation highlights several potential adaptations that could increase jumping performance: (1) the total average power required for the jump has to be provided by skeletal muscle but may be enhanced by elastic potential energy stored prior to or during the jump; and (2) the distance from the centre of mass to the most distal part of the limb could be increased by having relatively long legs.

This review will consider how animals can maximise jump distance, take-off velocity and/or acceleration, focussing on the role of muscle mechanics as constraints on jumping performance. To explore the potential constraints of muscle mechanics on jump performance, the review will present evidence for trade-offs in skeletal muscle performance and will discuss the effects of temperature and effects of body size on both muscle mechanics and locomotory performance. This review will also highlight various possible adaptations to improve jumping performance including alteration of muscle mechanics, increased muscle mass, increased leg length,

amplification of available muscle power or increased mechanical advantage of the muscles used.

### Trade-offs in skeletal muscle performance

Skeletal muscle can perform many different tasks during animal behaviour acting to rapidly produce high power output, to produce power efficiently over long periods of time, to produce high force for long periods of time, to produce force isometrically to stabilise a limb, to transmit force, or to absorb power to act as a brake (Dickinson et al., 2000; Kargo and Rome, 2002). During jumping, extensor muscles would ideally shorten rapidly whilst producing high power output to maximise take-off velocity and acceleration. However, the mechanical properties of muscle are determined by their composition, which in turn reflects trade-offs among the differing tasks performed by the muscle (Lindstedt et al., 1998). In mammalian muscles the fibre type of a muscle has been correlated to its daily activity patterns (Kernell et al., 1998), with slower fibre types occurring in muscles used for a larger percentage of the day. Kargo and Rome used modelling to demonstrate that the hind limb muscles of frogs are used in different task-specific ways (Kargo and Rome, 2002). Therefore, the composition and structure of extensor muscles used to power jumping will be compromised by these same muscles being used to perform other tasks.

In many animals, skeletal muscles contain different proportions of fibre types and within those muscles, fibre types may be separated into distinct regions or may appear as a mosaic (Putnam et al., 1980; Putnam and Bennett, 1983). The mechanical properties of the different muscles/fibre types and the proportions of different fibre types within muscles in jumping frogs appear to match the force/power output required by their different functions (Putnam et al., 1980; Putnam and Bennett, 1983; Lutz and Lieber, 2000; Rome, 2002). For example, in *Rana pipiens* the hindlimb muscles typically used to power jumping consist primarily (89%) of the fastest, most powerful, type 1 muscle fibres, which should maximise burst jumping performance and enable rapid escape from predators (Lutz et al., 1998; Lutz et al., 2002). In contrast, hindlimb muscles not used to power jumping are composed of far fewer (29%) type 1 muscle fibres (Lutz et al., 1998). As the percentage of myosin heavy chain in tibialis anterior muscle fibres from *Rana pipiens* increased from 0 to 100% there was a 57% increase in power output, a 22% rise in the force produced per cross-sectional area and a >30% increase in the velocity of shortening achieved at 50% maximal force (Lutz et al., 2002).

Many previous papers have demonstrated differences in mechanical properties between fast and slow muscles (Goldspink, 1996; Bottinelli and Reggiani, 2000), with a few studies examining correlations among different mechanical properties within a muscle *via* inter-individual variation (Bennett et al., 1989). However, several recent studies have used inter-individual analyses of whole-muscle performance to demonstrate trade-offs between maximum power output and

fatigue resistance in both isolated mouse and frog muscle (Wilson et al., 2002; Wilson and James, 2004; Wilson et al., 2004). Interindividual analyses of isolated whole gastrocnemius muscle performance of the toad *Bufo viridus* demonstrated trade-offs between fatigue resistance and both maximum power output and stress of the muscle (Wilson et al., 2004). In addition, this correlative analysis showed a significant positive relationship between power output and maximum stress (Wilson et al., 2004). Thus increases in maximum stress of an individual muscle lead to simultaneous increases in maximum power output and decreases in fatigue resistance (Wilson et al., 2004). Surprisingly, no significant correlations were detected between whole muscle performance of *B. viridus* and muscle fibre-type composition.

These trade-offs at the muscular level may translate themselves into trade-offs at the organismal level, with some animals excelling at explosive tasks such as sprinting or jumping but being poor at endurance tasks (Vanhooydonck et al., 2001; Van Damme et al., 2002). Since muscular design trade-offs appear to affect ecologically relevant performance traits they are likely to be under strong natural selection. Therefore, it can be expected that the skeletal muscle morphology, muscle mechanics and leg morphology of jumping animal species will be adapted to meet the requirements of their ecology and natural history. For example, the long, relatively thin legs of many high-performance jumping anurans are well adapted for arboreal life, but may be sub-optimally designed for performance in other contexts such as burrowing. Similarly, *Anolis* lizards that are good jumpers tend to have long hind limbs, which may negatively affect their ability to run across narrow substrates (Losos and Irschick, 1996).

### Temperature effects on skeletal muscle and jumping performance

Many animals are exposed to temperatures that can affect both jumping and skeletal muscle performance. In some ectotherms physiological adaptation or acclimation to extreme environmental temperatures is essential to maintain skeletal muscle and locomotor performance (Johnston and Temple, 2002). Previous studies on the effects of temperature indicate that skeletal muscle performance can limit locomotor performance.

Jumping ability of anuran amphibians is typically impaired by extreme low or high temperatures. A typical performance *versus* temperature curve would show reduced performance at low temperatures, a trend towards increased performance from low to warm temperatures, and often a sharp performance decrease at high temperatures (Hirano and Rome, 1984; Marsh, 1994; Navas et al., 1999). However, anurans occupy a variety of thermal environments, from cold high elevations to hot arid areas, such that the terms 'hot', 'cold' and 'extreme' become relative to the species under study. Thermal physiology of locomotion appears to differ among species to reflect variation in thermal ecology. For example, high-elevation tropical frogs in diverse genera and families (*Hyla*, *Eleutherodactylus*,

*Colostethus* and *Atelopus*) can move reasonably well at temperatures as low as 5°C (Navas, 1996; Navas et al., 1999), whereas some juvenile toads (*Bufo*) from tropical semi-arid regions are diurnal and jump best at 35°C (Navas et al., 2004). Adjustments in thermal physiology have also been observed within species, with differences in thermal sensitivity among populations of Australian striped marsh frog (*Limnodynastes peronii*). Jumping performance of *Limnodynastes peronii* differed among populations, with those populations from cooler climates tending to perform better at lower temperatures than those from warmer climates and *vice versa* (Wilson, 2001).

Studies of isolated skeletal muscle indicate that as temperature increases, skeletal muscle activation and relaxation times decrease, and maximum shortening velocity and power output increase (Marsh, 1994; Navas et al., 1999; Wilson et al., 2000). However, the rate of change of muscle mechanical properties alters greatly among different temperature intervals (Marsh, 1994). The rates of change of muscle performance and locomotor (including jumping) performance are often similar, suggesting that temperature constraints on muscular performance in turn limit locomotor performance. However, isolated muscle performance may significantly improve over certain temperature ranges, whereas locomotor performance may undergo much less change. Some of these differences in thermal sensitivity between locomotor and muscle performance are probably due to the importance of relatively temperature-insensitive mechanisms of storage and recovery of elastic strain energy (Marsh and Bennett, 1985; Navas et al., 1999). An extreme example of this occurs in insects that use a catch mechanism to largely avoid the constraints of temperature on jumping performance. Elastic strain energy is stored prior to the jump such that rapid, almost temperature independent, jumping responses can occur (see 'Energy storage mechanisms' section, below).

A number of physiological and biochemical traits would be candidates for improved activity at low temperatures in cold-adapted species. However, the actual mechanisms for improved activity at low temperatures are not fully understood. Most of the current traits identified relate to regeneration of ATP and as such are probably related to recovery processes in the muscle that allow repeated jumps. Enhanced expression of key metabolic enzymes is among the most important mechanisms allowing for locomotion at low activity temperatures in anurans. The skeletal muscle of the Australian striped marsh frog (*Limnodynastes peronii*) exhibits higher maximal activity of the enzyme lactate dehydrogenase (LDH; key in oxygen-independent glycolytic pathways) in individuals maintained at 20°C than in frogs kept at 30°C (Rogers et al., 2004). The mechanisms that allow a few anuran species to hop at temperatures above 40°C apparently also involve changes in muscle metabolic profile. In this case, protection of working enzymes seems to be a key aspect of thermal adaptation. The thermal stability of the citrate synthase of leg muscles of *Bufo granulosus* is much lower in adults than in the thermophilic juvenile toadlets, which are diurnal (Navas et al., 2007).

The temperature-dependent effects of skeletal muscle performance on locomotion can also affect ectotherm behaviour. For example, some lizards are more likely to exhibit aggressive antipredator responses (Hertz et al., 1982; Mautz et al., 1992) or longer flight distances (Rand, 1964; Rocha and Bergallo, 1990) when they are colder. The near isometric force development used during biting is less temperature sensitive than muscle power production during sprinting or jumping. Tree frog *Scinax hiemalis* individuals choose either to jump away from danger, or to feign death when approached by a predator (Gomes et al., 2002). The likelihood that the individuals would choose to jump away under laboratory conditions was found to increase with animal size and with temperature, indicating that the 'decision' to jump is probably based on the likely muscle performance of the individual. Among warm individuals, those that exhibited high absolute jumping performance (a function of body size and leg muscle physiology) were more likely to attempt to escape by jumping than to use stationary defensive measures (Gomes et al., 2002).

### Effects of body size

Effects of body size are pervasive, causing large changes in both muscle mechanics and jumping performance. Such effects provide another interesting context in which to explore links between muscle mechanics and jumping performance, therefore, this section of the review will describe these effects, then consider whether there are causal links between scaling of muscle mechanics and scaling of jumping performance.

#### Scaling of absolute jumping performance

A large amount of jumping performance data is available for frogs. Zug's extensive data set (Zug, 1978) was reanalysed (Marsh, 1994) to split the frog species studied into three groups according to morphology (as body shape varied considerably among groups and such variation would affect jump performance) and test temperature (which is known to have large effects on jump performance). Absolute maximum jump distance for each group scaled with body mass ( $M_b$ ) as either  $M_b^{0.19}$  or  $M_b^{0.20}$ , with large variation in performance within and among each group. In comparison, interspecific scaling relationships of jumping performance in *Anolis* lizards yields an exponent of  $M_b^{0.15}$  (Toro et al., 2004).

Intraspecific scaling relationships show much greater variation in results, with scaling relationships of adult frog species of between  $M_b^0$  and  $M_b^{0.40}$  (Rand and Rand, 1966; Emerson, 1978; Miller et al., 1993; Choi et al., 2000; Wilson et al., 2000). Intraspecific scaling relationships for maximal jump distance were found to vary from  $M_b^{0.19}$  to  $M_b^{0.44}$  in *Anolis* lizard species (Toro et al., 2003). Amongst these studies, both maximum jump distance and take-off velocity in adult (post-metamorph) striped marsh frogs were independent of body size (Fig. 1) (Wilson et al., 2000). In contrast, Wilson et al. found that both maximal jump distance and take-off velocity in juveniles (metamorphs) were highly dependent on body size,  $M_b^{0.53}$  and  $M_b^{0.23}$ , respectively (Fig. 1) (Wilson et al., 2000).

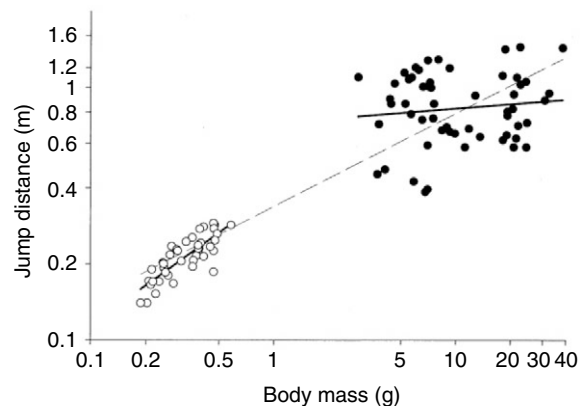


Fig. 1. Scaling of jump performance in metamorph (open symbols) and post-metamorphic (filled symbols) striped marsh frogs *Limnodynastes peronii*. The lines were fitted via least squares linear regression for metamorph and post-metamorphic data separately (solid lines) and all data combined (broken line). Based on Wilson et al. (Wilson et al., 2000).

Other studies have also found lower than expected jump performance immediately after metamorphosis (Emerson, 1978; Zug, 1978), so it may be that the slopes for some of the above frog scaling relationships are more positive than the adult data due to inclusion of juvenile data. However, removal of metamorph data greatly reduces the body size range and still leaves the adult data difficult to interpret. Emerson suggested that any jumping performance parameter that is independent of body size is likely to be the critical locomotory performance variable selected for (Emerson, 1978). In some species of frogs (Emerson, 1978) and some larger species of *Anolis* lizards (Toro et al., 2003), acceleration capacity was body size-independent. In contrast the frog jumping results of Wilson et al. suggest that, in striped marsh frogs at least, it is jump distance that is the key variable (Wilson et al., 2000).

In intraspecific studies of African desert locusts there is no significant change in maximum jump range or take-off velocity from the first up to and including the fourth instar of *Schistocerca gregaria* (Gabriel, 1985a; Katz and Gosline, 1993). However, over time adult locusts (sixth instar) initially increase jump take-off velocity, then level out at approximately double the velocity of juveniles. Therefore, in this species at least, developmental (ontogenetic) effects, rather than body size effects, have a more marked effect on jump performance. In juvenile locusts, leg length increases relative to body size to maintain jumping performance (Katz and Gosline, 1992). However, jumping performance in adults is improved by increasing the relative muscle mass available for jumping (Gabriel, 1985a) and reflects the need for higher jump velocity to enable a change in locomotory mode to flying (Katz and Gosline, 1993).

Intra-specific studies of mammalian jumping performance are limited in number, and very little change in jumping performance of black tailed jackrabbits (*Lepus californicus*) was reported (Carrier, 1995). The two smallest (juvenile)



Table 1. Interspecific body mass specific scaling exponents for maximum unloaded shortening velocity against body mass for different single muscle fibre types from a range of mammals

Fibre type	Scaling exponent	
	15°C <sup>a</sup>	12°C <sup>b</sup>
I (slow)	-0.18	-0.21
IIA	-0.07	-0.08
IIX	Not measured	-0.04
IIB	Not measured	No relationship

<sup>a</sup>(Rome et al., 1990); <sup>b</sup>(Toniolo et al., 2005).

jackrabbits in this study achieved approximately 20% lower maximal jump velocity, with adult rabbits all showing very similar jump velocity; the study animals, however, only spanned a fourfold body mass range.

#### Scaling of muscle mechanics

Unfortunately there is a distinct lack of data on scaling of muscle stress and shortening velocity in jumping animals [with the exception of unpublished data from *Rana catesbeiana* presented in Marsh's review (Marsh, 1994)]. Generally, however, as animal size increases, skeletal muscle shortening velocity and contraction kinetics become slower. A large comparative study considering skeletal muscle, from 72 species of animals from many taxonomic groups, found that length-specific shortening velocity scaled  $M_b^{-0.12}$  for running and flying animals, after the data had been corrected for the effects of experimental temperature (Medler, 2002). Medler's review gives a good indication of broad muscle shortening-velocity relationships but is unable to correct for fibre type changes, and uses data determined *via* different methods in different studies and laboratories. A few studies have isolated single fibres of specific fibre types, from the same muscle, in a large body mass range of mammalian species, to subsequently determine scaling relationships within the study. Similar scaling exponents to those reported by Medler for maximum shortening velocity have been found for type I muscle fibres [ $(M_b^{-0.11})$  (Widrick et al., 1997) and  $M_b^{-0.13}$  (Seow and Ford, 1991)]. However, these mammalian muscle scaling exponents have been determined using force-velocity studies (isotonic) that rely on curve-fitting techniques to estimate maximal shortening velocity (Marsh and Bennett, 1986), which they are prone to underestimate (Claflin and Faulkner, 1985; Widrick et al., 1997; James et al., 1998). Studies using the slack test, which directly measures unloaded shortening velocity, have demonstrated larger scaling exponents (-0.18 to -0.21) in slow fibres than have been found using force-velocity studies (Table 1). Widrick and coworkers (Widrick et al., 1997) further confirmed the scaling relationship of type I fibres found by Rome and coworkers (Rome et al., 1990) despite using a few different mammalian species. Data of Toniolo and coworkers (Toniolo et al., 2005) suggests that the fastest muscle fibres, which are of greater importance in maximal activities such as escape responses, have very similar maximum

unloaded shortening velocity in each species over a large body size range.

Intraspecific studies within anuran (Bennett et al., 1989; Marsh, 1994; Altringham et al., 1996), lizard (Marsh, 1988; Johnson et al., 1993) and fish (Wardle, 1975; James et al., 1998) species have highlighted that as body size increases there are usually decreases in temporal traits of whole muscle/muscle fibre bundle functions, including relative muscle shortening velocity and twitch activation and relaxation rates, i.e. muscle in smaller individuals of a species will tend to produce force quicker, shorten relatively faster and relax quicker. In many cases these muscles are of mixed fibre type and fibre type proportions will change with size, such that the scaling relationships observed are the summation of changes within and between fibre type with changing body size. As body mass increases intraspecific maximum muscle shortening velocity generally decreases, with a slope between -0.08 and -0.11 in fast muscle from frog (sartorius,  $V_{max}$ ; Fig. 2) (Marsh, 1994), fish ( $V_0$ ) (James et al., 1998), lizard ( $V_{max}$ ) (Marsh, 1988) and salamander ( $V_{max}$ ) (Bennett et al., 1989). However, in contrast Curtin and Woledge found no effect of body size on the maximum shortening velocity ( $V_0$ ) of fast myotomal muscle from dogfish (*Scyliorhinus canicula*) (Curtin and Woledge, 1988).

One analysis (Medler, 2002) found no significant relationship between maximal isometric stress and body mass. Intraspecific studies have also found that maximum isometric muscle stress and normalised power output are generally unaffected by body size (e.g. Bennett et al., 1989; Johnson et al., 1993; Marsh, 1994; Altringham et al., 1996; James et al., 1998). A significant though weak relationship does exist, however, between maximal isometric force production and maximal shortening velocity (Medler, 2002) ( $P_0=122V_{max}^{0.14}$ ). Medler argues that fast glycolytic fibres will tend to have relatively higher myofibrillar density, causing higher muscle stress (Medler, 2002).

#### How can jumping performance be maximised despite the muscle performance constraints imposed by body size?

It appears that within some species maximal adult jumping performance may be relatively independent of body size. The reasons for this body size independence are not fully understood, but they could include physiological or biomechanical properties, and may also include small body size ranges in adults studied and changes in body mass in adults in some species being caused by variation in body composition such as fat mass (Harris and Steudel, 2002) or egg mass. However, it is clear that skeletal muscle decreases in contractile speed with increasing body size both within and among species (for example maximal skeletal muscle shortening velocity decreases at approximately  $M_b^{-0.10}$  for most whole muscle studies performed). Therefore, it appears that during jumping in many species other factors are compensating for, or allowing uncoupling from, size related changes in the mechanical properties of muscle.

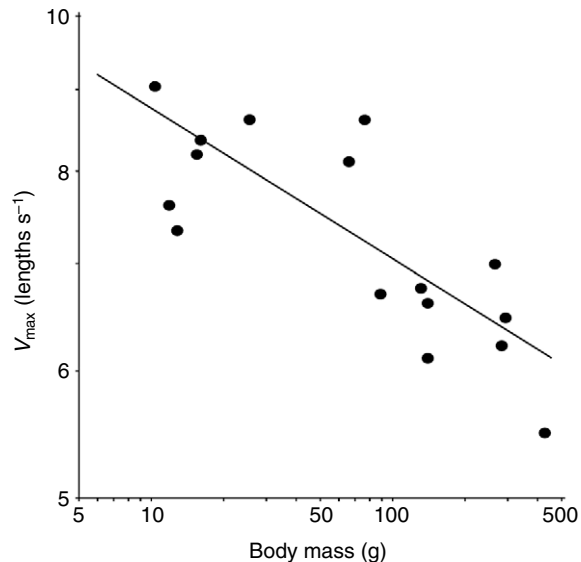


Fig. 2. Scaling of maximal muscle shortening velocity  $V_{max}$  of *Rana catesbiana* sartorius muscle at 20°C. Based on Marsh (Marsh, 1994). The scaling relationship for the data shown was  $M_b^{-0.094}$ .

There is evidence that juveniles in some species (including jumping jackrabbits) (Carrier, 1995) compensate for their smaller absolute body size by rapid development of locomotor morphology to attain high locomotor performance early in life (Herrel and Gibb, 2006). Such selective development is probably driven by predation leading to the requirement of juveniles to attain locomotory performance as high as adults.

#### Energy storage mechanisms

Both Emerson (Emerson, 1985) and Bennett-Clark (Bennett-Clark, 1977) have demonstrated that many animals covering a large body size range, including insects, frogs and mammals, require higher power outputs for jumping than could be directly delivered by skeletal muscle.

In general, smaller animals have smaller limbs and, therefore, a shorter distance over which to accelerate. Therefore, to achieve the same jumping performance the smaller animals will require higher force, greater peak power output and higher maximum shortening velocity to enable them to accelerate faster to achieve the same all-important take-off velocity (Bennet-Clark, 1977). As animals become smaller a point is reached where maximum skeletal muscle shortening velocity cannot continue to increase. A compounding problem is that as animals get much smaller they encounter greater losses in jump performance due to drag; however, drag effects are only significant in animals the size of smaller insects (Vogel, 2005). Therefore, smaller animals need to be more specialised, to increase storage of elastic potential energy prior to the jump, to amplify available muscle power output, enabling them to achieve similar jump distances to larger animals (Bennet-Clark, 1977). Power supply is clearly critical in determining jump distance, with most, if not all, jump specialist animals using energy storage to some extent to

enhance power. However, much smaller animals need larger power amplification due to the constraints imposed by drag and the mechanical properties of muscle.

Elastic energy storage is particularly notable in insects. In some insects such as click beetles (Evans, 1972), flea beetles (Brackenbury and Wang, 1995), locusts (Heitler, 1974) and fleas (Bennet-Clarke and Lucey, 1967), jumping performance is greatly enhanced *via* substantial storage of elastic strain energy. In some insects a catch mechanism is used, to allow muscular activation to occur while restraining movement of the 'catapult' mechanism used for jumping. In some animals, body weight may act as an effective catch, allowing initial muscle shortening to be uncoupled from whole body movement (Roberts and Marsh, 2003). Catch mechanisms allow power to be generated by the muscles and stored as elastic potential energy, *via* stretch of elastic structures before the jump takes place. Once the catch mechanism is released the power generated by the muscles during take-off is enhanced during elastic recoil of the elastic structure. The elastic recoil releases the elastic strain energy stored prior to take-off. Therefore, in a number of animals, energy can be stored during a relatively slow muscular contraction, yet be transferred rapidly when the catch mechanism has been released. Bennet-Clark suggests that such a catch mechanism allows over half of the energy generated during a slow muscular contraction to be stored in an elastic structure (Bennet-Clark, 1975). The release of the stored energy enhances the energy available to power the jump to 1.5 times that of the maximum power of the muscle, leading to an effective power amplification of up to 10 times that actually produced by the muscle during jumping. The energy storage materials are relatively small and lightweight compared to the muscle used to generate the power, therefore, representing a cost-effective mechanism for improving jumping performance. The effectiveness of a catapult mechanism is demonstrated by the finding that locusts kept at cold temperatures can jump just as far as those kept at higher temperatures (Gabriel, 1985b). The only decrease in performance is that the colder locusts take longer to perform the jump as the power of the jump is largely dependent on the energy storage mechanism, so at lower temperatures it just takes longer for the skeletal muscle to deform the storage element by the required amount.

In some mammals such as man (Kubo et al., 1999; Bobbert, 2001; Kurokawa et al., 2001) and bushbaby (Aerts, 1998), elastic energy storage in tendons has been found to increase countermovement jump performance. In the case of the bushbaby, elastic strain energy is stored in the internal connective tissue sheets of the vastus muscle, not only during preparatory crouching, but also during the early phase of knee extension, with a sudden release of energy late in take-off (Aerts, 1998). Use of a countermovement enables force enhancement due to stretch of active muscle (Edman et al., 1978), time for the extensor muscles to attain high force prior to shortening and energy storage in the tendons in series. During hopping in wallaby (Biewener et al., 1998; Ker et al., 1986), kangaroo (Alexander and Vernon, 1973) and kangaroo

rat (Biewener et al., 1981), similar principles apply with high muscle force, and in these cases limited muscle length change, during stretch of the muscle–tendon unit, leading to energy storage prior to muscle shortening. Also, in jumping lizards, power amplification during countermovement jumps has been invoked to explain the increased power output during jumping compared to running (Vanhooydonck et al., 2006a).

In frogs, however, no obvious countermovement is observed and no catch mechanism is known, yet the jumping performance of many frog species studied also appears to exceed that available from the skeletal muscle. These findings suggest that energy storage may be used to allow subsequent power amplification in these species (Marsh and John-Alder, 1994; Peplowski and Marsh, 1997; Navas et al., 1999; Wilson et al., 2000). Modelling of the frog plantaris muscle–tendon unit, combined with sonomicrometry measurements in plantaris muscle of jumping bullfrogs, demonstrates uncoupling of skeletal muscle and whole body movements during jumping (Roberts and Marsh, 2003). Rapid early shortening of plantaris muscle, without movement of the frog, causes stretch of tendons and consequent elastic energy storage, which subsequently enhances muscle power output during take-off. Such uncoupling of muscle shortening from whole body movement allows the muscle to produce more force and to shorten at a lower velocity than if the two were coupled, and allows a catapult-like mechanism to be used, without a catch being present.

In species where elastic energy storage is used the scaling of jump performance will reflect the power available for the jump, which will be affected by both scaling of skeletal muscle properties and potentially by scaling of elastic energy storage. Both the type of energy storage mechanism and the jumping technique vary among animal species, affecting jump performance (Alexander, 1995) (see final section of this review).

#### Limb morphology

When standard projectile equations are applied to jumping (see Eqn 1, 2 in Introduction), they suggest that increased hindlimb length and mass of jumping muscles, and beneficial alteration of the origin and/or insertion of jumping muscles, should improve animal jump performance (for a review, see Emerson, 1985). These predictions have been empirically confirmed in studies among species of frogs, concluding that, in comparison with non-jumping species, jumping specialists have longer hindlimbs, larger jumping muscles and a more proximal insertion of hip extensor muscles in jumping (for a review, see Emerson, 1985). For example, interspecific increases in frog take-off speed have been positively correlated with body mass-specific hindlimb thigh muscle mass and with body length-specific hindlimb length (Choi et al., 2003). In lizards, hindlimb length also explained a significant proportion of the variation in take-off velocity across different *Anolis* species (Toro et al., 2004). However, when *Anolis* muscle masses and limb segment lengths were entered into a multiple regression model, the mass of the knee extensors was the only

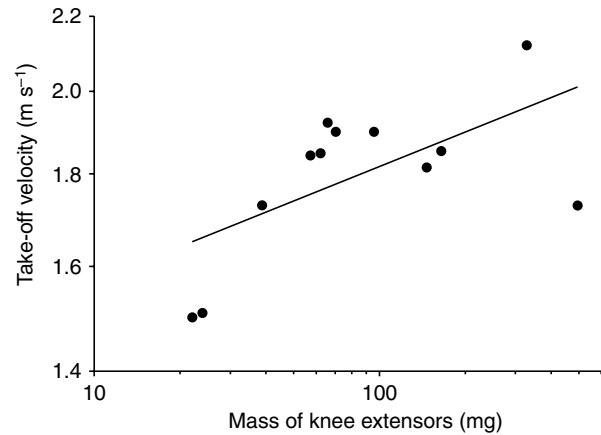


Fig. 3. The mass of the knee extensors is the best predictor of take-off velocity across 12 species of *Anolis* lizards. Data on take-off velocity were taken from Toro et al. (Toro et al., 2004); data on muscle masses were taken from Vanhooydonck et al. (Vanhooydonck et al., 2006b).

variable retained and was thus the best predictor of take-off velocity ( $r=0.62$ ;  $P=0.03$ ; see Fig. 3).

Relative hindlimb length (hindlimb length/body length) does vary among species and can affect performance. Frog (Emerson, 1978) and mammal species (Emerson, 1985) that are jump specialists have relatively longer legs. Frog (Rand, 1952; Zug, 1972; Choi and Park, 1996; Choi et al., 2003) and lizard species (Losos, 1990) with longer hindlimbs have generally been found to achieve greater jump distance and/or take-off velocity. In some smaller species of indriids such as galagos, disproportionately larger hindlimbs may serve to increase the time available for acceleration during take-off (Demes et al., 1996). Some animal species, such as within the lizards *Chameleo* and the frogs *Phylomedusa*, have large hind and front limbs but are not good at jumping; instead the elongated limbs are used for climbing in complex three-dimensional habitats (Pough et al., 2004). Within *Bufo marinus* (cane toads), individuals with relatively long legs are faster over 1 m and cover larger distances in 24 h (Phillips et al., 2006). However, variation in hindlimb length within a species does not necessarily cause a change in jump performance. Within and among many species of *Anolis* lizards limb dimensions generally increase geometrically (Toro et al., 2003), but *Anolis carolinensis* demonstrates negative allometry. Toro and coworkers (Toro et al., 2003) argue that the negative allometry in *Anolis carolinensis* may reflect weak selection for long limbs in adults due to their reliance on crypsis for predator avoidance. No effect of relative or residual hindlimb length on jump performance was found within species in some frog jumping studies (Stokely and Berberian, 1953; Emerson, 1978; James et al., 2005) and in one lizard jumping study (Losos et al., 1989). However, variation in residual hindlimb length has been found to correlate with variation in maximum jump take-off velocity within domestic cats (Harris and Steudel, 2002). Variation in hindlimb length among hemiclones of *Rana*

*esculenta* explained 77% of the variation in maximal jump distance, whereas body mass only explained 1% of the variation in performance (Tejedo et al., 2000).

Hindlimb muscle mass of juveniles and adults of frog species does appear to scale geometrically, whereas in just-metamorphosed through to juvenile frogs there is positive allometry in hindlimb muscle mass (Emerson, 1985). However, hindlimb muscle mass in frogs (Emerson, 1978) and mammals (Alexander et al., 1981) varies as a proportion of body mass as jumping species have proportionally larger extensor muscles than non-jumping species. There is some evidence that frog species with relatively greater thigh muscle mass achieve higher jump take-off velocity (expressed relative to body mass) (Choi and Park, 1996; Choi et al., 2003). Miller et al. (Miller et al., 1993) found that larger leopard frogs (*Rana pipiens*) achieved higher jump distances, had relatively heavier jumping muscles and relatively higher LDH activity. Bennet-Clark suggested that some smaller jumping animals have a relatively smaller jumping muscle mass, but that the jumping muscles become wider with respect to their length and that the skeleton they are attached to has to become relatively stronger (Bennet-Clark, 1977). However, in adult locusts the muscle mass of the femur is a higher percentage of body mass than it is in fourth instar locusts (Gabriel, 1985a), with an aligned increase in angle of muscle pennation (Gabriel, 1985b). In adult locusts the semilunar process is thickened and lengthened to create a stiffer spring for energy storage; this coupled with the change in muscle morphology leads to a greater capacity for energy storage and greater jump velocity (Gabriel, 1985b).

The greater force requirements for jumping in smaller animals lead to a change in muscle architecture with body size (Bennet-Clark, 1977). Larger animals tend to have muscles that are relatively long, relatively thin and relatively less pennate when compared to smaller animals. Some hip extensor muscles have a more proximal insertion on the tibia in jumping mammals than in non-jumping mammals (reviewed in Emerson, 1985). Such adaptations in smaller animals would lead to relatively higher muscle forces being applied for the same muscle mass [for a review on the effects of architecture on skeletal muscle mechanical performance, see Lieber and Fridén (Lieber and Fridén, 2000)]. However, the larger muscle forces involved in jumping may potentially reach levels that compromise safety factors of bone and tendon in larger animals, which may explain the relatively poor performance of larger jumping animals (e.g. Toro et al., 2003; Toro et al., 2004).

#### **Relative importance of skeletal muscle mechanics, limb morphology and muscle biochemistry in jump performance**

Modelling of jump performance can give us insights into the relative importance of the effects of different variables. The effects of changing skeletal muscle properties, jumping technique, mass distribution in legs, leg length, moment arms and tendon compliance on jumping performance in different

types of animals have been modelled (Alexander, 1995). In a human-like animal, catapult and countermovement jump techniques yielded similar jump performance, both of which outperformed squat jumps. However, in bushbaby and insect-like animals, catapult jump techniques were clearly better than both countermovement and squat jumps, which fits in well with the existence in these two types of animals of the different forms of 'catapult' jumping, discussed earlier in this review. In all cases, increasing muscle shortening velocity or series compliance yielded higher jumps in Alexander's model. However, in countermovement jumps, jump height was more sensitive to changes in maximum muscle shortening velocity than to alterations in series compliance, whereas in catapult jumps the reverse was true. These findings again reinforce the idea that smaller animals require substantial power amplification of muscle power output *via* energy storage in elastic structures to allow them to overcome the constraints of muscle mechanics (see section 'How can jumping performance be maximised despite the muscle performance constraints imposed by body size?'). In all cases longer legs yielded higher jumps in Alexander's model, but this effect was less marked in catapult jumps, especially when series compliance was relatively high. In Alexander's model the total mass of the legs had a greater effect on jump performance than the mass distribution within the legs.

Although many studies of adult animals have demonstrated that differences in jump performance among species are also linked with differences in the morphological, enzymatic and mechanical properties of muscles (Marsh, 1994), these need not necessarily apply to intraspecific correlates of locomotor performance. Very few studies have examined size-independent interindividual variation in the underlying factors explaining variation in adult jumping performance within species. Multiple regression analysis determined that 62% of variation in jump take-off velocity in domestic cats could be explained by variation in lean body mass residuals of hindlimb length and fat mass (Harris and Steudel, 2002), but was largely unaffected by variation in lean body mass, % of type IIX MHC content in lateral gastrocnemius muscle or residual muscle mass; i.e. cats with relatively long legs and relatively low fat mass achieved higher take-off velocities. Similar analysis in a species of tree frog (*Hyla multilineata*) demonstrated that 43% of variation in jump distance could be explained by variation in body length residuals of total hindlimb muscle mass and plantaris muscle pyruvate kinase activity (James et al., 2005), but was largely unaffected by residuals of plantaris muscle force, plantaris muscle power, plantaris activation rate, total leg bone length, lactate dehydrogenase activity of plantaris muscle or citrate synthase activity of plantaris muscle. These findings suggest that, in some species, differences in jumping performance among individuals may be related to morphological variables such as greater relative quantity of muscle and larger relative leg length, which would lead to greater available muscle power output and longer distance over which to accelerate during take-off, respectively. However, we need further analysis of



this type to fully quantify the importance of different factors that affect jump performance.

It is unlikely that relationships among morphological/physiological measures and jumping performance will be the same in all species. Some species, such as some toads and toad-like microhylids, rely on defence mechanisms such as secretion of poison to deter predators rather than relying on jump performance to escape. Such species have been found to have relatively poor jump performance and little of the specialisation of limb morphology seen in high performance jumpers (Marsh, 1994; Choi and Park, 1996). Variability in the jump performed may also be important in avoiding being caught by predators. Kargo and coworkers (Kargo et al., 2002) used a model of frog jumping to demonstrate that relatively small alterations in hip external rotation torque, which can be controlled by key muscles active during jumping, could cause large changes in take-off angle providing a relatively simple system for variability in jump response. Unpredictability of an escape response can increase the likelihood of escaping predation. Differences in the propensity of individuals to jump have been demonstrated both within a frog species (Gomes et al., 2002) (also see section entitled 'Temperature effects on skeletal muscle and jumping performance') and among lizard species (Tropidurinae) (Kohlsdorf and Navas, 2007). Species of Tropidurinae that lived in arid, relatively open, sand environments jumped less often and were not able to jump as high as those species that inhabited rocky more densely vegetated environments (Kohlsdorf and Navas, 2007). These differences in propensity to jump and in jumping performance reflected differences in habitat and were not related to phylogeny.

In conclusion, skeletal muscle mechanics can restrict jumping performance due to the limits of maximal shortening velocity and maximal power output affecting jump acceleration and distance. Skeletal muscle performance could cause greater limitations on jumping performance when temperature is low or animal size is small. However, animals use a range of adaptations to mitigate the potential restrictions imposed by the mechanical properties of muscle. Selective rapid development of locomotor morphology can be used to enable young animals to attain high locomotor performance early in life. In some very small animals specialist structures are used to enhance energetic storage, to amplify the power output available from skeletal muscle. Adaptations involving increased relative hindlimb length and relative mass of jumping muscles, and beneficial alteration of the origin and/or insertion of jumping muscles, can all be used to improve animal jump performance. However, we do need an integrative study to investigate within-species measures of jump performance related to fitness. Such a study would ideally use a species that covers a relatively large body mass range, is relatively good at jumping and uses jumping to escape. Such a study would need to determine whole body jumping performance, *in vivo* muscle strain and activation, *in vitro* maximal shortening velocity of a jumping muscle (to allow comparisons to previous studies), *in vitro* mechanical performance of muscle under simulated *in vivo*

jumping conditions and, preferably, consider limb muscle fibre type and muscle/bone morphology in some detail to investigate effects of development and growth on performance. Such studies could then investigate both body size-dependent and body size-independent effects of a wide range of realistic muscle mechanical and morphological variables on jumping performance within a species. Only after such studies have been performed may we get a much better understanding of how important skeletal muscle properties are in affecting jumping performance.

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