Beyond power limits: the kinetic energy capacity of skeletal muscle

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Muscle is the universal agent of animal movement, and limits to muscle performance are therefore an integral aspect of animal behaviour, ecology, and evolution. A mechanical perspective on movement makes it amenable to analysis from first principles, and so brings the seeming certainty of simple physical "laws" to the challenging comparative study of complex biological systems. Early work in biomechanics considered muscle energy output to be limited by muscle work capacity, W_{max}; triggered by seminal work in the late 1960s, it is now held broadly that a complete analysis of muscle energy output during impulsive contractions is to also consider muscle power capacity, for no unit of work can be delivered in arbitrarily brief time. This work adopts a critical stance towards this paradigmatic notion of a "power-limit", and argues that the *de facto* alternative constraint to muscle energy output is imposed by a characteristic "kinetic energy capacity", E_{max}, dictated by the maximum speed with which the actuating muscle can shorten. The two critical energies can now be directly compared, and define the "physiological similarity index", $\Gamma = E_{max}/W_{max}$. It is the explanatory power of this comparison that lends weight to a shift in perspective from muscle power to kinetic energy capacity, as is argued through a series of brief illustrative examples. Γ emerges as a key dimensionless number in musculoskeletal dynamics, and sparks novel hypotheses on functional adaptations in musculoskeletal "design" that depart from the eternal evolutionary null hypothesis of geometric similarity.

Movement is essential for all animals, and muscle is what drives animal movement (Alexander, 2003; Biewener and Patek, 2018; Dickinson et al., 2000; McMahon, 1984). What muscle can and cannot do is thus a fundamental question in zoology (Biewener, 2016; Daniel and Tu, 1999; Higham et al., 2016; Mendoza et al., 2023). Two rudimentary mechanical properties are thought to characterise each unit of muscle mass as a motor: its maximum work density, and its maximum power density (Bennet-Clark, 1977; Borelli, 1680; Gabriel, 1984; Hill, 1950b). No muscle contraction can violate these limits, and they are consequently thought to pose universal constraints on animal performance. A limiting work or power density have, in some form or another, been invoked to account for a remarkable diversity of non-trivial observations across the broad field of comparative animal biomechanics, including the maximum running speed (e. g. Hill, 1950b; Irschick et al., 2003; Meyer-Vernet and Rospars, 2015; Usherwood and Gladman, 2020), flight speed (Alexander, 2005; Pennycuick, 1968), swimming speed (e. g. Clemente and Federle, 2012; O'dor and Webber, 1991; Richards and Clemente, 2013; Richards and Sawicki, 2012; Wakeling and Johnston, 1998), and jump height (e. g. Bennet-Clark, 1977; Gabriel, 1984; Lutz and Rome, 1994; Marsh, 1994; Roberts et al., 2011; Sutton et al., 2016; Wilson and James, 2000); size-specific variations in animal posture (Usherwood, 2013); the prevalence of latched "power-amplifiers" in small animals (Alexander, 1988; Bennet-Clark, 1975; Gronenberg, 1996; Ilton et al., 2018; Longo et al., 2019; Patek, 2023); the mechanical benefits of in-series elasticity in explosive muscle contractions (e. g. Aerts, 1997; Alexander, 1995; Galantis and Woledge, 2003; Hill, 1950a; James et al., 2007; Lichtwark and Wilson, 2005; Mendoza and Azizi, 2021; Peplowski and Marsh, 1997; Roberts, 2016; Roberts and Azizi, 2011; Roberts and Marsh, 2003; Rosario et al., 2016; Sawicki et al., 2015, reviewed recently in (Holt and Mayfield, 2023)); the outcome of predator-prey interactions (Wilson et al., 2018); feeding performance (Camp et al., 2015); the limits to manoeuvrability (Williams et al., 2009; Wilson et al., 2013); or the transition from latch-mediated to direct muscle actuation in jumping animals (Sutton et al., 2019), to name but a few examples.

Both muscle power and work density appear to be remarkably conserved — they vary by at most one order of magnitude across animal size, ecological niche, and evolutionary history (Askew and Marsh, 2002; Close, 1972; Marden and Allen, 2002; Medler, 2002; Rospars and Meyer-Vernet, 2016). Animal size is however thought to determine whether it is the work or the power density that limits the energy output during impulsive muscle contractions (e. g. Alexander, 2003; Bennet-Clark, 1977; Biewener and Patek, 2018; Gabriel, 1984; Ilton et al., 2018; Longo et al., 2019; Patek, 2023; Schmidt-Nielsen, 1984; Usherwood, 2013; Usherwood and Gladman, 2020). Power is the amount of work done per time, and smaller animals are thought to have less time to complete muscle contractions (Alexander, 2003; Bennet-Clark, 1977; Biewener and Patek, 2018; Schmidt-Nielsen, 1984). Muscle energy output, the argument goes, is consequently constrained by muscle power capacity in animals below some critical size, but by muscle work capacity in animals above it (e. g. Alexander, 2003; Bennet-Clark, 1977; Biewener and Patek, 2018; Gabriel, 1984; Ilton et al., 2018; Longo et al., 2019; Schmidt-Nielsen, 1984; Usherwood, 2013; Usherwood and Gladman, 2020). This manuscript revisits this paradigm of a power-limit, and suggests an alternative mechanical framework to account for size-specific varia-

tions in muscle energy output during impulsive contractions.

Two laws to bind jump height

The limits to muscle energy output have long been a core problem in work on jumping animals, and the key arguments are thus perhaps best understood through this historical lens. Jump performance is thought to be bound by two "laws": Borelli's law, which encodes a work density constraint to muscle energy output (Borelli, 1680); and what arguably should be called Bennet-Clark's law, which prescribes a power density constraint (Bennet-Clark, 1977; Bennet-Clark and Lucey, 1967).

The argument for the work constraint typically runs as follows (Alexander, 2003; Biewener and Patek, 2018; McMahon, 1984; Schmidt-Nielsen, 1984): an animal that jumped to a height h has increased the gravitational potential energy of its centre-of-mass by an amount $E_{pot} = mgh$. This increase was paid for with mechanical work, done by muscle at the expense of chemical energy. The maximum mechanical work muscle can do depends on its volume, V, and on the maximum average stress, $\hat{\sigma}_{max}$, it exerts as it shortens by a maximum fraction of its length, ε_{max}, $W_{max} = V\hat{\sigma}_{max}\varepsilon_{max}$. An estimate for the maximum jump height then follows via conservation of energy, $E_{pot} = W_{max}$, where it is tacit that all external forces are much smaller than the muscle force — the jump is impulsive (see SI for a more detailed discussion of this subtle point). The physiological parameters $\hat{\sigma}_{max}$, ε_{max}, and the muscle volume per unit body mass, V/m, are typically considered size-invariant; animals small or large should consequently jump to the same height, and no higher than to $h_{max} \sim V\sigma_{\max}\varepsilon_{\max}(mg)^{-1}$. It is this prediction that is often referred to as *Borelli's law*.

The presentation of Bennet-Clark's law usually remains on more qualitative grounds. Schmidt-Nielsen explains (Schmidt-Nielsen, 1984): "The smaller the animal, the shorter its take-off distance. [...] The time available for take-off is very short, and muscle just cannot contract that fast". Alexander has it that "smaller jumping animals have smaller acceleration distances, and so have to extend their legs in even shorter times [...]. But no known muscle can complete an isolated contraction in so short a time." (Alexander, 2003). Biewener and Patek agree (Biewener, 2016): "Smaller animals have shorter limbs [...]; therefore, the [...] time available for acceleration during take-off is less". These representative accounts of Bennet-Clark's law have in common that they highlight the importance of time. Time is absent in the framework of Borelli's law, because it phrases the problem solely in terms of muscle work—the path-integral of Newton's second law. But no fixed amount of work can be done in an infinitely short amount of time, and time therefore ought to be considered explicitly when estimating bounds on muscle mechanical performance. It is this omission of time that prompted Bennet-Clark and others to challenge Borelli's law; and it is this challenge that eventually developed into the now almost ubiquitous notion of a "power-limit" to the energy output of muscle in impulsive contractions. This power-limit is thought to be tightened further by an intrinsic property of muscle which stems directly from the molecular mechanisms that underpin muscle contraction—muscle force typically varies inversely with muscle shortening velocity (Hill, 1938; Piazzesi et al., 2007). As a consequence of this force-velocity-relationship (FVP), the fraction of the work capacity that muscle can provide declines with the rate at which it is delivered, inducing complex trade-offs (Bobbert, 2013; Peplowski and Marsh, 1997; Roberts and Marsh, 2003).

Where a typical account of Borelli's law ends with the testable prediction that animals large and small should take-off with the same speed, a discussion of Bennet-Clark's law usually ends just here: from the essential textbooks quoted above, only Biewener and Patek provide a quantitative prediction for the allometry of take-off speed under a power-limit (Biewener, 2016). Why are quantitative predictions on muscle energy output less forthcoming when muscle power is thought to be the limiting constraint?

Materials and methods

In what follows, we analyse a minimalistic model of a muscle with constant force capacity F_{max}, displacement capacity δ_{max}, and absolute shortening speed capacity v_{max}. The objective of the analysis is to determine the maximum energy this muscle can inject as it contracts to accelerate a mass m from rest. One feature notably absent from this simple model is an elastic element in-series with muscle, with the crucial consequence that the muscle shortening speed and the speed of the mass are equal at any point in time. Keeping this seemingly simple observation in mind will be important in several stages of the energetic analysis. Initially, we approach the problem from the perspective of physical dimensions, and only consider the final result of the contraction—the total energy provided by the muscle. This dimensional analysis is then put to work to illustrate fundamental differences in how the muscle work capacity, $W_{max} \sim F_{max}\delta_{max}$, and the average power capacity, $P_{max} \sim F_{max}v_{max}$ relate to muscle energy output. Next, we consider the acceleration phase itself, and thus replace elemental dimensional considerations with exact Newtonian mechanics. During the acceleration phase, the mass gains kinetic energy, and both the muscle shortening speed v_m and displacement δ_m increase with contraction time t. The crucial task now is to monitor the dynamic progression of v_m and δ_m to ensure that the contraction is stopped before either of two elemental physiological limits—the displacement capacity δ_{max}, or the shortening speed capacity v_{max}—are breached; allowing longer contraction times would result in an overestimation of the energy output achievable by muscle. We then increase the complexity of the analysis one last time, and assess the effect of FVPs on muscle energy output, distinguished from the previous models by a muscle force that no longer remains constant throughout the contraction, but varies inversely with the speed of shortening.

Table 1 | A dimensionally consistent link between power output P, mass m, and energy output (or speed v) requires specification of one of three 'auxiliary variables': the contraction time, t, the contraction displacement, δ, or the average exerted force, $\hat{F}$. Because point-mass dynamics involve six elemental variables, but provide only three equations, only one parameter remains free, and its choice fully determines the remaining variables. The different instantiations of Bennet-Clark's law differ in their choice of auxiliary variable, and consequentially in how the same mass-specific power output is partitioned into muscle force vs. muscle shortening speed—the *de facto* limit on jump performance—they thus yield different predictions for the allometry of jumping speed. The choice of the auxiliary variable also controls the scaling of the remaining variables. In deriving these scaling predictions, we assumed a geometrically similar musculoskeletal system with size-invariant power density.

Free variables	Dependent variables	Scaling
P, m, t	$\hat{F} \sim \sqrt{Pmt^{-1}}$, $\delta \sim \sqrt{Pm^{-1}}t^{3/2}$, $v \sim \sqrt{Pm^{-1}t}$	$\hat{F} \propto m\sqrt{t^{-1}}$, $\delta \propto t^{3/2}$, $v \propto \sqrt{t}$
P, m, $\hat{F}$	$\delta \sim mP^2\hat{F}^{-3}$, $v \sim P\hat{F}^{-1}$, $t \sim mP\hat{F}^{-2}$	$\delta \propto m$, $v \propto m^{1/3}$, $t \propto m^{2/3}$
P, m, δ	$\hat{F} \sim (m\delta^{-1})^{1/3}P^{2/3}$, $v \sim (P\delta m^{-1})^{1/3}$, $t \sim (mP^{-1})^{1/3}\delta^{2/3}$	$\hat{F} \propto m^{8/9}$, $v \propto m^{1/9}$, $t \propto m^{2/9}$

Results and Discussion

Arbitrary speed with equal power — a problem of dimensions

Borelli's and Bennet-Clark's law both seek to estimate the maximum energy muscle can deliver during an impulsive contraction; the key difference between them can be illustrated with a dimensional argument: if the left-hand side of an equation is of dimension length per time [L T^{-1}], the right-hand side had better been, too, otherwise something has gone awry. Consider, then, the task of predicting the energy a muscle can deliver as it contracts against a mass m. Energy and work share the same dimension [M L^2 T^{-2}], so that, with Borelli, one may quickly surmise that $E \sim W_{max}$ or, in keeping with the focus of the jumping literature on take-off speed, $v \sim \sqrt{Em^{-1}} \sim \sqrt{W_{max}m^{-1}}$. Power, however, is of dimension [M L^2 T^{-3}], and it is consequently impossible to define an energy output using only P, or a speed using only P and m. Instead, dimensional consistency demands that one of three auxiliary variables be specified in addition (Table 1): (i) a displacement δ, so that $E \sim (P_{max}\delta)^{2/3}m^{1/3}$ or $v \sim (P_{max}\delta m^{-1})^{1/3}$; *or* (ii) a time t, so that $E \sim Pt$ or $v \sim \sqrt{Ptm^{-1}}$; *or* (iii) a force F, so that $E \sim P^2F^{-2}m$ or $v \sim PF^{-1}$ (these results are derived briefly via Newtonian mechanics in the SI). It is not obvious at all which variable—displacement, time or force—should be chosen. And lo!, all three have been: Bennet-Clark enforced the displacement to be geometrically similar, $\delta \sim m^{1/3}$, so that contractions with equal mass-specific power impart speeds that scale as $v \sim m^{2/9}$ (Bennet-Clark, 1977); this remains the most common quantitative implementation of Bennet-Clark's law (e. g. Biewener and Patek, 2018; Bobbert, 2013; Gabriel, 1984; James et al., 2007; Marsh and John-Alder, 1994; Sutton et al., 2016). Usherwood instead fixed a time via $t \sim \sqrt{\delta}$, leading to $v \sim m^{1/12}$ (Usherwood, 2013; Usherwood and Gladman, 2020, or, via a similar argument, $v \sim m^{1/6}$), and, last but not least, Meyer-Vernet and Rospars (Meyer-Vernet and Rospars, 2015, 2016) implicitly fixed the force to geometric similarity, $F \sim m^{2/3}$, so that $v \sim m^{1/3}$. A rather striking difference between the two laws has become apparent: for geometrically similar animals, Borelli's-law unequivocally predicts $v \sim m^0 \sim$ constant. Bennet-Clark's law, however, has been used to predict anything between $v \propto m^{1/12}$ to $v \sim m^{1/3}$ (Table 1). If the same mass-specific work output is uniquely tied to a maximum speed, but the same mass-specific power output can be correctly associated with different speeds, is it really proper to speak of a power-limit on muscle energy output?

Power limits and the hidden determination of centre-of-mass dynamics

To probe further the grounds on which the notion of a power-limit rests, revisit briefly the premise of its original development in the arthropod jumping literature (Bennet-Clark, 1977; Gabriel, 1984): (1) the time available for take-off increases with animal size. (2) There thus exists a critical size at which the available time exactly equals the time required for muscle to deliver its maximum work capacity. (3) This critical size splits jumping animals into two groups, distinguished by the muscle property that limits jump performance: in smaller animals, muscle energy output is dictated by muscle power; in larger animals, muscle work capacity reigns supreme. In the previous section, it was demonstrated that any dimensionally consistent link between power and energy requires the specification of one auxiliary variable, that this choice is not trivial *a priori*, and that it leads to different energy outputs for the same muscle power output. We now turn to Newtonian mechanics to uncover a hidden implication of this dimensional necessity, which calls into question the very idea of a power-limit to energy output.

Consider a jumping animal of body mass m. The maximum power capacity of its muscles is P_{max}, and it is allowed to accelerate for a time t prior to take-off. What is the energy it can impart to its centre-of-mass? It is tempting to conclude with $E \sim P_{max}t$ that the energy output is limited by the available muscle power. However, fixing mass, power and time places additional constraints on the muscle output during the acceleration phase, which render this conclusion incorrect for all but one special case. To understand this conclusion, note that Newtonian point-mass dynamics are governed by a set of three equations that uniquely link six elemental variables: Newton's second law, and its time- and path-integral, respectively, define the relation between acceleration, force, mass, speed, time, and displacement throughout the contraction. This mathematical structure dictates that the choice of any three parameters uniquely determines the remaining three

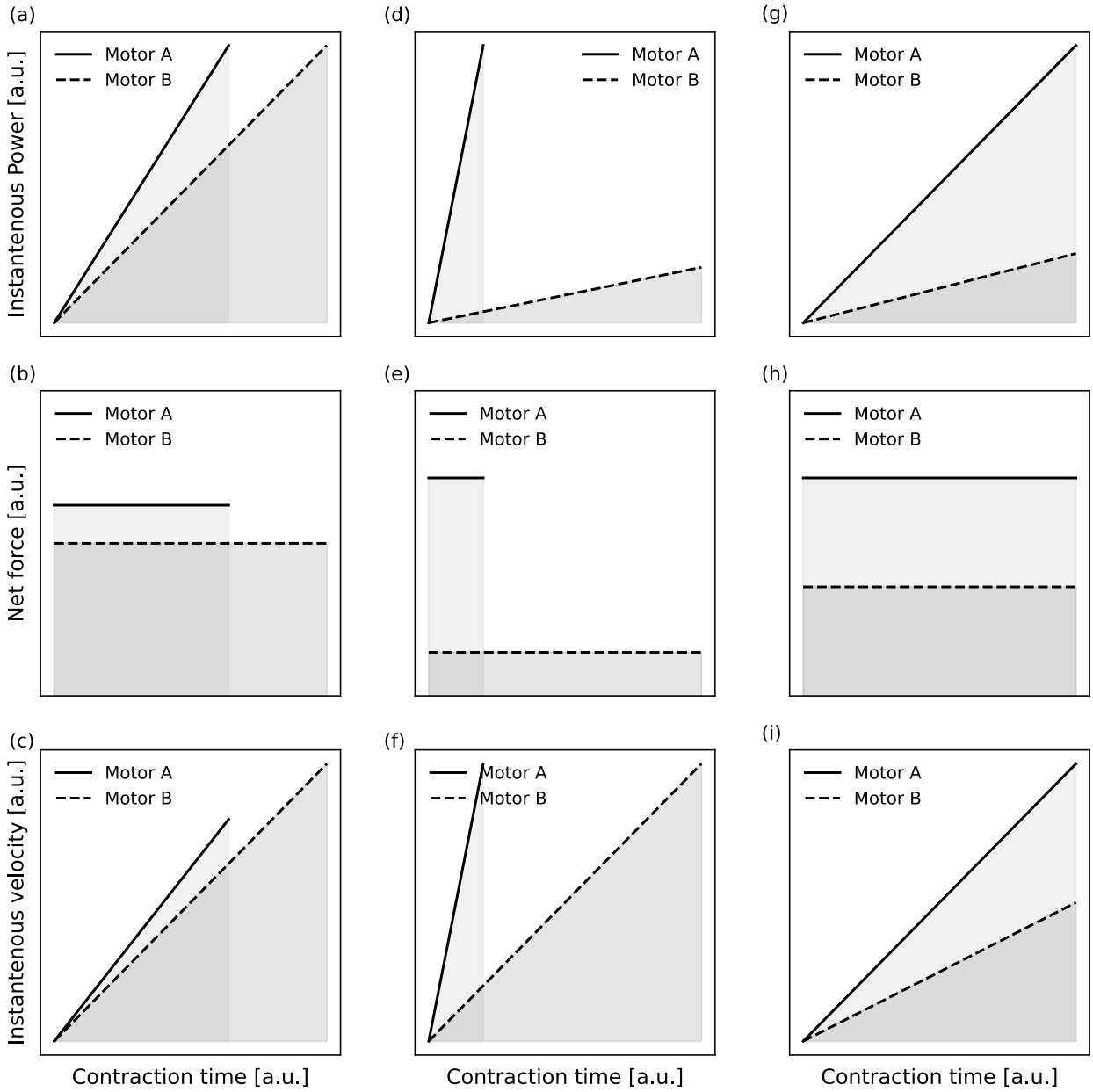

Figure 1 | Variation in muscle power is neither necessary nor sufficient to achieve variations in muscle energy output or speed, as can be illustrated with a thought experiment involving two hypothetical motors, Motor A and Motor B, accelerating a payload with mass m. We consider three different examples, distinguished by how motor power capacity is partitioned into motor force and speed of shortening; by how motor work capacity is partitioned into motor force versus displacement; and consequently by how motor displacement, speed, power and energy output vary with contraction time, t. The dynamic progression of muscle mechanical output is summarised in **a-i**: the energy output is equal to the shaded area in the first row, $W = \int Fv(t)dt$, and is related to the average power output via, $\hat{P} = Wt^{-1} = 1/2F_{\max}v_{\max}$; the impulse is equal to the shaded area in the second row, $I = \int Fdt$; and the displacement is equal to the shaded area in the third row, $\delta = \int v(t)dt$. In **(a-c)**, both motors provide the same power output, but Motor A delivers less energy. It generates a larger force, and thus delivers the same power with a smaller speed of shortening and with less displacement; in **(d-f)** both motors deliver the same energy, but Motor A is five times as powerful as Motor B, because its force capacity is larger. It consequently delivers the same energy in less time, and with less displacement; and in **(g-i)**, both motors have the same nominal power capacity, and are allowed to contract for the same time, but their energy output nevertheless differs, because Motor B has a smaller maximum force capacity, and thus fails to achieve its larger maximum shortening speed within the time available. Because any dimensionally consistent link between energy and power involves a complete determination of the contraction dynamics in terms of muscle force, displacement and shortening speed, great care must be taken to avoid predictions that appear physically possible, but are in fact physiologically prohibited by either the displacement or the shortening speed capacity of muscle (see text for further details).

variables. As an illustrative example, $E \sim P_{max}t$ at once demands $F_p \sim \sqrt{P_{max}mt^{-1}}$, and $v_p \sim \sqrt{P_{max}tm^{-1}}$. In other words, the energy will be equal to $E \sim P_{max}t$ only if the muscle force was exactly F_p throughout the contrac-

tion, and if the maximum shortening speed was exactly v_p at the end of it; it will differ for any other partitioning of P_{max} into muscle force and shortening speed. This point may appear subtle, but its consequences are surely troubling: *even with both P_{max} and contraction time t specified, the realisable muscle energy output cannot be predicted*, unless to prescribe a power output P_{max} is to imply that it can be delivered with arbitrary partitioning of the same unit power into variable muscle force vs. muscle shortening speed, i. e., independent of the available time. The same observation holds if energy and power are linked through choice of a displacement or force, i. e. regardless of how Bennet-Clark's law is implemented (see Tab. 1). Contrast this scenario with a determination of the energy output via the work capacity of muscle, which requires to define only two variables, $E \sim \sqrt{W_{max} m^{-1}}$. It consequently does not matter whether W_{max} is partitioned into a small force and large displacement capacity (which would take a long time, and involves low power), or into a large force and a small displacement capacity (which will be completed rapidly, and requires large power, Figure 1 d-f)—any muscle with work capacity W_{max} will do, because the governing equations remain underdetermined, and retain one residual "degree of freedom" that can absorb arbitrary work partitioning.

Taken together, dimensional arguments and Newtonian mechanics provide two key observations: due to the need for dimensional consistency, the question "how much energy can a motor with power P_{max} inject into a mass m" cannot be answered without specification of exactly one further auxiliary variable (see Table 1); and due to the fundamental structure of Newtonian mechanics, any such choice uniquely defines all remaining variables—the muscle force, displacement and shortening speed throughout the contraction are now fully determined. It is this determination that is the essential distinction between the different instantiations of Bennet-Clark's law discussed above, and that brings about the variation in the speed they predict (Figure 1)—a key result to which the discussion will return shortly. For now, we conclude that contractions with equal mass-specific power output cannot be tied uniquely to an energy output or a speed thus imparted (Figure 1). A muscle which provides the same mass-specific power P/m over a contraction time t or $4t$ imparts a speed that differs by a factor of two (Figure 1 a-c); a muscle which provides a power P/m or a power $5P/m$ will impart the same speed if the exerted force differed by a factor of five, too (Figure 1 d-f); and two muscles with equal mass-specific power capacity P_{max}/m may deliver unequal amounts of energy over the same contraction time t, if the same maximum power involves different partitioning into muscle force and shortening speed, respectively (Figure 1 g-i). Variation in muscle power is thus neither necessary nor sufficient to achieve a variation in the energy output of impulsive contractions; equal mass-specific power output can lead to *arbitrarily different* speeds.

Some readers may feel ill at ease with the conclusion that muscle power capacity is irrelevant for the energy output of impulsive contractions. And rightly so, for muscle surely cannot deliver the same unit of work over arbitrarily short times. If it is not power that limits energy output in these instances, then what is?

Beyond power-limits: The kinetic energy capacity of muscle

The notion that muscle power capacity limits jump speed has been called into question in the past (e. g. Adamson and Whitney, 1971; Bobbert, 2013; Farley, 1997; Knudson, 2009; Ruddock and Winter, 2015; Winter, 2005; Winter et al., 2016). But the harshness with which this criticism was sometimes expressed masked its own failure to address the fundamental issue and valid concern unearthed by the careful observations of Bennet-Clark and many others since: any account of muscle mechanical performance that ignores the dimension of time risks to arrive at conclusions that violate physiological or physical constraints, for no muscle can do a unit work in arbitrarily short contraction times. It is true enough that the mechanical quantity which uniquely ties speed, mass, and contraction time is the impulse, and not the power (Adamson and Whitney, 1971; Knudson, 2009; Ruddock and Winter, 2015; Winter, 2005; Winter et al., 2016); but pointing this out merely addresses a symptom instead of the root of the problem: what limits the contraction time? A holistic account of the limits to muscle mechanical performance has to keep track of the key mechanical parameters that characterise each muscle, and enforce that none are violated: muscle cannot exert a force larger than F_{max}, cannot contract by more than δ_{max}, and cannot shorten faster than with v_{max} (Figure 2 a.. There are also other constraints, for example muscle activation times and force-velocity effects etc, and many muscles attach to the segments they move via tendons, so introducing in-series elasticity. Neither are appropriately considered by this minimalist mechanical perspective.). Together with a mass to be moved, this specifies *four* mechanical parameters for a generic musculoskeletal system, but point mass dynamics only have *three* degrees of freedom. Which of the four parameters are fixed and which is variable was the subject of a mechanical analysis recently presented in detail elsewhere (Labonte, 2023); the results of relevance for the problem at hand are briefly summarised below.

Historically, the maximum amount of energy muscle can inject has been assessed via the path-integral of Newton's second law. Although it is equally possible, valid and reasonable to assess limits to speed via the time integral of Newton's second law, and thus phrase the problem in terms of the delivered impulse, we stick with this tradition and write:

$$\begin{aligned} F =& m\frac{dv}{dt} \\ \int F dx =& m\int \frac{dv}{dt}dx = m\int v dv \\ W =& \hat{F}\delta_{max} = \Delta E_{\max} \end{aligned} \tag{1}$$

No muscle can deliver more energy than the above expression defines, as is forever enshrined in Borelli's-law. But, as Bennet-Clark pointed out (Bennet-Clark, 1977), muscle may in fact be hindered from delivering this maximum amount of energy. What stops it? Two cogent

arguments provide an answer to this question.

First, one may recast the energy output as an explicit function of a critical contraction time, t_c:

$$W = \int F dx \frac{dt}{dt} = \int F v(t) dt = \int^{t_c} \frac{F^2}{m} t dt = \frac{1}{2} \frac{F^2}{m} t_c^2 \quad (2)$$

which used $v = dx/dt = Fm^{-1}t$. This writing finally brings us back full circle to the core premise of Bennet-Clark's law: the take-off t_c time limits muscle energy output. This assertion itself appears intuitive. But what exactly is it that limits this time? One possible answer is to borrow a characteristic time from elsewhere, for example by invoking a characteristic frequency through mechanical analyses (e. g. Thangal and Donelan, 2020; Usherwood, 2013; Usherwood and Gladman, 2020), or via a neuro-physiological or sensorimotor control framework (e. g. More and Donelan, 2018; More et al., 2010). More commonly, however, the time limit is recast in terms of a constraint on displacement or force instead (e. g. Biewener and Patek, 2018; Bobbert, 2013; Gabriel, 1984; James et al., 2007; Marsh and John-Alder, 1994; Meyer-Vernet and Rospars, 2015, 2016; Sutton et al., 2016). Indeed, two limits physiological limits are imposed by muscle itself: muscle cannot contract by more than its maximum shortening distance, so that $t_c = \sqrt{2\delta_{max} m F^{-1}}$, and thus $W = F\delta_{max}$ — the result is the familiar Borelli-limit to speed, $v_{\mathrm{Bo}} \sim \sqrt{W_{max}/m} \sim \sqrt{F\delta_{max} m^{-1}}$. But muscle also cannot contract faster than with an maximum absolute shortening speed v_{max}. Reaching this speed takes a time $t_c = v_{max} m F^{-1}$, so that $W = 1/2 m v_{max}^2$ — muscle energy output is not only limited by its work capacity, but also by its *kinetic energy capacity*, $E_{max} = m v_{max}^2$. The associated bound on speed has recently been referred to as the Hill-limit, $v_{\mathrm{Hi}} \sim \sqrt{E_{max}/m} \sim v_{max}$ (Labonte, 2023; Labonte et al., 2023).

Alternatively, one may consider the limit to shortening speed explicitly. Consider again conservation of energy:

$$\int F dx = m \int v dv \quad (3)$$

Evaluating this expression requires choice of integration limits, and the textbook approach is to consider the displacement as fixed, and the velocity as variable. Energy output is then limited by the muscle's work capacity, W_{max}, and one concludes with Borelli that maximum speed should be independent of size. However, one may equally well fix the upper integration boundary of the velocity integral, and consider the displacement as variable instead. The energy output is then limited by the kinetic energy capacity, E_{max}, and speed is bound by the Hill-limit instead, as above.

Both routes suggest a critical need to consider not only the displacement, but also the shortening speed capacity of muscle when evaluating the maximal energy it can provide, and to thus compare the work capacity with the kinetic energy capacity. There is no reason why W_{max} and E_{max} should be equal — they depend on fundamentally different physiological processes and mechanical properties. Which capacity limits the energy output can be assessed through inspection of their ratio (Figure 2):

$$\Gamma = \frac{[\text{Shortening speed limit}]^2}{[\text{Displacement limit}]^2} = \frac{E_{max}}{W_{max}} = m \frac{\int^{v_{max}} v dv}{\int^{\delta_{max}} F dx} \quad (4)$$

For $\Gamma < 1$, the kinetic energy capacity is limiting, the muscle shortening speed is fixed, and the muscle displacement is variable. For $\Gamma > 1$, the work capacity is limiting, the muscle displacement is fixed, and the shortening speed is variable (Figure 2 b). Γ has recently been argued to constitute an important dimensionless number for musculoskeletal dynamics, because it can be interpreted in a number of meaningful ways: musculoskeletal systems which operate with equal Γ share the same "effective inertia" or normalised mass; deliver the same fraction of their work and power capacity; operate at the same fraction of their speed and displacement capacity, or their kinetic energy and work capacity; and share the same ratio of a characteristic inertial to a characteristic maximum force (Figure 2 b. For a more detailed discussion, see Labonte, 2023; Labonte et al., 2023). To avoid giving one interpretation priority over any other, they may be emphasised equally by asserting that Γ is an index of the degree of *physiological similarity* across musculoskeletal systems (Labonte, 2023).

Muscle energy capacity, force-velocity properties, and in-series elasticity

Muscle is a complex motor, and some of this complexity has been ignored in the minimalist mechanical analysis presented above. One idiosyncratic property of muscle that demands explicit discussion is the variation of relative muscle force F_m with muscle shortening speed, v_m: muscle produces more force during isometric contractions with zero muscle shortening speed, $v_m \sim 0$ than during concentric contractions, and muscle force drops to zero for contractions with $v_m \sim v_{max}$ (Hill, 1938; Piazzesi et al., 2007). This FVP is important, because it imposes yet another distinct limit on muscle energy output: maximum work is only delivered in quasi-instantaneous contractions which reach the maximum displacement with vanishing muscle shortening speeds (Alexander, 2003), and is smaller during any other contraction. More recent work on the allometry of jump performance has suggested that Borelli's law breaks down in small animals because of such "force-velocity-effects", and not because of power limits (Bobbert, 2013): a given absolute speed requires higher muscle strain rates in smaller animals, which have shorter muscles; contractions which involve larger muscle shortening speeds have reduced relative work output; smaller animals should consequently jump to smaller heights (Bobbert, 2013). The same argument was invoked more recently by Sutton et al. to provide an explanation why latch-mediated jump actuation is only beneficial in small animals (Sutton et al., 2019). How do FVPs affect the energy output of muscle?

In order to evaluate the impact of FVPs, consider two instances of the simple musculoskeletal system shown in Figure 2 a; one system has a muscle that generates constant force, one has a muscle with FVPs, and both share the same maximum muscle shortening speed. Let both muscles contract to the same shortening speed, v_m—the

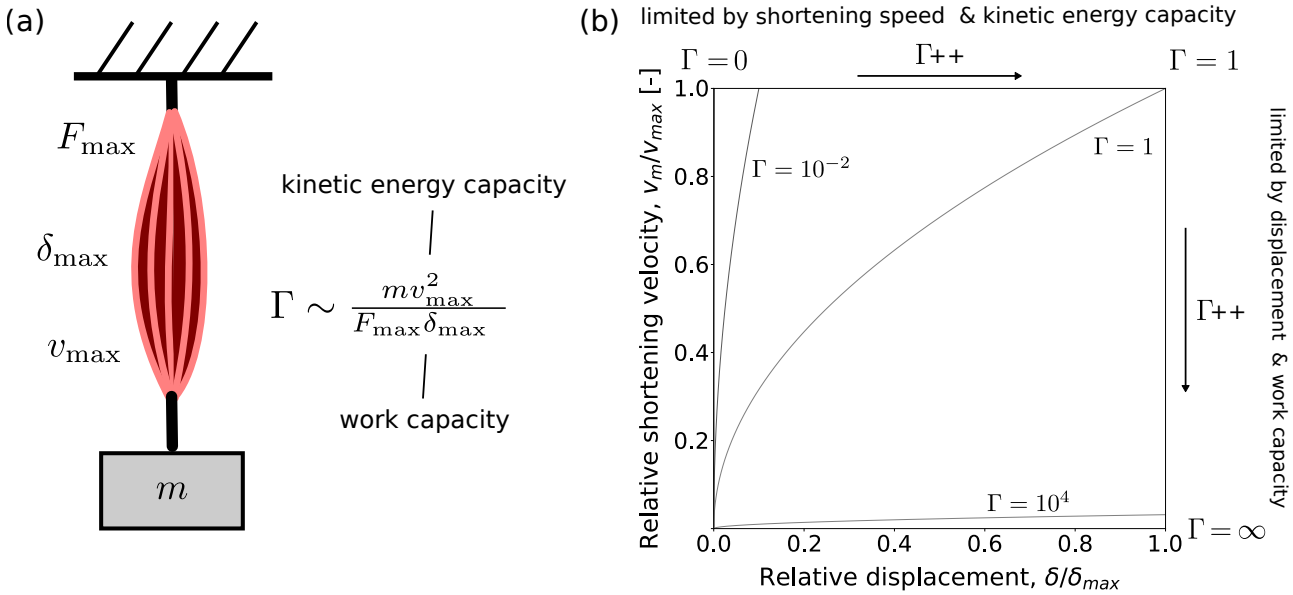

Figure 2 | **(a)** A minimalistic model of a musculoskeletal system is characterised by a maximum muscle force $F_{\max}$, a maximum muscle displacement capacity, $\delta_{\max}$, and a maximum muscle speed of shortening, $v_{\max}$. This mechanical system has four dimensional parameters, but point mass dynamics only leave three parameters "free". Which parameters are free and which are fixed is determined by the magnitude of the dimensionless "physiological similarity index", Γ. **(b)** One interpretation of Γ emerges from the inspection of "equation of motion landscapes", in which the dynamic progression of the displacement and speed is monitored as the muscle contracts (Labonte, 2023). For $\Gamma \to 0$, muscle acquires shortening velocity rapidly and with a minimal fraction of its displacement capacity. The contraction always ends with maximum shortening speed, but involves variable muscle displacement; it becomes quasi-instantaneous. For $\Gamma \to \infty$, the muscle has contracted by its maximum displacement long before it has reached any appreciable fraction of its maximum shortening speed. The muscle always shortens maximally, but achieves variable shortening speeds; the contractions becomes quasi-static. The transition from a shortening speed to a displacement limit occurs at a limiting value of $\Gamma = 1$, the critical value at which muscle reaches the maximum displacement and shortening speed at exactly the same time.

energy output is consequentially identical, $W \sim E \sim mv_m^2$. However, due to "force-velocity-effects", the FVP muscle exerted a lower displacement-averaged force, $\hat{F} < F_{max}$, and thus had to contract over a longer displacement to deliver the same work $\delta \sim W\hat{F}^{-1}$; FVPs altered the partitioning of work into average force vs. displacement. Let both muscles now contract over the same distance, δ_{max}, so that the work delivered is $W \sim \hat{F}\delta_{max}$. For a constant force muscle, $\hat{F} \sim F_{max}$ and the muscle delivers its maximum work capacity. For a muscle with FVPs, however, any increase in muscle shortening velocity reduces the average force, $\hat{F} < F_{max}$; the energy output, and consequently the achieved muscle shortening speed, of the FVP muscle is smaller than its nominal work capacity. This thought experiment provides the conclusion that muscle energy output is unaffected by FVPs if the contraction is shortening speed-limited, and is reduced only in displacement-limited contractions. Whether shortening speed or displacement is limiting is determined by the magnitude of Γ (Figure 2 b); $\Gamma << 1$ indicates a shortening speed limit for both a constant force and FVP muscle (Labonte, 2023). Because Γ is a function of size in geometrically similar animals, smaller animals are more likely to be limited by muscle shortening speed, and their jump performance are thus insensitive to FVPs—*the opposite* of the interpretation provided by Bobbert and Sutton et al (Bobbert, 2013; Sutton et al., 2019, A more technical discussion for a linear FVP is provided in the SI, where we show that the maximum reduction in energy output due to FVP is a factor of two for $\Gamma \approx 1$—negligible compared to the orders of magnitude of energy density that can be lost to the decrease in kinetic energy capacity.). We stress that we challenge the interpretation, not the main result: both Bobbert and Sutton et al correctly infer that only large animals have access to the full work capacity of their muscles via careful numerical simulations, and provide meaningful and novel insights. However, we posit that the reduction in performance in small animals is not the result of FVPs, but is instead a manifestation of the differential size-specific variation of the kinetic energy versus work capacity of geometrically similar musculoskeletal systems, $E_{max} \propto m^{5/3}$ vs $W_{max} \propto m$, and thus $\Gamma = E_{max}/W_{max} \propto m^{2/3}$ (This interpretation is also more consistent with the results of the dimensional analysis provided in the SI of Sutton et al., 2019). Because the kinetic energy capacity constrains energy output even for a muscle that does not have FVPs, this is a distinction in kind, and not just in emphasis.

FVPs are also often invoked to explain a key functional benefit of the in-series elasticity introduced by tendons: in dynamic contractions, tendons can decouple limb and muscle shortening speed, and muscle can consequently achieve similar absolute limb speeds with lower muscle shortening speeds, so increasing the average force and power (Aerts, 1997; Astley and Roberts, 2012; Farris et al., 2016; Kurokawa et al., 2001; Marsh, 2022; Roberts and Marsh, 2003; Robertson et al., 2018); in quasi-static "latched" contractions, muscle can contract arbitrarily

slowly against elastic elements, and so avoid both force-velocity-effects and supposed muscle power limits to performance, before explosively releasing the stored energy (Bennet-Clark, 1975; Bennet-Clark and Lucey, 1967; Gronenberg, 1996; Longo et al., 2019; Patek, 2023). A large body of careful work has been dedicated to such amplification of muscle power via in-series elastic elements, be it in dynamic or in "latched" quasi-static contractions (for recent reviews, see Holt and Mayfield, 2023; Longo et al., 2019; Patek, 2023). There is no doubt, of course, that elastic elements can amplify muscle power. But a reasonable argument is to be had whether the biological function of these "springs" is to amplify speed rather than power as such, at least in the context of "latched" jumps, where speed is usually the focal performance metric. The kinetic energy capacity of a spring is orders of magnitudes higher than that of muscle; it is limited by the elastic wave speed, $v_e \sim \sqrt{Y_m \rho_s^{-1}}$, where Y_m is the Young's modulus of the spring, and ρ_s is its density. For reasonable values of $Y_m \sim 10^9 Nm^{-2}$ and $\rho_s \sim 1000 kgm^{-3}$, one finds $v_e \sim 1000\ \mathrm{m\,s^{-1}}$; a muscle with a maximum strain rate of $\dot{\varepsilon}_{max} \sim 10\ \mathrm{L\,s^{-1}}$ would need to have fascicles with a length of 100 m to reach the same absolute speed. Because jumping performance in small animals is likely limited by the kinetic energy capacity of muscle, we suggest that (i) their springs are "work enablers", allowing them to overcome the constraint on energy output imposed by a limiting kinetic energy capacity; and (ii) that power amplification is an epiphenomenon instead of the biological purpose of in-series elasticity. The outcome of this somewhat semantic debate is clearly immaterial for the validity of the long list of fundamental insights that have been derived from the study of power amplification due to biological "springs" (Gronenberg, 1996; Ilton et al., 2018; Longo et al., 2019; Patek, 2023).

Last, FVP properties provide an opportunity to illustrate why the kinetic energy capacity is not just a power limit in energy clothing. For a constant force muscle, a contraction that delivers maximum average power also delivers the muscle's maximum kinetic energy capacity. That this is a correlative and not a causal relationship is evident as soon as the driving force varies with displacement or velocity. For a FVP muscle, the maximal kinetic energy capacity is still associated with the largest possible muscle shortening speed, but both maximal instantaneous and the average power are maximal for contractions which are terminated at a smaller fraction of the maximum muscle shortening speed (typically between one third to one half, see Askew and Marsh, 1997; Labonte, 2023; Sawicki et al., 2015).

Biological relevance and testable predictions

The framing of muscle performance in the conceptual terms of a limiting work and power density is a textbook staple, and has been invoked to explain an extraordinary large and diverse array of observations in the biomechanical literature (see introduction). Our analysis suggests that attributing these observations to a competition between a limiting work and power density may well be misleading, and that the *de facto* responsible alternative constraint on muscle energy output is the characteristic kinetic energy density, $E_\rho \sim m/m_m v_{max}^2$ where m_m is the muscle mass. Indeed, E_ρ differs from the power density P_ρ and the work density W_ρ in at least key three aspects, and this difference provides simple and intuitive explanations for key observations in comparative biomechanics: First, in contrast to P_ρ and W_ρ, E_ρ retains a size-dependence (Figure 3 a): geometrically similar larger musculoskeletal systems have a larger kinetic energy density, $E_\rho \sim m^{2/3}$. As a result, larger animals are generally faster (Garland, 1983; Labonte et al., 2023). Second, in contrast to P_ρ and W_ρ, E_ρ can be geared, $E_\rho = m/m_m v_{max}^2 G^{-2}$, where G is a dimensionless gear ratio (Figure 3 b, Labonte, 2023). As a result, two staples of biomechanical analyses that may ring mutually contradictory can in fact both hold: gearing is usually interpreted in terms of force-velocity trade-offs; a lower gear ratio increases the instantaneous velocity of the driven mass at the expense of the transmitted force. But gearing leaves the work and power capacity unaffected, for it amplifies displacement and velocity by just as much as it attenuates force. How, then, can a muscle make things move more quickly via gearing if its putatively limiting work and power capacities have remained unchanged? The answer is that for as long the energy output remains below the work capacity, a reduction of the gear ratio can in fact enable muscle to do more work, because it increases its kinetic energy density (see McHenry, 2011; Olberding et al., 2019; Osgood et al., 2021, for related results). Third, in contrast to P_ρ and W_ρ, E_ρ is a function of the mass that is driven (Figure 3 c). This is perhaps the least intuitive idiosyncrasy of E_ρ: *increasing the payload can enable muscle to deliver more energy* (see Sawicki et al., 2015, for a related finding on muscle power output). As a result, where E_ρ is limiting, animals can achieve the same speed even if they contract against payloads that are increasing multiples of their own body mass. As a striking illustration of this prediction, consider rhinoceros beetles, which can carry up to 30 times their own body mass without changing speed (Kram, 1996).

Even those readers who have by now grown convinced that muscle power holds little sway in impulsive contractions may remain sceptical if they are left with the impression that muscle power is relegated to biomechanical irrelevance altogether. This is decisively not so: *instantaneous* power is of crucial importance whenever external forces "remove" muscle work at approximately the same rate at which it is delivered, such as may well be the case during steady-state flight or swimming, or during movements at low Reynolds numbers (Clemente and Federle, 2012; Vogel, 2008). The *average* power output muscle sustains over time can be an eminently sensible metric to rank performance, as is for example done with bicycle or rowing ergonometers. Both scenarios somewhat resemble the relevance of motor power in engineering design — if a given payload is to be moved with a certain speed against a known external force, the motor must be capable to provide at least the instantaneous power defined by the product of said force and speed.

A useful shift in perspective?

The idea of a power-limit to the energy output of muscle has become common biomechanical vernacular. It is

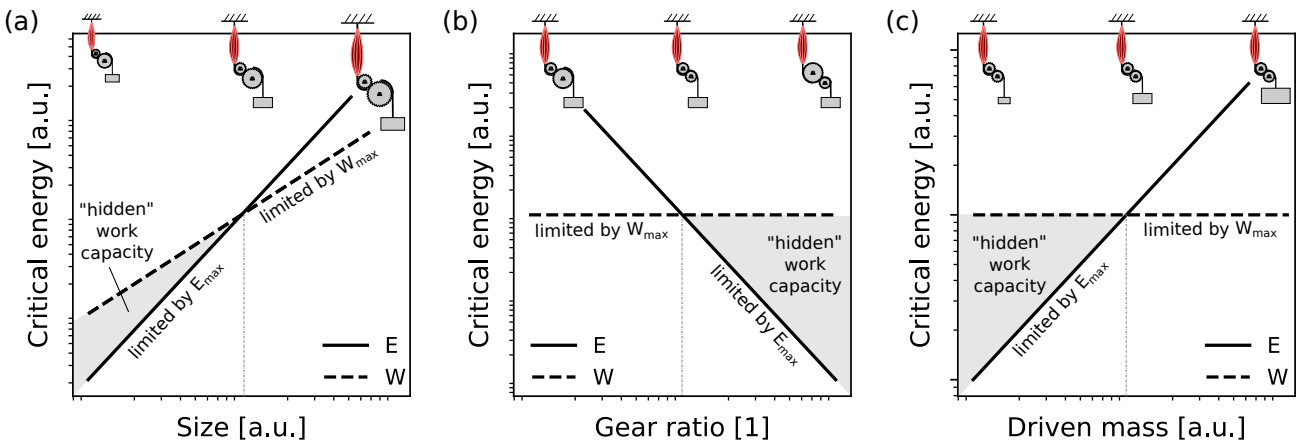

Figure 3 | The energy output of muscle is limited by two critical energies: its *work capacity*, $W_{max} = \int^{\delta_{max}} F_{max} d\delta$, and its *kinetic energy capacity*, $E_{max} = m \int^{v_{max}} v dv$. The ratio of both energies defines the 'physiological similarity index', $\Gamma = E_{max}/W_{max}$. E_{max} and W_{max} differ in their dependence on biomechanical parameters, and this differences has meaningful consequences for biomechanical performance across animal size and musculoskeletal "design". **(a)** Both E_{max} and W_{max} increase with size for geometrically similar musculoskeletal systems, but at different rates, $W_{max} \propto m$ vs. $E_{max} \propto m^{5/3}$. As a consequence, small animals are more likely to be limited by their kinetic energy capacity, and large animals are generally faster. **(b)** The work capacity is unaffected by changes to the gear ratio G for an otherwise invariant musculoskeletal system, $W_{max} \propto G^0$, but gearing changes the kinetic energy capacity, $E_{max} \propto G^{-2}$. As a consequence, where the energy output is limited by the kinetic energy capacity, it can be increased by changing the gear ratio, such that small animals benefit from smaller gear rations, and large animals benefit from larger gear ratios. **(c)** For the same musculoskeletal system, the work capacity of muscle is independent of the payload, $W_{max} \propto m^0$, but the kinetic energy capacity is directly proportional to it, $E_{max} \propto m$. As a consequence, small animal can respond to an increase in pay load by delivering more energy; the increase in load releases "hidden work capacity". All three characteristics of E_{max}, its variation with animals size, gear ratio, and payload, distinguish it from the power capacity of muscle, and so help explain several observations in comparative biomechanics (ee text for details).

rooted in the fundamental objection that muscle needs time to inject energy, and that muscle work capacity alone therefore does not tell the whole performance story. Supported by a series of arguments based in Newtonian mechanics, we have suggested that this conclusion is partially wrong, and thus only partially right. Variation in muscle power is neither necessary nor sufficient to vary the energy output of impulsive muscle contractions, and muscle power by itself consequently does not pose a limit to either energy output or speed. The problem is not that small animals do not have enough time to do work, the problem is that their muscles have a lower maximum shortening speed, and consequently a lower kinetic energy capacity: neither infinite power nor an infinitely long contraction time would help to overcome this limit. A limit to shortening speed is tacit in any dimensionally consistent expression that links muscle power, mass and energy, and consequently shares many of the features that are typically associated with a power-limit, including shorter contraction time scales and a reduced mechanical performance in small animals. The conclusion therefore neither can nor should be that the large body of work that analysed problems in biomechanics in the conceptual terms of a power-limit is "wrong", that it lost any significance, or that the fundamental issues it raised are any less seminal. Much rather, the question ought to be whether a shift in perspective, to muscle shortening speed instead of muscle power, and to a kinetic energy density instead of power density, brings any meaningful advantages, or if it is at best technically correct, but for all intents and purposes practically irrelevant.

In favour of this shift, four brief arguments may be presented. First, expressing putative energy-limits directly in terms of energy enables meaningful comparison, for distinct limits now share the same dimension (Figure 3). Second, this comparison provides straightforward explanations for a series of observations in comparative biomechanics that are cumbersome if not impossible to explain in the framework of a size-invariant work and power density: why larger animals are generally faster (Figure 3 a), why gearing can trade force against velocity (Figure 3 b), and why small animals can be seemingly indifferent to large variations in payload (Figure 3 c). Third, in its reliance on auxiliary variables, analysing impulsive contractions in terms of muscle power makes it exceedingly easy to unintentionally demand of muscle something it cannot do. An explicit account of the key mechanical variables that limit every contraction — via the physiological similarity index, Γ — side-steps this difficulty, and provides a clear framework to ensure that mechanical analyses remain not only physically but also physiologically plausible. It is both clearer and less ambiguous to bind speed through an explicit limit on shortening velocity, than to introduce this limit through the backdoor, by treating the problem as if it were one of muscle power. Fourth, the notion of a size-invariant work and power density leaves remarkably little room for adaptive variation in musculoskeletal design. Inspection of the kinetic energy density, in turn, permits interesting speculation. To give but two examples: (i) systematic variations in gear ratio with size can, in fact, enhance the work output of musculoskeletal systems, such that small animals would benefit

from small gear ratios, and large animals will benefit from large gear ratios (Biewener, 1989; Labonte, 2023; Labonte et al., 2023; Usherwood, 2013); (ii) the maximum energy output can be independent of muscle mass, and instead depend solely on fascicle length, gearing, and intrinsic muscle speed. Thus, small animals may be able to reduce the fraction of the body mass allocated to muscle, without suffering from a decrease in locomotor speed, as appears to be the case in reptiles compared to mammals (Labonte et al., 2023). These hypotheses no doubt require scrutiny, but they follow readily from inspection of the kinetic energy density, and cannot be extracted through the lens of a limiting work or power density.

Although this text has criticised the notion of a power-limit to the energy output of impulsive muscle contractions, it was written in undiminished admiration of the groundbreaking work that has been conducted within this conceptual framework. Deciphering the mechanical limits that bind muscle performance across animal size and environments remains challenging enough, and any tool that permits progress should be used. Time only will tell if the kinetic energy density and the physiological similarity index belong into this category, alongside the notion of a power-limit.

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