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REVIEW

The importance of comparative physiology: mechanisms, diversity and adaptation in skeletal muscle physiology and mechanics

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ABSTRACT

Skeletal muscle powers animal movement, making it an important determinant of fitness. The classic excitation–contraction coupling, sliding-filament and crossbridge theories are thought to describe the processes of muscle activation and the generation of force, work and power. Here, we review how the comparative, realistic muscle physiology typified by *Journal of Experimental Biology* over the last 100 years has supported and refuted these theories. We examine variation in the contraction rates and force–length and force–velocity relationships predicted by these theories across diverse muscles, and explore what has been learnt from the use of workloop and force-controlled techniques that attempt to replicate aspects of *in vivo* muscle function. We suggest inclusion of features of muscle contraction not explained by classic theories in our routine characterization of muscles, and the use of phylogenetic comparative methods to allow exploration of the effects of factors such as evolutionary history, ecology, behavior and size on muscle physiology and mechanics. We hope that these future directions will improve our understanding of the mechanisms of muscle contraction, allow us to better characterize the variation in muscle performance possible, and enable us to infer adaptation.

KEY WORDS: Excitation–contraction coupling, Force–length, Force–velocity, Eccentric, History dependence, Phylogenetic comparative methods

Introduction

Skeletal muscle generates the force, work and power required for animal movements, making it an important determinant of behavioral capabilities (Syme and Josephson, 2002; Miles et al., 2018; Nelson et al., 2018) and fitness (Lappin and Husak, 2005; Husak et al., 2006). Skeletal muscle uses a relatively consistent physiological mechanism of contraction across taxa; in response to activation by the nervous system, interactions between the contractile proteins actin and myosin produce force and do work. However, the diversity of movements powered by skeletal muscle suggests significant capacity for variation. Moreover, the use of a molecular-scale motor to drive organismal-scale movements suggests an extensive force transmission system and, therefore, significant structural and functional complexity (Williams and Holt, 2018).

General features of skeletal muscle structure and function

Skeletal muscle is a highly organized, multi-scale tissue (Williams and Holt, 2018; Holt, 2020). Sarcomeres, sub-cellular structures containing contractile protein filaments, are considered to be the functional units of muscle. Thin filaments, containing a helical actin polymer (Holmes et al., 1990; Holmes, 2009) and a regulatory troponin–tropomyosin complex (Hanson and Lowy, 1963), project from the Z-disks at the ends of the sarcomere and overlap with the central thick filaments, which contain a myosin polymer. These contractile protein filaments are held in place by a sarcomeric cytoskeleton (Horowits et al., 1986; Gautel and Djinović-Carugo, 2016), including the large protein titin (Horowits et al., 1986; Maruyama, 1976; Wang et al., 1979), and create a highly ordered lattice structure when viewed in three dimensions (Hodge et al., 1954; Millman, 1998; Shimomura et al., 2016). Sarcomeres are arranged in series and in parallel in muscle fibers, and are enveloped by the sarcoplasmic reticulum (SR), an internal calcium (Ca^{2+}) store made up of a network of interconnected tubules. Muscle fibers are organized into entire muscles with orientations ranging from parallel to perpendicular to the line of action of the muscle (Gans, 1982; Kier and Smith, 1985; Askew and Marsh, 2001; Kargo and Rome, 2002; Taylor-Burt et al., 2018). Muscle fibers and entire muscles are surrounded by connective tissues (Purslow and Trotter, 1994; Scott and Loeb, 1995; Azizi and Roberts, 2009; Huijing, 2009; Sleboda et al., 2020) and connected to the skeleton by tendons (Alexander et al., 1982; Gronenberg et al., 1997; Roberts and Azizi, 2011).

The classic framework for understanding muscle contraction includes the excitation–contraction coupling (ECC) and crossbridge and sliding-filament theories. Together, these theories describe the process of force generation in response to activation by the nervous system. According to ECC theory, action potentials in motorneurons activate muscles and cause Ca^{2+} release from the SR. This Ca^{2+} binds to troponin, moving tropomyosin and permitting myosin heads to bind to actin and form crossbridges (Ebashi and Endo, 1968). According to the crossbridge and sliding-filament theories, these bound myosin heads then undergo a conformational change that acts to slide the actin filament past the myosin filament, generating force and potentially doing work. Upon deactivation, Ca^{2+} is returned to the SR and the muscle relaxes. Single activation pulses give rise to short twitch contractions, whereas high frequency activation pulses do not leave sufficient time for Ca^{2+} to be removed and result in tetanic contractions at fusion frequency. The formation of crossbridges and the sliding of filaments are thought to give rise to the isometric force–length and isotonic force–velocity relationships observed in maximally stimulated muscles *in vitro* (Hill, 1938; Huxley, 1957; Gordon et al., 1966). According to the force–length relationship, isometric force is maximal at an intermediate sarcomere length corresponding to optimum actin–myosin overlap (Fig. 1). Force declines at long lengths owing to reduced overlap, and at shorter lengths owing to excessive overlap

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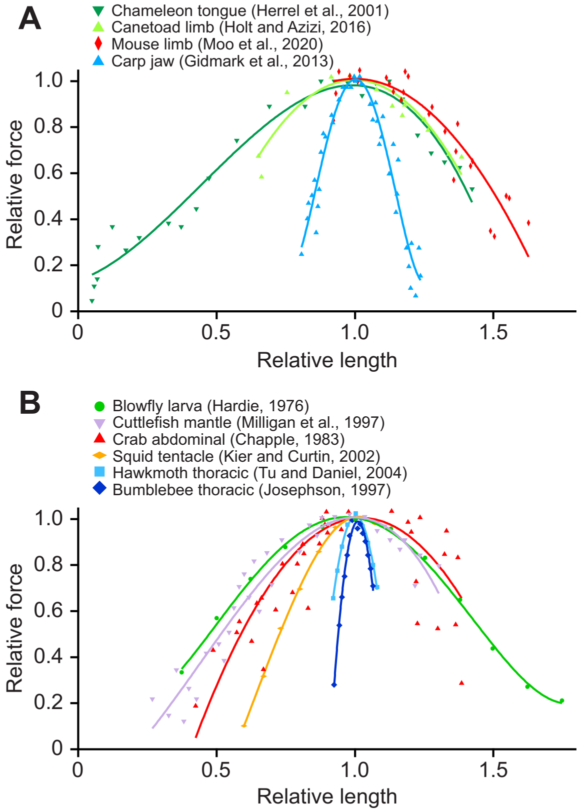

Fig. 1. Comparison of skeletal muscle force–length curves across vertebrates and invertebrates, and across muscles with a variety of functions, highlighting variation in curve width. (A) Vertebrates; (B) invertebrates. All digitized data points were normalized to peak force and optimum fiber or sarcomere length, and fit with a polynomial function. The chameleon tongue and blowfly larva muscles have been characterized as supercontracting muscles, and the cuttlefish body wall muscle is obliquely skeletal. All other muscles are thought to be typical skeletal muscles. Not all invertebrate sarcomere lengths are reported but the crab abdominal and squid tentacle muscles have sarcomere lengths of 10.8 μm (Chapple, 1983) and 1.5 μm (Kier and Curtin, 2002; Shimomura et al., 2016), respectively.

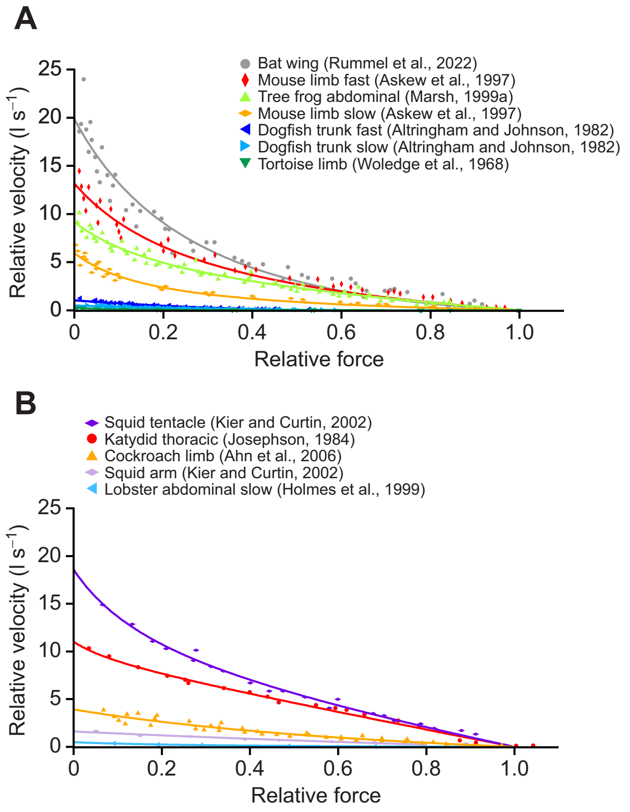

Fig. 2. Comparison of skeletal muscle force–velocity curves across vertebrates and invertebrates, and across muscles with a variety of functions, highlighting variation in V_{max} and curvature. (A) Vertebrates; (B) invertebrates. All digitized data points were fit with a hyperbolic–linear equation (Marsh and Bennett, 1986). Not all invertebrate sarcomere lengths are reported, but the squid arm, squid tentacle, katydid thoracic and cockroach limb muscles have sarcomere length of 12.5 μm, 1.5 μm (Kier and Curtin, 2002; Shimomura et al., 2016), 3.1 μm (Josephson, 1984) and 3.5 μm (Fourtner, 1976), respectively.

potentially interfering with crossbridge binding (Gordon et al., 1966; Walker and Schrodt, 1974; Herzog et al., 1992a). According to the isotonic force–velocity relationship, the force a muscle can produce declines monotonically with increasing shortening velocity (Fig. 2), thus limiting power (Rome et al., 1988; Schiaffino and Reggiani, 2011). This decline is thought to result from reduced crossbridge binding probability at faster shortening speeds and opposing crossbridge forces resulting from insufficiently rapid crossbridge detachment (Huxley, 1957; Alcazar et al., 2019).

ECC and the crossbridge and sliding-filament theories have dominated our understanding and comparative study of skeletal muscle since the 1950s. However, these theories do not adequately describe muscle performance. Deviations from the typical force–length and force–velocity relationships with changing muscle activation level (Rack and Westbury, 1969; Brown et al., 1999; Holt et al., 2014; Holt and Azizi, 2014, 2016), high muscle forces during lengthening (Abbott and Aubert, 1952; Nishikawa, 2016), and the dependence of muscle activation and force on contractile history (Abbott and Aubert, 1952; Sandercock and Heckman, 1997; Askew and Marsh, 1998; Josephson and Stokes, 1999a; Fukutani and Herzog, 2019) are routinely observed. Mechanisms such as changes to actin–myosin lattice spacing (Williams et al., 2013; Tune et al., 2020; Rockenfeller et al., 2022), cooperative crossbridge binding (in which the binding of one crossbridge increases the likelihood of additional binding; Daniel et al., 1998; Tanner et al., 2007) and changes to titin upon muscle activation (Kellermayer and Granzier, 1996; Herzog et al., 2012; Nishikawa et al., 2012) have been proposed to explain these deviations.

Journal of Experimental Biology has a long and rich history of the study of muscle physiology that is comparative (i.e. studying functionally diverse muscles across a range of taxa) and realistic (i.e. studying muscles under conditions somewhat relevant to *in vivo* muscle function). Here, we explore the role that this type of study has had in the development of classic theories, and highlight the diversity possible within, and deviations from, such theories. We suggest potential new directions for the study of comparative muscle physiology, including the routine characterization of a wider range of muscle properties and the use of phylogenetic comparative methods.

Comparative skeletal muscle physiology

Comparative study is the heart of understanding the broad diversity of skeletal muscle physiology and mechanics across organisms and how they affect their movement. Such work may compare muscles within a single organism to understand variation across muscles performing different functions (e.g. Altringham et al., 1993; Kier and Curtin, 2002; Ahn et al., 2006; Azizi, 2014; Fuxjager et al., 2016; Tune et al., 2020). However, it is more commonly understood to mean the comparison across organisms that vary in factors such as ecology, behavior and size, often focusing on extremes (e.g. Josephson and Young, 1987; Josephson et al., 2001; Taylor, 2000; Tu and Daniel, 2004; More et al., 2010; Miles et al., 2018; Nelson et al., 2018; Sleboda et al., 2020; reviewed in Green et al., 2018; Clark et al., 2023). Such variation greatly affects the demands on muscles, and so potentially the underlying physiology, with the resulting physiological variation presumably reflecting adaptation (Gould and Lewontin, 1979). However, trade-offs often limit simultaneous optimization of different tasks (Garland et al., 2022). Therefore, organisms with different functional demands often show different underlying physiology, whether to maximize force production, power or contraction frequency, for example. Here, we review the comparative study of skeletal muscle physiology, focusing on the observed variation in muscle mechanical performance and physiology in the context of the ECC, crossbridge and sliding-filament theories of contraction. We highlight the relationship between muscle physiology and performance, and, where possible, examine effects of ecology, behavior and size.

Comparative study of excitation–contraction coupling

Comparative physiology has demonstrated extensive variation in ECC. Such study has largely focused on twitch times and fusion frequencies, as they define the upper limit of repetitive movements. Some of the earliest comparative work showed that although locust flight muscles only develop brief twitches *in vivo*, they can contract tetanically, similar to frog limb muscles, if stimulated at a higher frequency (Weis-Fogh, 1956). Variation in ECC kinetics has been shown across muscle types, spatially across the body, and with body size. Tetanic fusion occurs at 20 and 50 Hz in slow and fast muscles in the sculpin (fish; Altringham and Johnston, 1988), activation and relaxation kinetics slow nearly 2-fold rostro-caudally along the body of many species of fish (Altringham et al., 1993; Rome et al., 1993; Davies et al., 1995; Swank et al., 1997; James et al., 1998; D'Aout et al., 2001), and increased twitch times with increased body size have been observed in fish (James et al., 1998) and iguanas (Johnson et al., 1993). Such variation in muscle performance has organismal-level functional consequences, such as permitting the higher stride and tailbeat frequencies used at smaller body sizes (Kram and Taylor, 1990).

Much of our study of ECC has focused on the exceedingly high contraction frequencies required for sound production (Josephson, 1973; Josephson and Young, 1985; Rome et al., 1996; Schaeffer et al., 1996.; Elemans et al., 2008, 2011; Nelson et al., 2018; Schuppe et al., 2018). Such study has yielded insights into the functional importance of contraction rate, and the physiological mechanisms responsible. Passerine bird species that use high-frequency wing claps in courtship displays have wing-muscle kinetics that are twice as fast as species without such displays (Fuxjager et al., 2016), and variation in kinetics is suggested to have contributed to speciation in manakins (birds; Miles et al., 2018). Rattlesnake tail-shaker muscles operate at frequencies as high as 90 Hz owing to an increase in SR volume (Schaeffer et al., 1996; Conley and Lindstedt, 2002), and SR volume negatively correlates with twitch times across cicada (hemipteran insect) species (Josephson and Young, 1987). The Atlantic toadfish can call intermittently at 200 Hz owing to large amounts of the Ca^{2+} binding protein parvalbumin (Heizmann et al., 1982; Tikunov and Rome, 2009), a troponin isoform with a low Ca^{2+} affinity (Rome et al., 1996; Rome, 2006), and fast crossbridge kinetics (Rome et al., 1996, 1999). In contrast, the Pacific midshipman fish uses low amplitude Ca^{2+} transients to call continuously at frequencies of 100 Hz (Harwood et al., 2011; Nelson et al., 2018).

This array of studies demonstrates the diversity in both contraction rates and the physiological mechanisms responsible for those rates across muscles. However, none of the above mechanisms require substantial deviation from classic ECC theory. The range of physiological changes seen suggests that there is not a rate-limiting step (Mead et al., 2017), and the mechanism used may depend on the behavior required and trade-offs incurred (Josephson, 1973; Schaeffer et al., 1996; Nelson et al., 2018). For example, the use of parvalbumin in the intermittent calling of Atlantic toadfish may not work in the continuously calling Pacific midshipman fish, as parvalbumin would saturate (Nelson et al., 2018). Moreover, given constant muscle-fiber volume, increases in SR volume seen in the rattlesnake tail-shaker muscle come at the cost of reduced contractile-protein volume and force production (Lindstedt et al., 1998), potentially explaining why increased SR volume is a common strategy in sound production, where force and power requirements might be lower than in locomotion. Hence, although exceedingly high-frequency contraction can be achieved within classic ECC theory, trade-offs may limit the use of these high frequencies to movements requiring little force or power.

Although significant variation in contraction kinetics occurs within classic ECC theory, comparative physiology has demonstrated significant deviations from this theory in muscles that produce sustained force or contract asynchronously. Sustained force has been observed in the forearm muscles of ranid frogs (Peters and Aulner, 2000; Navas and James, 2007) and the jaw muscles of southern alligator lizards (Nguyen et al., 2020), both used in prolonged mate-holding behaviors (Wells, 1977; Nguyen et al., 2020). These muscles fail to relax fully before the subsequent contraction during prolonged bouts of activity, developing high sustained forces. The mechanisms responsible, and the extent to which they deviate from classic ECC theories, are unclear. Activation and relaxation kinetics can vary widely across muscles, and fatigue prolongs relaxation (Edwards et al., 1975; Allen et al., 1989). Hence, sustained force could be explained by the slow contraction kinetics of these muscles (Peters and Aulner, 2000; Navas and James, 2007; Nguyen et al., 2020) and an early onset of fatigue. However, sustained force can develop in the absence of the declines in peak force typical of fatigue (Navas and James, 2007). Hence, we might expect that these muscles would exhibit changes in Ca^{2+} handling or crossbridge kinetics that go beyond previously observed variation, potentially deviating from classic ECC theories.

Asynchronous muscle is arguably the clearest and best studied example of a deviation from the classic ECC theory. It is thought to have evolved multiple times in insect flight and sound-producing muscle (Pringle, 1949; Cullen, 1974; Josephson and Young, 1981; Dudley, 2000; Iwamoto, 2011). In contrast to the classic ECC framework, in which there is a synchronous relationship between motorneuron action potentials and muscle contractions, the contraction of asynchronous muscle is decoupled from action potentials. Low-frequency neural input to asynchronous muscle maintains Ca^{2+} at a level that permits crossbridge cycling (Jewell and Ruegg, 1966), and force cyclically rises and falls as a result of delayed stretch activation and shortening deactivation (Machin and Pringle, 1960; Pringle, 1978; Dickinson and Tu, 1997). For example, in insect flight, the thoracic muscle is stretched during wing upstroke. This increases muscle activation after a short delay, which increases muscle force, drives muscle shortening, and generates work and power during the downstroke. A variety of potential mechanisms for delayed stretch activation have been proposed, including a stretch-activated troponin isoform (Agianian et al., 2004), connections between myosin heads and troponin that move tropomyosin upon stretch (Perz-Edwards et al., 2011), a stretch-dependent transition from weakly to strongly bound crossbridges (Iwamoto and Yagi, 2013), and cooperative crossbridge binding (Iwamoto and Yagi, 2013). A variety of coordinated changes may be required for delayed stretch activation (Cao and Jin, 2020), and the precise mechanism may vary across species if asynchronous muscle indeed has multiple independent origins.

Delayed stretch activation and shortening deactivation in asynchronous muscle seem to represent a fundamental departure from the classic ECC framework; force develops in response to mechanical, rather than chemical (Ca^{2+}), stimuli (Hooper et al., 2008; Cao and Jin, 2020). This departure is thought to permit high contraction frequencies while avoiding the reduced-force trade-off associated with increasing SR volume. The removal of the need to cycle Ca^{2+} in each contraction allows for the maintenance of contractile protein volume, and therefore force and power (Josephson et al., 2000a; Josephson and Young, 1981; Syme and Josephson, 2002). Hence, asynchronous muscle contraction is thought to represent an adaptation that allows for flight in the smallest insects, whose body size requires high wingbeat frequencies (Josephson et al., 2000b). More detailed comparative studies across insect species and beyond may elucidate whether this mechanical activation represents an adaptation seen only in asynchronous muscle, or illustrate whether this phenomenon contributes to muscle performance to varying degrees across a wider range of muscles.

Comparative study of the sliding-filament and crossbridge theories of muscle contraction

The sliding-filament and crossbridge theories of muscle contraction predict that the isometric force a muscle can produce depends on the degree of overlap between actin and myosin, and that the force it can produce during shortening depends on shortening speed.

Actin–myosin overlap and the force–length relationship

The first support for the sliding-filament and crossbridge theories of muscle contraction was provided by images of sarcomeres in frog muscle that showed length of the myosin-containing region remaining constant during shortening while the actin-only region shrank, suggesting the sliding of actin filaments past myosin (Huxley and Niedergerke, 1954). A subsequent study in locust flight muscle suggested that this was a generalizable mechanism of contraction (Weis-Fogh, 1956). The sliding-filament and crossbridge theories have been further supported by the apparent ubiquity of isometric force–isometric length relationships and the relationship between peak muscle force and contractile protein filament length. These theories predict that the instantaneous length of a given sarcomere, and the variation in contraction protein filament length across muscles, determines the amount of overlap and therefore the number of potential crossbridges that could be formed and force that could be generated (Gordon et al., 1966; Josephson, 1975; Taylor, 2000). Isometric force–length relationships have been described in limb, abdominal, thoracic and jaw muscles across vertebrates and invertebrates (Fig. 1; Weis-Fogh, 1956; Gordon et al., 1966; Zachar and Zacharová, 1966; Herzog et al., 1992b; Tu and Daniel, 2004; Guschlbauer et al., 2007; Gidmark et al., 2013; Bohm et al., 2019, Moo et al., 2020). And although actin and myosin filament length are relatively consistent in vertebrates (Walker and Schrodt, 1974; Herzog et al., 1992a), more than 10-fold variation has been observed across invertebrates (Hoyle, 1969; Taylor, 2000; Hooper et al., 2008; Shimomura et al., 2016). This variation in contractile protein length appears to correlate with stress (Taylor, 2000) and have functional importance. Crayfish muscles with 10.5 µm sarcomeres (Zachar and Zacharová, 1966) produce a maximum isometric stress of 65 $N\,cm^{-2}$, whereas frog muscles with 2.6 µm sarcomeres produce only 35 $N\,cm^{-2}$ (Hodgkin and Horowicz, 1960). Moreover, across 22 species of mantis shrimp, the resting sarcomere length of the muscle actuating the raptorial appendage is ∼25% longer in species requiring high forces for prey capture (Blanco and Patek, 2014).

Despite the support for the sliding-filament and crossbridge theories provided by the dependence of force on actin–myosin overlap, considerable variation seems to exist in the width of the normalized force–length curves (Fig. 1). Some caution should be taken with these comparisons owing to the variety of methods used across labs and muscles. Nevertheless, in the squid mantle, the shape of the force–length relationship varies across muscle fibers from different regions under identical conditions (Thompson et al., 2014). The shape of the force–length curve has functional implications. Broader curves allow for higher forces over larger ranges of motion and in some cases are presumed to reflect adaptation. For example, supercontracting muscles in which myosin filaments are thought to pass through the Z-disk and interact with actin in adjacent sarcomeres have been described in both invertebrates and vertebrates, and are thought to allow for the large strains required in ballistic tongue projection in chameleon feeding (Hoyle et al., 1965; Hardie, 1976; Wainwright et al., 1991; Herrel et al., 2001; Anderson and Deban, 2010). In addition, obliquely striated muscles, in which sarcomeres are at an oblique angle to the long axis of the muscle fiber and can rotate during shortening, have been suggested to allow for broader and more variable force–length relationships and may permit distention of the body wall in feeding leeches (Rosenbluth, 1965; Kier, 1985; Gerry and Ellerby, 2011; Taylor-Burt et al., 2018). Supercontracting and obliquely skeletal muscles expand our notions of the variation possible largely within crossbridge and sliding-filament theories. However, significant variation in force–length curve width is observed across muscles with more typical sarcomeres (Fig. 1). A variety of mechanisms have been proposed to explain this variation in width, including variation in troponin isoform and actin–myosin lattice structure, and phosphorylation of troponin (Gordon et al., 2000; Josephson and Stokes, 1987; Thompson et al., 2014; Tu and Daniel, 2004; Williams et al., 2013; Rockenfeller et al., 2022). Furthermore, the very narrow curves of stiff flight muscles (Josephson, 1997; Josephson et al., 2000b; Tu and Daniel, 2004) suggest that the passive properties of muscle may be related to the shape of the force–length curve (Hardie, 1976). Detailed comparative study of force–length relationships, especially across muscles with varying *in vivo* strains, lattice structures and passive properties, may further our understanding of the mechanisms of muscle contraction and the scope for variation and adaptation in the shape of the force–length relationship.

The force–velocity relationship

The shortening side of the isotonic force–velocity relationship is arguably the most characterized feature in comparative muscle physiology (Fig. 2; Hill, 1938, 1950; Medler, 2002; Alcazar et al., 2019). Shortening force–velocity relationships are typically characterized by maximum unloaded shortening velocity (V_{max})

and their curvature. More than 40-fold variation in $V_{\max}$ has been reported across muscles and species (Fig. 2; Altringham and Johnston, 1982; Josephson and Stokes, 1987; Chan and Dickinson, 1996; Holmes et al., 1999; Kier and Curtin, 2002; Astley, 2016; Anderson and Roberts, 2020; Rummel et al., 2022). Moreover, the shape of the relationship varies from highly curved to almost linear (Fig. 2; Woledge, 1968; Josephson, 1984; Schiaffino and Reggiani, 2011; Alcazar et al., 2019). This variation in $V_{\max}$ and curvature of the force–velocity relationship has important functional consequences. The two-fold variation in ankle extensor $V_{\max}$ across 14 frog species positively correlates with jump performance (Astley, 2016), and a flatter force–velocity relationship, which results in higher powers, is associated with increased calling frequency in two species of tree frogs (Marsh, 1999a).

Variation in $V_{\max}$ and curvature is largely attributed to variation in myosin isoforms and contractile-protein length. Slower myosin isoforms decrease $V_{\max}$ and increase curvature (Bottinelli et al., 1991; Medler, 2002; Schiaffino and Reggiani, 2011), and muscle fibers with shorter sarcomeres have a higher $V_{\max}$ owing to the increased number of serial sarcomeres (Josephson, 1975; Kier and Schachat, 1992; Kier and Curtin, 2002), Thus, such variation can be explained within classic crossbridge and sliding-filament theories. However, interaction between the contractile proteins and structural elements of muscle also modulate the force–velocity relationship. The requirement of muscle to move both its own mass and external loads has been suggested to reduce $V_{\max}$, decrease curvature, and restrict the region of the force–velocity relationship over which a muscle can operate (Günther et al., 2012; Richards and Clemente, 2013; Holt et al., 2014; Ross et al., 2020; Ross and Wakeling, 2016; Richards and Eberhard, 2020). Hence, in larger muscles and animals, we might expect that observed shortening velocity would be lower than predicted from myosin kinetics. In muscles with a substantial tendon, stretch and recoil of this elastic element can decouple muscle shortening speed from myosin kinetics, leading to very rapid yet forceful shortening (Peplowski and Marsh, 1997; Azizi and Roberts, 2010; Ilton et al., 2018; Longo et al., 2019). Variation in the elastic properties of these tendons is a major determinant of jump performance across three frog species (Roberts et al., 2011; Mendoza and Azizi, 2021).

In contrast to the extensive comparative study of the shortening force–velocity relationship, the lengthening side of the relationship has received little attention, and almost nothing is known about how this property varies across species (Abbott and Aubert, 1952; Flitney and Hirst, 1978; Josephson and Stokes, 1999a; Pinniger et al., 2006). The high forces generated during active muscle lengthening are unexplained, but have been suggested to be due to an increased number of crossbridges, increased force per crossbridge, and the engagement of a passive element such as titin (Edman et al., 1982; Harry et al., 1990; Nishikawa, 2016; Herzog, 2018). Comparative study of the lengthening force–velocity relationship, especially across muscles that experience differing degrees of lengthening *in vivo* and have differing titin properties, may provide insight into both the mechanism responsible for high forces during lengthening and the scope for variation and adaptation in this property.

Lessons from comparative skeletal muscle physiology

Comparative muscle physiology has demonstrated extensive, functionally important variation in skeletal muscle performance within classic theories of contraction. However, it has also demonstrated deviations from these theories, such as the asynchronous contraction in insect flight muscle, variation in force–length curve width and high force during active lengthening. Some of this variation is probably functionally important and represents adaptation; asynchronous muscle likely maintains muscle power at the high wingbeat frequencies required for flight in small insects (Josephson et al., 2000b), and supercontracting muscle likely allows for extreme tongue elongation in chameleon feeding (Herrel et al., 2001). However, what is not clear is the extent to which these deviations from classic theories represent adaptation in specific muscles with high functional demands, or whether they also reflect a fundamental limitation of the capacity of classic theories of contraction to explain performance in all muscles. These limitations to the classic theories of contraction become increasingly apparent when we consider muscle mechanical performance under some of the complex conditions relevant to its *in vivo* function.

Realistic study of skeletal muscle

Much of the early study of muscle physiology, and many of the previously referenced comparative studies, focused on maximally activated isometric or isotonic contractions (Fig. 3A). Although providing valuable insight into some mechanisms of muscle contraction, and potentially remaining a convenient way to explore muscle diversity, these approaches fail to replicate the transient activation patterns and constantly changing forces that muscles experience, and their resultant length changes, during movement. The force, work and power a muscle can generate under such conditions deviates significantly from predictions based on maximally stimulated isometric and isotonic contractions (Malamud and Josephson, 1991; Stevens, 1993; Marsh and Olson, 1994; Franklin and Johnston, 1997; Askew and Marsh, 1998; Josephson, 1999; Lichtwark and Wilson, 2005; Holt et al., 2014). Hence, the early focus on muscle performance under quasi-static, isometric and isotonic conditions meant both that we lacked accurate predictions of muscle performance during movement, and that our understanding of muscle contraction was limited to the physiological mechanisms that dominate under such conditions. However, technological, physiological and conceptual advances have gradually increased our ability to study muscle physiology under conditions more relevant to some movements.

The workloop technique, in which muscles are driven through cyclical length changes and periodically stimulated, has been used to replicate aspects of *in vivo* muscle function and allow for the determination of force, work and power production under such conditions (Fig. 3B–E; Machin and Pringle, 1960; Josephson, 1985; Ahn, 2012). The workloop technique initially used simple sinusoidal length change trajectories, which roughly approximated muscle length change during cyclical movements (Fig. 3B). Development of techniques to study *in vivo* muscle length changes (Griffiths, 1987, 1991; Marsh et al., 1992) allowed for the more accurate replication of *in vivo* contraction cycles *in vitro* (Fig. 3C,D; Marsh et al., 1992; Marsh and Olson, 1994; Wakeling and Johnston, 1998). Perturbed workloops, which examined the effects of rapid length perturbations (Fig. 3E; Libby et al., 2020; Tytell et al., 2018), have allowed us to better replicate *in vivo* muscle function in complex environments (Daley et al., 2006, 2009; Sponberg and Full, 2008; Daley and Biewener, 2011). And more recently, force-controlled approaches, in which muscles are activated and an external load is prescribed, have allowed us to avoid the artificial specification of muscle length change used in workloop experiments (Fig. 3F; Marsh, 1999b; Richards and Clemente, 2013; Richards and Eberhard, 2020; Robertson and Sawicki, 2015) and potentially expand our study to non-cyclical movements such as jumping.

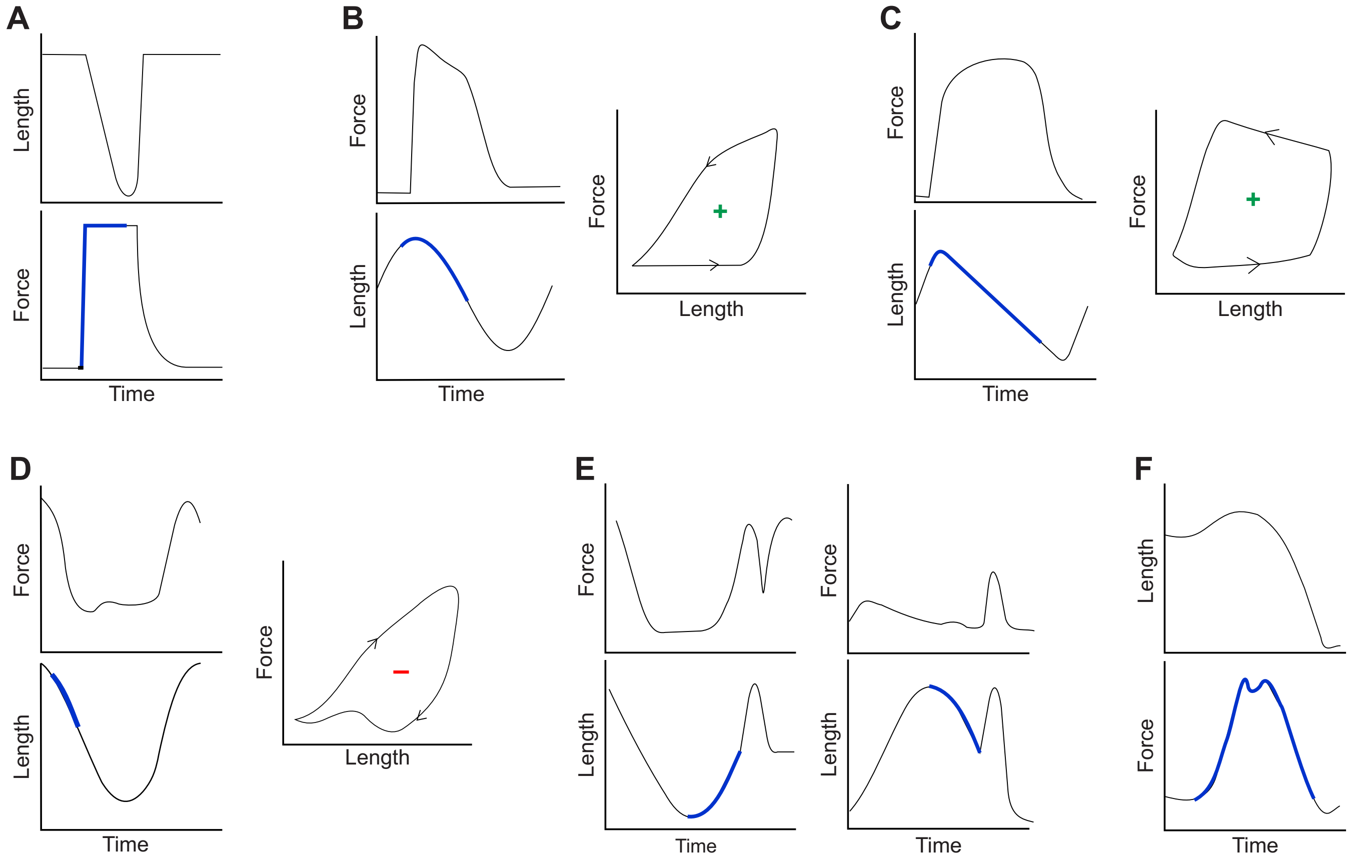

Fig. 3. Schematic showing the development of the study of muscle performance under increasingly realistic conditions. (A) In simple isotonic contractions, a muscle is activated (bold), a resistive force is prescribed (bottom), and the resultant length change and shortening velocity (top) are measured (data from Holt and Azizi, 2016). (B) The workloop technique initially applied a sinusoidal length change to the muscle (bottom left), transiently stimulated it (bold) and measured the force produced (top left; adapted from Askew and Marsh, 1997). Measured force is plotted against length in a workloop, and the work done is calculated as the area contained within the loop (Josephson, 1985). The arrows indicate the direction of muscle length change, and a counterclockwise loop indicates positive work (right). Subsequent workloop studies used the same approach to replicate (C) asymmetric length changes (adapted from Askew and Marsh, 1997) and (D) active lengthening (adapted from Ahn et al., 2006). (E) Perturbed workloops impose rapid stretches (bottom) (adapted from Libby et al., 2019), and demonstrate that higher forces (top) are produced by perturbations during lengthening (left) than during shortening (right). (F) Force-controlled experiments activate muscle (bold) and allow it to contract against simulated forces (bottom) and measure the resultant length change (top) (adapted from Richards and Eberhard, 2020).

Workloop studies using simple sinusoidal length changes have shown that the work and power a muscle produces varies greatly with length change and stimulation conditions (James et al., 1995; Bahlman et al., 2020; Curtin and Woledge, 1996; Franklin and Johnston, 1997; Harwood et al., 1998; Josephson and Stokes, 1989). Adjusting cycle frequency in mouse limb muscles (James et al., 1995), increasing muscle strain in zebra finch flight muscles (Bahlman et al., 2020) and advancing muscle stimulation so that it precedes the start of shortening in fish myotomal muscles (Franklin and Johnston, 1997) all increase power. Workloop studies that more closely replicate *in vivo* muscle function have shown that the asymmetric length changes (Fig. 3C) seen in systems requiring high power, such as treefrog calling and bird flight (Girgenrath and Marsh, 1997; Askew and Marsh, 2001; Biewener et al., 1998; Ellerby and Askew, 2007), increase power output (Askew and Marsh, 1997; Holt and Askew, 2012). Moreover, two cockroach limb extensors can have dramatically different functions (Fig. 3D) despite apparently similar muscle properties and *in vivo* length change and activation patterns (Ahn et al., 2006). Workloop studies replicating perturbed locomotion (Fig. 3E; Daley et al., 2009; Daley and Biewener, 2011) have demonstrated that the force production and energy absorption resulting from the sudden changes in muscle length that occur during perturbation contribute to stabilization (Brown and Loeb, 2000; Sponberg and Full, 2008; Biewener and Daley, 2007; Daley et al., 2009; Libby et al., 2019), but that such responses are strongly dependent on a muscle's condition prior to perturbation (Libby et al., 2019; Tytell et al., 2018). For example, four times more energy was dissipated by a cockroach limb extensor muscle during a sudden stretch when the muscle was being stretched prior to the perturbation compared with when it was shortening (Fig. 3E; Libby et al., 2019). Force-controlled studies that simulate the muscle's *in vivo* loading environment have demonstrated that the inertial load the muscle operates against limits the performance space a muscle can access during movement. For example, the drag force generated during swimming likely confines frog ankle extensor performance to a small region of its force–velocity curve (Richards and Clemente, 2013). This effect of load to be moved has major implications for human musculoskeletal modelling, in which the properties of muscle determined in small muscles *in vitro* are scaled up, largely without consideration of loading (Günther et al., 2012; Ross and Wakeling, 2016).

Some of the observed effects of workloops and force control on muscle performance are predicted by classic theories of contraction. Generation of significant work and power requires muscles to generate high forces and change length rapidly and extensively during the shortening phase of the contraction cycle. Therefore, contraction frequency cannot exceed ECC kinetics, strain cannot exceed the range of lengths over which actin and myosin overlap substantially, and the combination of contraction frequency and length change must result in intermediate shortening velocities at which high power can be generated (Josephson, 1999). Some of the effects of perturbation have also been explained by classic theories. For example, if a muscle operates at short lengths, a sudden stretch will increase actin–myosin overlap according to the sliding-filament and crossbridge theories, thus increasing force, resisting stretch and stabilizing the body (Tu and Daniel, 2004).

Despite the potential for classic theories of contraction to explain some aspects of muscle performance demonstrated using workloop and force-controlled techniques, muscle performance also deviates from the predictions of maximally stimulated isometric force–length and isotonic force–velocity relationships (Stevens, 1993; Marsh and Olson, 1994; Franklin and Johnston, 1997; Askew and Marsh, 1998; Josephson, 1999; Lichtwark and Wilson, 2005). Much of this deviation can be attributed to history dependence, the descriptions of which fall into two, not necessarily mutually exclusive, categories. The first focuses on increased rates of muscle activation with stretch and increased rates of deactivation with shortening (Askew and Marsh, 1998; Josephson and Stokes, 1999b; Sandercock and Heckman, 1997), whereas the second focuses on enhancement of force after stretch and the depression of force after shortening (Abbott and Aubert, 1952; Edman et al., 1982; Askew and Marsh, 1998; Edman and Tsuchiya, 1996; Fukutani and Herzog, 2019). Activation-based effects are thought to result from mechanical effects on ECC processes, such as the accelerated removal of Ca^{2+} from troponin during shortening (Askew and Marsh, 1998; Caputo et al., 1994) and an increased sensitivity of troponin to Ca^{2+} at longer lengths (Josephson, 1999). Force-based effects have been suggested to result from changes to crossbridge binding kinetics (Holt and Williams, 2018; Joumaa et al., 2012) and increased titin stiffness with activation and crossbridge cycling (Edman et al., 1982; Herzog et al., 2006; Powers et al., 2017; Dutta et al., 2018; Nishikawa, 2020). Such effects appear to be amplified, and potentially dominate muscle performance, under perturbed conditions (Libby et al., 2019). However, history dependence cannot explain the differing mechanical function of two cockroach extensor muscles despite similar force–length and force–velocity properties and *in vivo* activation and length change patterns (Ahn et al., 2006). These differences have been related to, but not explained by, small dynamic differences in the actin–myosin lattice spacing of these muscles (Tune et al., 2020). This suggests that there is much we still do not understand about the determinants of performance, and its variation across muscles, under conditions that replicate *in vivo* function.

Force-controlled experiments that demonstrate the potential limitation to the force–velocity performance space that can be accessed by muscles during movement highlight that *in vivo* muscle performance is not solely a consequence of actin–myosin interactions, as suggested by classic theories of muscle contraction, but rather an emergent property arising from these protein kinetics, structural elements of muscle and external loads imposed by factors such as gravity and viscosity (Holt et al., 2014; Günther et al., 2012; Richards and Clemente, 2013; Ross and Wakeling, 2016; Richards and Eberhard, 2020; Ross et al., 2020). Force-controlled approaches also offer the potential to understand mechanisms of muscle contraction that dominate performance across morphologies, environments and scales (Richards and Eberhard, 2020). For example, limb morphologies with lower mechanical advantages and larger body sizes will restrict muscle performance to a smaller fraction of its potential space, thus potentially making the maximum shortening velocity dictated by myosin kinetics less relevant to *in vivo* function.

Hence, classic theories of muscle contraction can provide some explanation for muscle performance under somewhat realistic contractile conditions. Yet it appears that poorly understood features of skeletal muscle physiology, such as the effect of actin–myosin lattice spacing, the role of titin in active muscle, mechanical activation and effects of the load, have important roles in determining *in vivo* muscle performance. The study of muscle performance under more realistic conditions suggests that these features contribute to mechanical performance in all muscles, thus highlighting the fundamental limitations of classic theories of contraction. Improved comparative methods, and better integration of these methods with realistic studies, may provide greater insight into the physiological mechanisms of muscle contraction and the scope for variation and adaptation in performance.

Future directions for comparative, realistic muscle physiology

Studies of comparative muscle physiology were hugely influential in developing classic theories of muscle contraction, and the comparative study of ECC, force–length and force–velocity relationships has demonstrated the diversity possible within classic frameworks. However, comparative and realistic study have clearly demonstrated the ubiquity and physiological relevance of features of muscle contraction not explained by classic theories. The adaptive value of such features has been implied by their necessity for achieving behavioral performance impossible under classic frameworks. For example, workloop studies across a diversity of organisms suggest that some form of mechanical activation is common across muscles, that it can enhance muscle power during the cyclical contractions commonly seen in locomotion, and that it is highly exaggerated in asynchronous insect flight muscle. Here, we suggest two complementary future directions for comparative muscle physiology that may build on such findings. Firstly, we suggest expanding our current approach to the comparative characterization of muscle to include features of muscle contraction that are commonly seen but are not well explained by classic theories. Secondly, we advocate for more intentional design of comparative studies to elucidate physiological mechanisms and adaptation.

Expanding our comparative characterization of muscle contraction

Our typical model for comparative muscle physiology has been to characterize muscles responsible for extreme performance according to classic theories of muscle contraction by, for example, determining their twitch times and force–length and force–velocity properties. However, features of muscle contraction not explained by such theories, such as stretch activation, force–length relationship width and the lengthening force–velocity relationship, are rarely characterized. Consequently, we lack understanding of how these features vary across muscles and taxa. For example, workloop studies of the myotomal muscles of Antarctic rock cod seem to suggest a greater degree of history dependence than in other muscles (Franklin and Johnston, 1997; Askew and Marsh, 1998); however, we lack the systematic study of history dependence to conclusively demonstrate this. We suggest that adding the characterization of features of muscle contraction not explained by classic theories, and the elements of muscle suggested to be responsible for these features, to our standard approach to comparative muscle physiology would provide insights into how our classic theories of contraction need to be amended. For example, if titin stiffness is responsible for the high forces during lengthening, then we would expect the low stiffness of titin in slow rabbit muscle (Prado et al., 2005) and northern watersnake jaw muscle (Close et al., 2014) to result in lower forces during active lengthening in these muscles compared with those with stiffer titin isoforms. Likewise, if the lattice structure of muscle contributes to the shape of the force–length curve, then we might expect that beetle flight muscles with myosin–actin ratios of 3:1 and lobster claw muscles with ratios of 12:1 (Hayes et al., 1971; Shimomura et al., 2016) would have different-shaped force–length relationships.

Extending (phylogenetic) comparative muscle physiology

The review of comparative, realistic muscle physiology presented here represents a huge body of work and also gives the impression of relatively few, somewhat randomly chosen taxa that have been extensively studied. This sampling likely results from several factors. Firstly, organisms found locally are easier to study than those found far from centers of scientific research (e.g. the general understudy of remote, tropical taxa; Zuk, 2016). Secondly, the long history of the ‘Krogh principle’ in comparative physiology has promoted the idea that certain taxa are best suited for studying particular phenomena (Sanford et al., 2002; Clark et al., 2023). And lastly, the study of muscle performance is technically complex and requires live, rather than museum, specimens (Muñoz and Price, 2019). These challenges are not new to comparative physiology and have been reviewed recently (e.g. Green et al., 2018; Huey et al., 2019; Clark et al., 2023). Thus, our goal here is to describe their implications for the study of muscle physiology, with ideas for future directions.

Limited, haphazard sampling challenges the study of both adaptation and the physiological mechanisms underlying variation in muscle performance. For example, the apparently high degree of history dependence in Antarctic rock cod muscle (Franklin and Johnston, 1997) may represent an adaptation to their cold environment and may share features of mechanical activation with asynchronous muscle. However, we currently lack the systematic studies required to make any such inferences. In the case of adaptation, phylogenetic comparative studies have become the primary means of study. Such studies require sampling many taxa that differ in factors – ecological, behavioral or environmental – thought to affect selection on the trait of interest. For example, a study of 68 anuran (frog and toad) species from around the world has shown that jumping power varies with body size and microhabitat (Mendoza et al., 2020). In contrast, for many of the phenomena we review above, often just a handful of distantly related taxa have been examined (Josephson et al., 2001; Tu and Daniel, 2004; Sleboda et al., 2020), with very little understanding of potential variation among more closely related species. For example, the only evidence for the higher efficiency of asynchronous compared with synchronous muscle comes from comparison of one beetle (Josephson et al., 2001) and one locust species (Josephson and Stevenson, 1991).

In the case of studying the physiological mechanisms responsible for exceptional performance, many features of muscle may differ between two extreme examples, with the functional implications of such differences remaining unclear. For example, titin homologs, troponin isoform, muscle stiffness and presence of myosin–tropomyosin bridges have all been reported to vary between synchronous and asynchronous muscle (Cao and Jin, 2020; Dickinson and Tu, 1997; Iwamoto, 2011; Josephson et al., 2000b). With so many differences between each pair of muscle types, the key factors necessary to produce their salient features are uncertain. If additional taxonomic sampling shows that some taxa have intermediate levels of complexity and performance, we can see which components matter more for producing variation in muscle performance. Moreover, we can map such differences on a phylogeny as ancestral-state estimates (Schluter et al., 1997) to understand the evolutionary trajectory of changes, possibly allowing us to infer adaptation to changing behavioral or environmental conditions (Martins, 2000).

A key concern about such broad sampling is how to study enough taxa to be able to conduct robust phylogenetic analyses (Garland et al., 2005; Moen et al., 2022). In comparative physiology, simply collecting sufficient data for a phylogenetic comparative study can be formidable. Of the few existing skeletal muscle studies that include phylogenetic analysis, many use morphological or histological techniques, rather than measurement of active muscle properties (Blanco and Patek, 2014; Bonine et al., 2001, 2005; Cieri et al., 2020, 2022; Scales et al., 2009). Thus, expansion to multiple species in order to conduct phylogenetic comparative analyses may seem an unreasonable goal in studies of realistic muscle contraction. However, some methods of testing adaptation with phylogenies can show clear results with as few as 10 species (Cressler et al., 2015; Ho and Ané, 2013; Moen et al., 2022). In such cases, it is ultimately the effect size – the phenotypic differences between taxa – that matter more than the number of species, per se. Moreover, we see room for collaboration and cooperation across labs, where each may be conducting intensive studies of a single species and can combine their results in broader comparative efforts for understanding mechanism and adaptation. A key to such efforts will be standardization in methodology so that data are comparable across labs. Some recent studies of active muscle properties across closely related taxa (Vanhooydonck et al., 2014; Astley, 2016; Miles et al., 2018) suggest promise in the future of phylogenetic comparative studies of muscle physiology.

Acknowledgements
We thank David Labonte and three anonymous reviewers for helpful comments.

Competing interests
The authors declare no competing or financial interests.

Funding
D.S.M. is supported by National Science Foundation grant IOS-1942893 and N.C.H. is supported by Human Frontiers in Science Program grant RGY0073/2020.

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