REVIEW

Springs, steroids, and slingshots: the roles of enhancers and constraints in animal movement

Timothy E. Higham · Duncan J. Irschick

Abstract Whole-body movement is an essential part of life for many animal species, and is used to evade predators, capture prey, and perform many other behaviors. In many cases, the ability to perform rapid movements may be crucial to fitness as doing so may allow animals to do things like effectively capture an elusive prey or to elude a chasing predator. A significant body of research has been devoted toward the musculoskeletal and neurobiological basis of animal movement, with large reviews and volumes written on locomotion and feeding. Biologists have also defined how movement can be quantified and compared among different species. Arnold (Am Zool 23:347–361, 1983) first clearly explained that the ability to perform an ecologically important task could be labeled and quantified as maximum performance abilities, a point that is elaborated upon later (Garland and Losos, Ecological morphology: integrative organismal biology. University of Chicago Press, Chicago, 1994; Irschick et al., Evol Ecol Res 10:177–196, 2008). Some commonly examined performance traits include maximum sprint speed, maximum acceleration or deceleration, maneuverability, maximum aerobic capacity (VO_{2max}), bite force, and rapidity of tongue projection, among other examples. Although the ability to perform such movements can be limited by muscle physiology, there are several situations in which the limits of muscle physiology are circumvented with a range of specializations. Here, we synthesize the literature dealing with movement (primarily ballistic) enhancers. Our goal is both to encapsulate the current state of knowledge of enhancers, and also to provide a broader evolutionary framework that might explain in which ecological contexts they have evolved, and how they can be studied in the future. Some common mechanisms for enhancing movement include elastic energy storage (e.g., tendons and other materials) in vertebrates and invertebrates, or hormonal changes (e.g., increased testosterone levels).

Keywords Power amplification · Elastic energy · Sprinting · Maximum performance · Jumping · Muscle

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Introduction

Many animals move at some stage of their life history, and therefore, this demand has profoundly shaped the diversity of form, behavior and physiology (Biewener 2003). Animals regularly employ movement for many important activities, such as capturing prey, eluding predators, finding mates, thermoregulating, and defending territories. Two behaviors have been studied in particular, namely feeding and locomotion, as each involves complex movements. In the latter case, jumping, running, walking, and other forms of locomotion often require substantial neuromuscular input, and are often power-intensive, and thus, demanding for the musculoskeletal system (Zehr and Sale 1994). While locomotion is studied in different ways, many

researchers have focused on the causal factors driving variation in maximum locomotor performance (Arnold 1983; Garland 1994; Husak 2006; Irschick et al. 2008). Maximum locomotor performance is typically defined as the ability of animals to perform an ecologically relevant locomotor task at a maximum level. Some common examples include maximum sprint speed (Garland 1984; Bauwens et al. 1995; Usherwood and Wilson 2005), maximum jump height (Kubo et al. 1999), maximum acceleration or deceleration (Huey and Hertz 1984; Williams et al. 2009; McElroy and McBrayer 2010), maneuverability (Tan and Wilson 2011), and maximum aerobic capacity (V_{O2max}) (Taylor et al. 1981; Hoyt and Kenagy 1988; Hammond et al. 2000; Ellerby et al. 2003), among other examples (see Irschick and Garland 2001). While less often studied in the context of maximum performance, some aspects of feeding are directly comparable to these locomotor performance traits, such as bite force, the rapidity of chewing or biting, and the rapidity of tongue projection (Anderson and Deban 2010; Herrel et al. 2005). Because the ability to perform rapid movements is likely to be favored by natural or sexual selection (Irschick et al. 2008), animals have evolved many mechanisms for enhancing performance (Table 1).

At a broad level, a performance enhancer is any morphological (e.g., a tendon), physiological (e.g., hormonal) or behavioral (e.g., a way of using the limbs) trait that notably improves some aspect of movements. Enhancers can act over short time periods, such as when hormone levels increase, or when certain behaviors are employed, or they can be more permanent, such as through a modification of, or addition to, existing structures. Such morphological features can be within structures (e.g., a series of elastic elements) or could be related to the external structure itself (e.g., limb length). In this vein, performance enhancers span an enormous range of biological features. Despite a large and emerging body of work on enhancers, there has been little effort toward a synthetic view of their abundance, and how and why they have evolved. Our goal is both to encapsulate the current state of knowledge of enhancers, and to provide a broader evolutionary framework that might explain how and why they have evolved, and how they can be studied in the future. Rather than be exhaustive, we aim to reveal the diversity and ecological context of enhancers through key examples. We focus on those behaviors that involve high-powered movements, such as sprinting, jumping, or the projection of tongues. We focus on three questions. (1) How do different enhancers increase movement? (2) For a given behavior, such as jumping or running, are there common mechanisms of performance enhancement across divergent taxa? (3) How are enhancers related to the diversity of morphological form and movement across a variety of animal species?

We discuss two ways of enhancing movement. (1) Maximizing physiological performance. Enhancers in this context maximize movement within the boundaries of neuromuscular physiology, and thus, include temporal adaptations (e.g., training) or modifications (e.g., altered hormonal levels, temperature changes). They involve well-documented systemic structural and neuromuscular adaptations that allow animals to run quickly, jump far, or perform other high-performance behaviors. Such evolutionary modifications appear to be the most predominant method for enhancing movement at a macroevolutionary level. (2) Circumventing neuromuscular limits via alternative structures. This mechanism for enhancing movement has received considerable attention over the past 40 years in both invertebrates and vertebrates. Most commonly, elastic structures are slowly stretched by muscles, thereby storing energy. These structures then recoil, releasing the stored energy very quickly, thus amplifying power output (e.g., Hustert and Baldus 2010). In this sense, they allow animals to "break the rules" and achieve new levels of performance that might not otherwise be possible. The ability of jumping frogs to perform beyond the limits of their neuromuscular system is a well-studied example (Roberts et al. 2011; Astley and Roberts 2012).

Trade-offs and mechanical constraints on performance

To understand how and why the enhancers have evolved, it is important to first consider the constraints placed on movements as a result of trade-offs with other factors (Fig. 1). In addition, mechanical or physiological limits pose constraints on the ability to move, and enhancers often circumvent these constraints. Ultimately, the only way that we can define an enhancer is by first identifying how the movement is constrained.

Gould and Lewontin (1979) and Lauder (1996) have discussed how the evolution of morphology can be constrained by various factors, such as development, and how it is unrealistic to expect that morphological and functional traits will evolve freely. Indeed, they note that basic constraints often emerge from the nature of the morphological structures that animals possess. Muscle function can dictate locomotor performance in a wide variety of animals (Dorn et al. 2012; Garland 1994; Higham et al. 2011; Kohlsdorf and Navas 2012). Muscles are in turn regulated by an integrated set of nerves, soft tissues, and bones. While muscles present some advantages, they are also often limited in their ability to generate high forces at high contraction speeds due to the force–velocity relationships of muscle (Josephson 1999). Therefore, animals that have an ecological need to perform some locomotor task very rapidly might be constrained by how muscles work. For

Table 1 Examples of performance enhancers in animal movement

Animals	Behaviors	Enhancer category[a]	Structures	Mechanism	References
Lamnid sharks and tuna	Swimming	1	Muscle	Internal red muscle	Bernal et al. (2005)
Human	Sprinting	1	Muscle	Testosterone	Husak and Irschick (2009)
Fence lizard	Sprinting	1	Muscle	Testosterone	Klukowski et al. (1998)
Drosophila	Flight	2	Thorax	Elastic storage	Dickinson and Lighton (1995)
Frog	Jumping	2	Tendon	Elastic storage	Roberts et al. (2011), Roberts and Marsh (2003); Astley and Roberts (2012)
Guinea fowl	Jumping	2	Tendon	Elastic storage	Henry et al. (2005)
Froghopper	Jumping	2	Legs	Elastic storage	Burrows (2003)
Bushbaby	Jumping	2	Tendon	Elastic storage	Aerts (1998)
Flea	Jumping	2	Resilin	Elastic storage	Haas et al. (2000), Bennet-Clark and Lucey (1967)
Shore bug	Jumping	2	Legs	Elastic storage	Burrows (2008)
Wallaby	Hopping	2	Tendon	Elastic storage	Biewener et al. (1998)
Kangaroo	Hopping	2	Tendon	Elastic storage	Alexander and Vernon (1975)
Kangaroo rat	Hopping	2	Tendon	Elastic storage	Biewener et al. (1981)
Dragonfly	Flight	2	Wings	Elastic storage	Donoughe et al. (2011)
Turkey	Running	2	Tendon	Elastic storage	Roberts et al. (1997)
Ant	Prey capture	2	Jaws	Elastic storage	Spagna et al. (2008)
Chameleon	Prey capture	2	Tongue	Elastic storage	de Groot and van Leeuwen (2004)
Seahorse and pipefish	Prey capture	2	Tendon	Elastic storage	Van Wassenbergh et al. (2008, 2009)
Salamander	Prey capture	2	Tongue	Elastic storage	Deban et al. (1997)
Mantis shrimp	Stunning prey	2	Forelimbs	Elastic storage	Patek et al. (2004), Claverie et al. (2011)

[a] This includes (1) increasing physiological limits, (2) circumventing neuromuscular limits via alternative structures
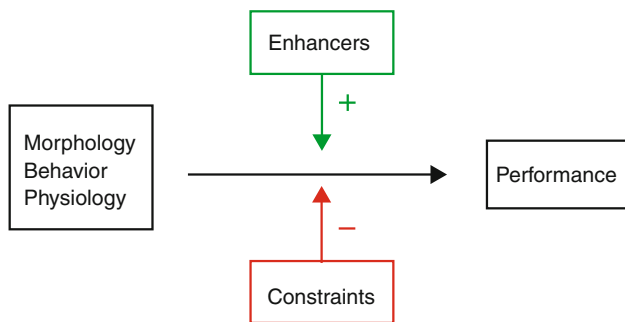

Fig. 1 The relationship between morphology, physiology, and behavior on performance. Enhancers can positively impact the relationships with performance, whereas constraints can negatively impact the relationships with performance

very small animals, it is possible to obtain high locomotor performance from extremely fast muscle due to the high force to body mass ratio (Wu et al. 2010), but for larger animals, this is not a viable possibility.

Another constraint concerns the multiple interacting functions of animal phenotypes. For example, while the ability to breathe and move has been largely decoupled in mammals, there is evidence that the respiration and locomotion conflict with one another in lizards (Carrier 1987, 1991). Lizards breathe by actively moving their ribs to alter the volume of the thoracic cavity, and the hypaxial and epaxial muscles driving the movements of the ribs are also involved in moving and/or stabilizing the body for locomotion. Thus, reptiles experience trade-offs with respect to their ability to locomote via limb and body movement, a fact which may explain the poor endurance of lizards relative to endotherms, such as mammals.

While trade-offs are often portrayed as being insurmountable, in fact, some animals can exhibit mechanisms for reducing or even eliminating them. One way of avoiding constraints is utilizing an alternative mechanism for a specific behavior. For example, gular pumping in varanid lizards is a way of eliminating the respiration constraint outlined above (Owerkowicz et al. 1999). During locomotion, varanids use a positive pressure gular pump to increase lung ventilation. This effectively avoids the axial constraint that is evident during costal aspiration found in other tetrapods. Another mechanism of avoiding constraints is through redundancy of functional units, such as muscles or anatomical structures. The fins of fishes are a wonderful example of multiple control surfaces in which forces can act on the environment (Blake 2004; Lauder and Drucker 2004). Many fishes will employ their body and caudal fin for escape maneuvers, whereas the paired fins can be used for steady swimming and/or routine maneuvers

(Webb 1975, 2006; Walker and Westneat 2000; Walker 2004). This effectively relegates a fin (or pair of fins) to a certain function, but enables performance to be maximized for that given behavior. Although this is useful for animals exerting forces in all directions on their surrounding fluid, this is not an option for most terrestrial animals that exhibit minimal contact with the surface on which they are exerting force. This minimal contact will likely reduce the number of options for overcoming trade-offs or constraints, but this requires a broad-scale study examining animals that live in different media.

In addition to utilizing multiple functional units to circumvent trade-offs, animals can also exhibit physiological flexibility and/or redundancy. For example, muscular trade-offs (speed vs. endurance) can potentially be avoided by maximizing the flexibility of function within a single limb, fin, wing, or even within a single muscle. Given that the limbs of terrestrial vertebrates have multiple muscles acting at a single joint (i.e., synergists), it is possible that specific muscles are "tuned" to a specific behavior (Higham and Biewener 2008). For example, one propulsive muscle might be effective at driving movement at high running speeds. Thus, this muscle would be preferentially recruited as the animal runs faster (also dictated by fiber type). At the same time, another muscle might be effective at generating high forces quickly (high power), which is beneficial for ballistic behaviors such as jumping. Thus, this muscle would be preferentially recruited during jumping behaviors or any other behavior that requires high power (e.g., accelerating or maneuvering). This flexibility in muscle function would potentially allow an animal to maintain a high level of performance under varying circumstances. However, this also reduces the amount of muscle dedicated to a single behavior, which is still a compromise. Muscle redundancy also permits a wide range of finely tuned force patterns, which increases the range of joint moments that can be generated (Prilutsky et al. 1996). Future work assessing the potential for animals to be "physiological masters of all trades" might reveal novel ways in which evolution has shaped the interaction of phenotype and environment.

Moreover, it is important to note that some kinds of trade-offs may make sense theoretically, but are not always supported by empirical data. One of the most commonly cited trade-offs is that between speed and endurance during locomotion. This trade-off is based on the notion that slow- and fast-twitch muscle fibers each play different roles, and there is limited space in any animal's body to have large numbers of each kind. If a muscle were predominantly comprised of slow-twitch muscle fibers, then one would expect that it should be involved primarily for long-distance (endurance) events, thus, precluding its ability to engage in high-power locomotion, such as fast

accelerations. However, few studies have examined this trade-off at the organismal level, and it is indeed possible that the potential trade-off between speed and endurance only occurs in animals that have a high capacity for speed and/or endurance (Sorci et al. 1995). In general, there seems to be little evidence for this trade-off when different individuals within a species are compared (e.g., lizards, Garland et al. 1990; Sorci et al. 1995; frogs, Wilson et al. 2002), although exceptions include one study comparing different lizard species (Vanhooydonck et al. 2001), one using *Xenopus* (Herrel and Bonneaud 2012) and a study using laboratory mice that have evolved in response to selection for high voluntary wheel running (Dluglosz et al. 2009).

Enhancing rapid movements

Below, we focus on two categories of performance enhancers. These categories define a set of conditions that differ between enhancers, although a specific feature might be involved in both of these categories. These categories typically do not define any taxonomic group given that a certain taxon may exhibit more than one (or all) of these. Because they have been so well studied, many of our example concern enhancers that maximize ballistic locomotor performance (high speeds and/or accelerations). In contrast, we do not focus on enhancers involved in endurance performance, which is largely beyond the scope of this paper.

Increasing physiological limits

This category of performance enhancers concerns those traits that increase the performance within basic physiological "rules". This category includes both behavioral and physiological features that can elevate performance. We acknowledge that the potential mechanisms in this category are almost limitless, which increases the complexity when trying to pinpoint the basis for an increase in performance. For example, any stage in a cascade of events (that lead to an increase in performance) could be the source of the enhancement. Although this increases the challenge, it must be acknowledged that anything that directly increases performance, evidenced by empirical results, should be considered as a performance enhancer.

Increasing, but not surpassing, muscle performance

Within a population or species, there is considerable variation in locomotor performance. This can be due to several factors, including muscle performance, which can be altered in several ways (discussed below). Modulating

muscle performance (within the muscle itself) is an example of an "incremental enhancer" given that the degree of response (level of enhancement) is often related to the "dose" of the variable (e.g., hormone level or amount of training). This is in contrast to the alternative view of locomotor enhancers (e.g., elastic energy storage), which simply cause the system to exceed the limits defined by the neuromuscular system alone.

Although circumventing neuromuscular performance by quickly returning stored elastic energy (as occurs with tendons) is arguably the most studied aspect of performance enhancement, several other factors can incrementally increase performance. For example, increasing the mass of a muscle can result in elevated values of physiological cross-sectional area (PCSA), which is positively correlated with increased muscle force (Powell et al. 1984). Thus, any factor that can increase the mass of a muscle will ultimately enhance, or increase, neuromuscular performance, which would have the potential to enhance the ability to move rapidly. In addition to muscle mass, the contractile properties (e.g., contraction velocity) of a given muscle can be altered by several different factors, including hormones and increased use (Lomo et al. 1974; Salmons and Henriksson 1981; Girgenrath and Marsh 2003). For example, when the external oblique muscle of gray tree frogs is supplemented with testosterone (to approximate breeding season levels), they exhibit shorter twitches, faster shortening velocities, and larger masses (Girgenrath and Marsh 2003).

Anyone who has watched baseball or football over the last several decades is aware of the purported performance advantages of steroids, such as synthetic testosterone (T), or similar chemicals. There is a compelling body of evidence to show that steroids like testosterone have dramatic impacts on locomotion in vertebrates. For example, increasing the amount of T in the humans will raise muscle mass by increasing muscle protein synthesis (Griggs et al. 1989), the number of satellite cells, and the number of myonuclei per unit area. The impact on non-human animals is less clear (reviewed in Husak and Irschick (2009). In fish, exogenous T seems to improve burst speed by enhancing muscle traits in much the same way as for humans, but in lizards, the outcomes are conflicting. Some studies show that exogenous T improves maximum burst speed (Klukowski et al. 1998), whereas other studies show little or no effect (O'Connor et al. 2011).

There are several explanations for this difference between humans and other animals in regards to T sensitivity. First, most of the studies that have examined the influence of T on locomotor performance have done so in a laboratory environment in which the animal is likely to be under duress, and the hormonal impacts of this duress are poorly understood. A lack of general information about normal fluctuations in hormone levels in various animal species makes any manipulative study challenging, especially because there are seasonal hormonal rhythms in many animal species, unlike humans (O'Connor et al. 2011). Challenges in obtaining blood samples and assessing hormone levels accentuate this problem. Second, in humans, training and a high-protein diet are essential elements in improving locomotor performance in combination with steroid use, but these factors have hardly been studied in other animals, or seem in some cases (e.g., training in lizards) to diminish performance (O'Connor et al. 2011), in some cases, by causing physical damage (Garland et al. 1987). However, training in lizards can be beneficial and crucial (Huyghe et al. 2010). These findings imply a fundamental divide among different groups (lizards, mammals, and fishes) in their muscle physiology, and suggests that more studies are needed across broad groups of vertebrates to understand the relative roles of stress, training, and hormones for either constraining or enhancing locomotor performance (Husak et al. 2007).

Optimizing the temperature of muscle

The arrangement of morphological structures, and their integrated function can act as a significant enhancer, which ultimately enables animals to occupy seemingly uninhabitable environments. One of the best-studied examples is the ability of some ectotherms to perform at high levels at low temperatures. Temperature acts as a significant constraint on locomotion because of its negative impact on the power output capacities of muscles, its tendency to increase twitch duration, and also reduce cycling frequencies (Angilletta et al. 2010; Bennet 1984; Rome et al. 1992). Much of this research has been performed with fish muscles (Syme 2006). The focus on fish is logical, as many fish require rapid locomotion while occupying low water temperatures. The effects of temperature on muscle pose a conundrum for cold-water fishes, as red muscle is typically located close to the external surface of the body. In such a position, the muscle would be cooled by the surrounding water and would, thus, be susceptible to the impacts of low water temperature.

Several kinds of fast-moving pelagic fish, such as tuna, lamnid sharks, and thresher sharks appear to have overcome this environmental obstacle by a unique structural arrangement that allows them to maintain relatively high temperatures for internal layers of red muscle in cold water (Bernal et al. 2005; Syme and Shadwick 2011). For example, the salmon shark, which occurs in cold Northern Pacific waters, possesses red muscles that only function effectively at relatively high temperatures (20–30 °C). The low temperature of the surrounding water (6–8 °C) poses a severe constraint, which the shark overcomes through a

unique arrangement of muscle, and a counter-current temperature-regulatory system (Bernal et al. 2005). These elevated internal muscle temperatures enable them to move long distances and swim quickly to capture prey in otherwise prohibitively cold waters. This evolution of an integrated set of morphological structures in these sharks allows them to function ecologically like endothermic mammals, but these animals also incur similar metabolic costs, which require them to continually acquire high-energy food.

Behavioral changes that increase performance

Behavioral changes can alter maximum performance in several ways, and these changes are often driven by dynamic ecological conditions. Although this is a relatively unexplored area of performance enhancement, it is clear that two distinct behavioral changes can occur. First, a behavior could be performed prior to the event of interest, and is thus deemed a "pre-performance" behavioral adjustment. Alternatively, enhancement might arise during the event of interest, and is deemed a "within-performance" behavioral adjustment. A range of examples is provided below.

Many examples exist of behavioral adjustment prior to executing a high-performance event, including mammals that hyperventilate prior to a dive to maximize dive duration (Butler and Jones 1997), or ectotherms that bask in the sun to raise body temperature to within an optimal range (Kaufmann and Bennett 1989). Similarly, many flying insects will activate their flight muscle prior to flight, without any motion of the wings. This behavior, which is analogous to shivering, warms the muscles and body and facilitates effective locomotor performance (Casey et al. 1981).

Postural shifts induced by variation in habitat structure also have the possibility of altering performance. Given that kinematics will dictate the operating lengths of muscles, anything that alters posture can potentially impact how much force a muscle can generate. For example, it was suggested by Vanhooydonck et al. (2006) that different species of *Anolis* lizards have different levels of potential energy storage prior to a jump due to the differences in femur protraction prior to the onset of a jump. Thus, postural shifts will alter the ability of elastic tendons to store energy. This is a relatively unexplored area, requiring thorough examination.

Behavioral adjustments during high-performance events also appear to be commonplace. Fishes and birds will exploit environmentally induced vortices to enhance locomotion (Liao 2007). Salmonids, for example, will seek portions of the habitat that exhibit reduced flows, such as behind logs and boulders. Performance enhancers can also emerge during, and as a result of, group activities. This is most common in aquatic and aerial locomotion, where the position of an individual relative to other individuals can enhance locomotion (e.g., reduce the costs associated with locomotion). These biotically generated flows that enhance the performance of another individual have been studied in several vertebrate groups, including schooling fish, flying birds, and swimming mammals, such as dolphins (Alexander 2004). In a school, fish can swim for longer with lower respiratory rates and lower tail-beat frequencies (Liao 2007). If the school adopts a diamond formation, a fish that swims behind and between two members can exploit the lower velocity that results from the thrust wakes generated by the two preceding members. This is predominantly two-dimensional (within a single plane), but there are likely benefits gained in three-dimensional schools from vortices shed from pectoral fins and other structures (Liao 2007). Studying the dynamics of groups can be technically challenging, but future work in this area will likely reveal many performance enhancing group activities.

Circumventing neuromuscular limits via alternative structures

Biological springs

As reviewed by Roberts and Azizi (2011), biological springs are structures that deform when a force is applied to them, and then recoil when the application of force stops. This storage of elastic strain energy can appear in many biological forms, including series-elastic elements within muscles, tendons external to muscle, aponeuroses, skin, and skeletal structures (Wainwright et al. 1978; Aerts 1998; Biewener 1998; Alexander 2002; Roberts and Marsh 2003; Azizi and Roberts 2009; Patek et al. 2011; Roberts and Azizi 2011). In addition, there is more than one way to load an elastic structure, including contractile elements of muscles and gravitational potential energy (Anderson and Pandy 1993).

Storage of energy in series elastic elements has been studied in detail over the past 40 years (e.g., Alexander and Vernon 1975; Komi and Bosco 1978) and has been reviewed recently by Roberts and Azizi (2011) and by Patek et al. (2011). Studies tend to distinguish between energy conservation, power amplification, and power attenuation (Roberts and Azizi 2011), all of which can occur when tendons are stretched by muscular contractions (Dickinson and Lighton 1995). Although distal tendons (of ankle extensors) are commonly examined in terrestrial vertebrates, intramuscular connective tissue sheaths and other elastic structures can also be utilized for power amplification. One such system is found in bushbabies, in which vastus muscle–tendon complex can store elastic energy and amplify power by up to 15 times (Aerts 1998).

Spring-like structures typically function either as energy savers or power amplifiers (Table 1; Gronenberg 1996; Roberts 2002; Claverie et al. 2011). The former is common in animals that exhibit a large fluctuation in kinetic energy during locomotion (Alexander 2003). Some structures, such as stiff tendons, are most useful for large animals (e.g., kangaroos), which can use the force of gravity to exert a substantial tensile force on the structure (Alexander and Vernon 1975). Pollock and Shadwick (1994) examined the scaling of muscle cross-sectional area (and therefore maximum force) and found that larger mammals have stronger digital flexors and ankle extensors than if they were geometrically similar to small mammals. Unlike muscles, tendons had dimensions (length and crosssectional area) that were predicted by isometry. Thus, the capacity for storing elastic energy in tendons scaled with mass exponents that were significantly greater than 1 for digital flexors and ankle extensors indicate that the mass specific energy storage increases in larger animals (Pollock and Shadwick 1994). Future research examining variation in energy storage between individuals and/or populations might reveal key relationships between ecology, form, and function.

Spring-like structures have likely evolved independently in many disparate animal species (Roberts et al. 1997; Biewener et al. 1998; Roberts 2002; Henry et al. 2005; Sensenig and Schultz 2003, 2004). The ecological need for power-amplification systems becomes evident when one considers the trade-offs faced by muscles. The instantaneous contraction velocity of muscle depends on several physiological factors, such as the length of the muscle when activated, the activation timing, innervation, enzymatic composition, and sarcomere length (Gronenberg 1996; Marsh 1999). Muscle power ultimately depends on the contraction velocity of muscle and the force generated by that muscle. However, high contraction speeds are necessarily linked to low force production, highlighting a trade-off between force and velocity (Hill 1938; Herrel et al. 2009). In addition, many animals may have a need for rapid movements that are faster than the contraction velocity of muscle, such as many arthropods that jump, fly, or perform predatory strikes (Gronenberg 1996). Indeed, many studies have observed movements of animals (or structures) that exceed the contraction velocity of muscle, and therefore, the neuromuscular limits (Fig. 2).

Prey capture and enhancers

Just as extremely rapid movements are important for locomotion, they also play a role during feeding, especially in sedentary animals for which rapid locomotion is challenging. In each of the below cases, animals have evolved unique structures that allow them to project their tongues at extremely rapid speeds, in some cases, far faster than
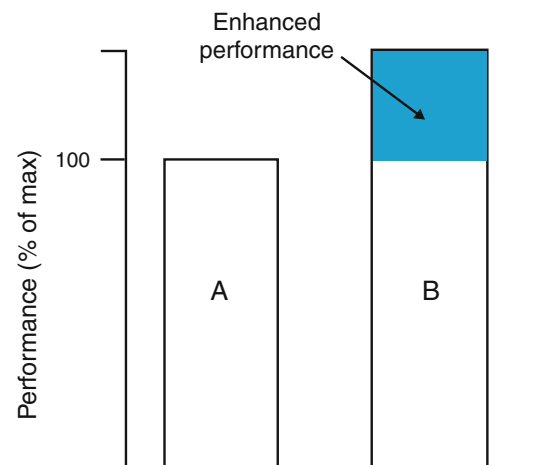

Fig. 2 Hypothetical performance (relative to maximum) under two scenarios. Maximum performance in this case is within the neuromuscular limits (limit is 100 %). For scenario *A*, maximum performance does not exceed the limit imposed by the neuromuscular system. The *shaded region* in *B* represents the enhancement beyond the neuromuscular limit. Thus, scenario *B* represents the condition in which the limits of the neuromuscular system are circumvented

typical muscle dynamics would allow. Some frog species project their tongues extremely rapidly to capture prey, often over durations of 30 ms (Nishikawa 2000). Many animals use their tongues actively to feed, and these movements are often short (roughly within 2 % of body length), and fueled by standard processes of muscle activation and shortening. However, in the salamander genus *Hydromantes*, their tongues can be projected fully within a few milliseconds, and up to complete body length (Deban et al. 1997). This remarkable performance is driven by specialized groups of muscle fibers that "squeeze" the tongue, thus propelling it forward in a ballistic trajectory and at very high accelerations and velocities. Chameleons also have evolved a unique musculature for propelling their tongues to very long lengths (de Groot and van Leeuwen 2004), albeit at a far slower pace than for *Hydromantes*. What unites these two examples is the evolution of morphological innovations that allows these very sedentary animals to consume mobile prey, thereby, overcoming a severe constraint on their locomotor morphology.

Two of the most rapid movements in the animal world are the strike of the mantis shrimp and the snapping of the jaw of trap-jaw ants. Mantis shrimp possess an external appendage, which is used for killing or stunning prey, or for territorial defense. These animals will unfurl their appendages at extremely high velocities (above 60 ms^{-1}), which is driven by a spring-like mechanism that stores and then releases energy (Patek et al. 2004). Trap-jaw ants have repeatedly evolved oversized mandibles that can be "cocked", and then close rapidly once a spring which

stores elastic energy is released. These jaws are multifunctional, and can be used for defense and locomotion, such as when they are snapped against the surface, allowing them to jump (Patek et al. 2006)! The dual usage of their jaws could explain why these jaws have evolved several times within ants. Much like a catapult, the trap-jaws are opened slowly and then kept in a wide locked position until a trigger hair on the mandible is stimulated, in turn stimulating several neurons, which release the trap jaw. The jaws reach speeds of over 64 ms^{-1}, which is higher than even the mantis shrimp strike (Patek et al. 2006).

Extremely fast prey capture in adult bay pipefish (*Syngnathus leptorhynchus*) and newborn seahorses (*Hippocampus reidi*) is also driven by elastic storage mechanisms (Van Wassenbergh et al. 2008, 2009). In the former, inverse dynamical modeling, based on high-speed kinematics, revealed that power enhancement stems from tension being built up in the tendons of the post-cranial muscle prior to prey capture (Van Wassenbergh et al. 2008). This results in values of instantaneous muscle-mass-specific power up to 5,795 W kg^{-1}. This catapult-like mechanism is also apparent in newborn seahorses given that peak instantaneous power requirements during prey capture exceed the maximum mechanical power output of muscle (Van Wassenbergh et al. 2009), which is approximately 1,100 W kg^{-1} (Curtin et al. 2005). A thorough investigation into other groups of fishes, and into the detailed mechanisms involved, is needed to fully understand power amplification during prey capture. Regardless, these examples add to the growing list of performance enhancers related to fast prey capture among vertebrates and invertebrates.

Jumping and enhancers

Because of its biomechanically simple yet dynamic nature, jumping has captured the interest of scientists for many years, and limits to maximum jumping performance have been examined in many species (Lutz and Rome 1996; Roberts and Marsh 2003; Toro et al. 2004; Henry et al. 2005; James et al. 2007; Vanhooydonck et al. 2006). Moreover, jumping fulfills an ecological need in many animals for capturing prey or escaping predators. Jumping is also widely used by a wide range of animals that span many different sizes, including insects, frogs, lizards, and mammals (Bennet-Clark and Lucey 1967; Aerts 1998; Roberts et al. 2011; Astley and Roberts 2012; Vanhooydonck et al. 2006; Legreneur et al. 2012). Within all these groups, there is evidence that jumping may sometimes require more power than could be provided by the muscles alone, thus, providing a rich model for studying performance enhancers.

Jumping is vitally important for frogs, and they have been a model system because of their many morphological specializations, such as elongated hindlimbs, and a short trunk and forelimbs. Several studies have documented that elastic structures permit power outputs that exceed the maximum power output of the muscles involved (Roberts et al. 2011). This result is puzzling, as there appears to be no anatomical catapult mechanism, which would enable frogs to store elastic energy. Using a relatively simple model, Roberts and Marsh (2003) explored the limits to muscle-powered accelerations during jumping in frogs. They found that a series elastic element which stored elastic energy and variable muscle mechanical advantage increases the work output of muscles. This system acts like a variable leverage catch mechanism, permitting power amplification during jumping. More recent work assessed whether variation in the jumping capacities of various species of frogs could be predicted based on available muscle power (Roberts et al. 2011). In this study, the power during jumping was determined using force plates, and the peak power output of the plantaris muscle, which is important for jumping was assessed under in vitro conditions. There was no correlation between available muscle power and jump power, indicating that the series elastic element can disconnect the link between muscle and jump performance.

Insects often exhibit remarkable specializations that enhance jumping performance (Bennet-Clark and Lucey 1967; Burrows 2003, 2006b, 2008; Sutton and Burrows 2011). For example, fleas (specifically the rabbit flea, *Spilopsyllus cuniculi*) contract a depressor muscle, which stores potential energy in resilin, a rubber-like protein that lowers stiffness and increases the deformation of structures in which it is found (Haas et al. 2000; Donoughe et al. 2011). This stored energy is then released by contracting a small muscle that alters the point of action of the depressor muscle (Bennet-Clark and Lucey 1967). This permits the hindlimb to extend rapidly like a catapult, resulting in remarkably long jumps for their size. Ultimately, fleas use the end of the tibiae to apply forces to the ground (Sutton and Burrows 2011). Other small insects, such as froghoppers and shore bugs, can also store energy prior to jumping. Froghoppers have a greater acceleration than any known animal, reaching a takeoff velocity of 4.7 ms^{-1} in less than 1 ms (Burrows 2003, 2006a). The forces and accelerations generated during jumping in multiple species of froghoppers could not be produced by direct contractions of muscles, underscoring the storage and rapid release of this energy (Burrows 2006a).

Interestingly, this biomechanical trick enables these very small insects to overcome, in part, inherent constraints on jumping. Small animals are typically capable of rapid accelerations, but the short durations over which their limbs contact the ground during jumping limit the total jump distance. By comparison, larger animals typically

accelerate at far lower levels, but compensate through experiencing relatively long takeoff durations. Despite these trade-offs, larger animals typically jump farther distances than small animals (i.e., compare a human to a flea), but the amplification mechanisms of small insects enable them to partially make up this disparity. Smaller animals appear to utilize trigger muscles to control the timing of catapult mechanisms, whereas larger animals may employ variable mechanical advantage to control the springs. However, the latter remains to be confirmed.

Conclusions and future directions

The breadth of enhancers is striking, as they have evolved in vertebrates (e.g., frogs, bushbabies), and invertebrates (e.g., trap-jaw ants, froghoppers), and for many different purposes, ranging from rapid jumping (froghoppers), to prey capture (mantis shrimp, salamanders, chameleons) and defense (trap-jaw ants). In many of these cases, spring-like or catapult-like structures play a key role, and allow animals to exert relatively little power, yet produce very impressive levels of performance. Enhancers also come in many different flavors, encompassing morphological, physiological, and behavioral traits. Although it is clear that many factors can enhance the movement, quantitative studies identifying the precise increase in performance are rare (but see studies such as Roberts et al. 2011). In many cases, species that exhibit rapid movements are studied, and an enhancer is implicated. One could argue that anything that results in variation in muscle function is an enhancer, which could include general body conditions. However, we would limit performance enhancers to those traits that directly increase performance, and this requires empirical links to be determined. It is also possible that factors that enhance locomotion under certain conditions might actually decrease performance under different conditions.

The type of enhancer exhibited by a specific species appears to depend on the behavior that is being performed (running, jumping, etc.; Table 1). Enhancers that maximize or increase physiological limits are likely to be important for achieving relatively high speeds during continuous locomotion, such as running. In contrast, extremely explosive behaviors, such as jumping, rely predominantly on enhancers that "break the rules" of physiology, including those that circumvent neuromuscular limits. The "gain" achieved is therefore likely to be greater for the latter given the degree to which power is "amplified". However, future quantitative comparisons would help illuminate this topic.

Our survey raises new questions. First, how, and under which conditions, did elastic storage mechanisms evolve? How many independent origins of power amplification have occurred among vertebrates and invertebrates? While our survey indicates many independent evolutionary origins of enhancers, in most cases the morphological and behavioral mechanisms are very different, and it would interesting to determine if there exist similar morphological and behavioral pathways in very different kinds of animals. A promising tool for exploring the evolution of elastic energy storage is evolutionary robotic analyses, which utilizes genetic algorithm optimization to search for the solutions (Sellers et al. 2010). In this case, evolutionary robotic techniques could be used to build musculoskeletal models to explore the biomechanics of extinct animals. A similar idea would be to employ physics-based animation to explore the "enhancer space" of animals. These models could explore the theoretical range of morphologies that could exist and how much performance would decline with modification or removal of the enhancers. A final question is what kinds of limits exist on the enhancement of different kinds of performance. For example, do limits exist for enhancing maximum sprint speed, and if so, which kinds of morphological or functional factors are the key constraints?

Enhancers are often related to a specific ecological task. The rapid locomotion of small insects such as froghoppers is largely driven by the need for these animals to escape predators rapidly, as their small size places severe constraints on their ability to jump long distances. The ability of some sharks to swim rapidly in cold water has likely occurred because of an ecological opportunity to capture prey that was available in such waters, such as marine mammals. However, there remain many areas for future research. First, what is the nature of the costs that could occur as a consequence of evolution of performance enhancers? For example, storing energy in a tendon prior to jumping can maximize power output. However, this likely compromises the control and ability to fine-tune the position of the body. However, this lack of control might (or not) influence these animals in a more natural environment has not been studied. Another example comes from energetic costs to the enhanced performance by elevated plasma T in lizards. Exogenous testosterone can result in diminished growth, smaller fat-body masses (Klukowski et al. 1998), and a weakened immune system, among other effects (Hau 2007). There is often substantial variation in T levels among individual animals, yet how this variation might enhance or constrain locomotion, or result in other costs, has not been well studied, especially in a more ecological context. Second, while the nature of some kinds of performance enhancers is well understood for some smaller animals (e.g., froghoppers), the nature of enhancers for larger animals such as large mammals or other animals remains more opaque. While elastic elements clearly play a role in enhancing locomotion in some animals (Roberts 2002), the complex enhancement of frog muscles suggests

that other similarly complex mechanisms may be at play in other animals, and deserve to be studied. These and other questions, thus, provide a rich template for future researchers.

Finally, genetics undoubtedly plays a fundamental role in performance. It was noted recently that 'performance enhancing' genes have been identified in almost all male Olympic sprinters and power athletes (Enriquez and Gullans 2012). These 'power genes' likely dictate how well athletes can perform if they maximize their training. This type of enhancement falls within the limits of neuromuscular physiology, but may account for variation between individuals. This is an exciting area for future work, especially from a comparative perspective.

Performance enhancers as key innovations

One of the most controversial ideas in evolutionary biology is that of key innovations (e.g., Bond and Opell 1998; Hodges and Arnold 1995; Alfaro et al. 2009) which are morphological or behavioral traits that provide some key attribute or advantage, and which allows a lineage to exploit novel habitats, often leading to increased diversification. Whether any of the enhancers we have discussed represent key innovations has not been addressed, and stands as an open question. It is possible that several enhancers not only increase performance but also open up new habitats or predatory options (or at least made them more accessible). Subsequent diversification, because of the enhancer, is therefore a possibility and suggests that enhancers might have played a key role in the evolution of movement (Fig. 3). For a performance enhancer to be considered as a key innovation, it should be synapomorphic within the group of interest, provide a functional advantage over the ancestral state, and result in an expansion in the

"adaptive zone" of the group (Bond and Opell 1998). This should result in an increase in species diversity (increase in the number of taxa within the clade). Future research could assess if, and to what degree, performance enhancers are key innovations. If this is the case, performance enhancers likely play a significant role in evolution.

Indeed, recent work by Spagna et al. (2008) revealed that trap-jaw ants of the genus *Odontomachus* exhibit substantial variation in their ability to generate force with their jaws (for predation and locomotion), and this might be due to recent selection pressures rather than from deep phylogenetic signal. Future work on a range of taxa addressing these possibilities in a phylogenetic framework will be especially useful. Through the course of evolution, it is also possible that certain aspects of an enhancer are more labile than others. Recent work by Claverie et al. (2011) examined the evolution of the predatory appendages of a mantis shrimp, *Gonodactylaceus falcatus*, and found that the functional units (muscle, spring, and hammer) belong to different developmental modules and thereby permit independent evolution of each part. Whether this is a common feature of enhancers remains a key question.

Although our understanding of performance enhancers is growing, especially with respect to the mechanisms of enhancement, we know little about the evolution of enhancers and what role they play in diversification. If we use the mantis shrimp as an example, it is likely that performance enhancers have undergone complex evolutionary changes that have significant impacts on the ability to enhance movements. An integrative approach is necessary and should be taken in future research.
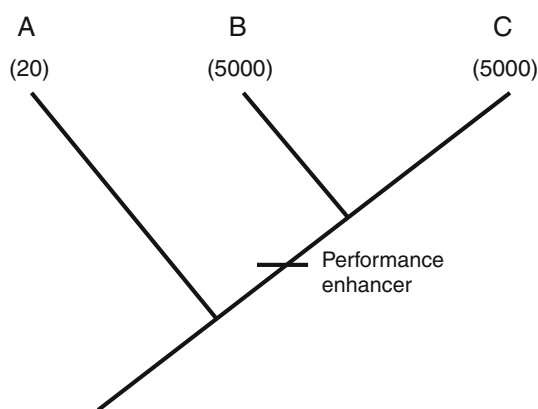
Fig. 3 Performance enhancers as key innovations. In this hypothetical scenario, the evolution of a performance enhancer resulted in the diversification of clades *B* and *C* (relative to *A*). The number of taxa within each clade is in *parentheses*

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