

COMMENTARY

Thermal robustness of biomechanical processes

Jeffrey P. Olberding^{1,*} and Stephen M. Deban²

ABSTRACT

Temperature influences many physiological processes that govern life as a result of the thermal sensitivity of chemical reactions. The repeated evolution of endothermy and widespread behavioral thermoregulation in animals highlight the importance of elevating tissue temperature to increase the rate of chemical processes. Yet, movement performance that is robust to changes in body temperature has been observed in numerous species. This thermally robust performance appears exceptional in light of the well-documented effects of temperature on muscle contractile properties, including shortening velocity, force, power and work. Here, we propose that the thermal robustness of movements in which mechanical processes replace or augment chemical processes is a general feature of any organismal system, spanning kingdoms. The use of recoiling elastic structures to power movement in place of direct muscle shortening is one of the most thoroughly studied mechanical processes; using these studies as a basis, we outline an analytical framework for detecting thermal robustness, relying on the comparison of temperature coefficients (Q_{10} values) between chemical and mechanical processes. We then highlight other biomechanical systems in which thermally robust performance that arises from mechanical processes may be identified using this framework. Studying diverse movements in the context of temperature will both reveal mechanisms underlying performance and allow the prediction of changes in performance in response to a changing thermal environment, thus deepening our understanding of the thermal ecology of many organisms.

KEY WORDS: Thermal sensitivity, Performance, Movement, Locomotion, Feeding, Temperature, Muscle

Introduction

Environmental temperature is one of the most important drivers of biological evolution. For example, organismal function can be disrupted by protein denaturation at extremely high temperatures or by freezing at extremely low temperatures. Although spectacular adaptations in some organisms push thermal limits, such as Taq polymerase in thermophiles (Chien et al., 1976) or antifreeze compounds in fish, amphibians and arthropods (DeVries and Wohlschlag, 1969; Duman, 2015), most life must operate within the relatively narrow temperature range (approximately 0–40°C). Within this range, physiological processes that involve chemical reactions proceed at a rate that is directly related to temperature, reducing the performance of many biological functions at lower temperatures. A long history of research has explored the diverse effects of temperature on biological functions and the ways in which organisms are suited to

their thermal environment (Angilletta and Angilletta, 2009; Huey and Stevenson, 1979). Physiological adaptation can shift thermal optima of processes to better suit environmental conditions over long time scales, but cannot remove sensitivity to temperature entirely (Autumn et al., 1994; Hochachka and Somero, 2002; Johnston and Altringham, 1985). Instead, endothermy and behavioral thermoregulation have repeatedly evolved to compensate for the effects of low temperatures on chemical processes by raising reaction temperature. However, the underlying thermal sensitivity of these processes persists when reaction temperature cannot be controlled. Organismal functions that maintain performance regardless of temperature therefore appear exceptional.

Movement in animals is accomplished through the coordinated function of many systems – respiratory, circulatory, sensory, nervous and musculoskeletal – all of which involve temperature-sensitive chemical processes. Gas exchange across respiratory surfaces and through tissue is strongly dependent on temperature for many animals (Mortola and Frappell, 2000). In systems with active pumping, rates of circulation of air, water, blood or hemolymph depend on temperature through thermal effects on muscular pumps (Bennett, 1984), but even passive diffusion relies on Brownian motion and is temperature dependent. Synaptic processes and nerve conduction velocity also decrease at lower temperature, even in cold-specialized species (Abramson et al., 1966; Chatfield and Battista, 1948; Katz and Miledi, 1965a,b; Montgomery and Macdonald, 1990; Rosenberg and Sugimoto, 1925; Weight and Erulkar, 1976). Finally, strong temperature effects on muscle contractile properties are well documented (Bennett, 1984; James, 2013; Olberding and Deban, 2017), even in lineages that have evolved in low-temperature environments (Huey et al., 1989; Wakeling and Johnston, 1998).

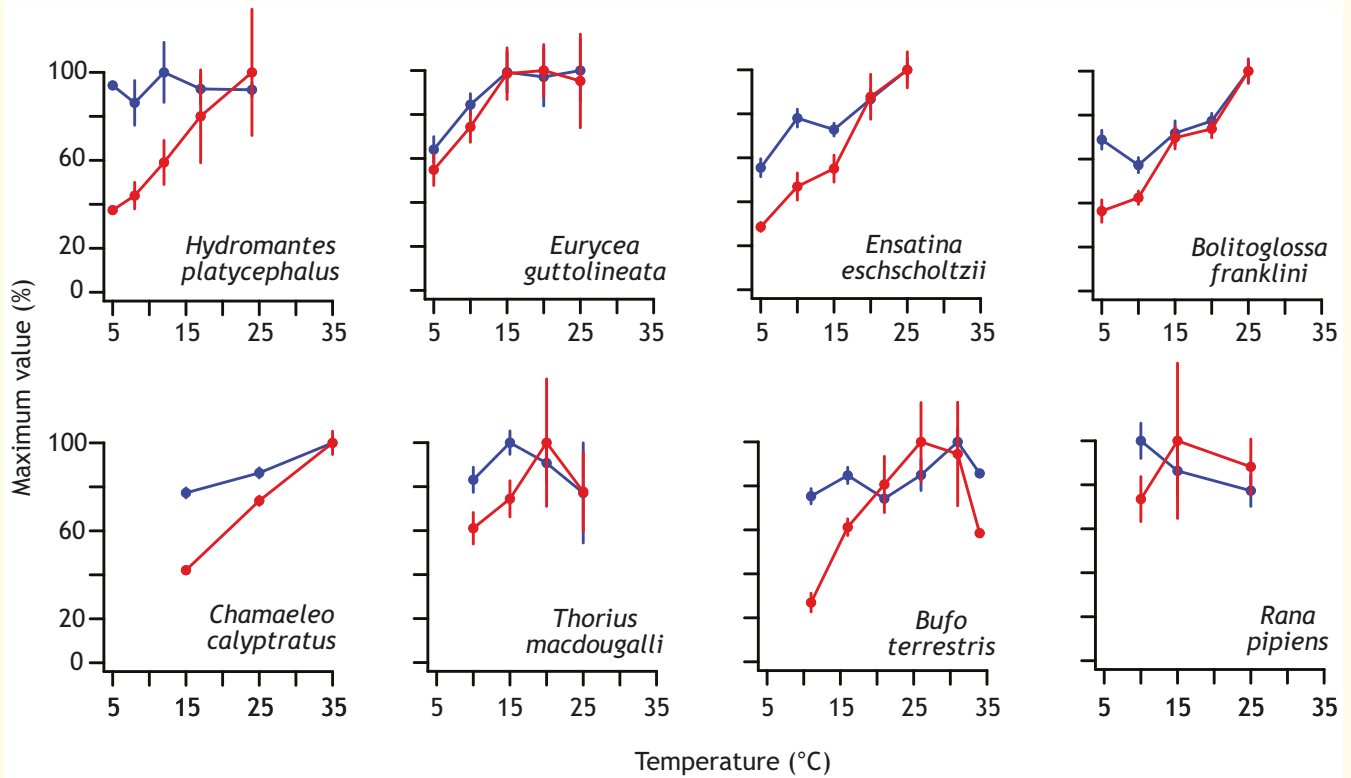
The temperature-dependent function of these physiological processes can limit performance of movements in terms of their rate, responsiveness, efficiency and endurance, and define the thermal ecology of organisms. At lower temperatures, decreased rates of oxygen and nutrient delivery and carbon dioxide and waste elimination can limit endurance in movements that are maintained for long durations (John-Alder and Bennett, 1981; Weinstein and Full, 1994). Additionally, movement efficiency could decrease at lower temperatures if anaerobic respiration is used instead of aerobic respiration, which produces more ATP for a given amount of fuel. The ability to respond to the environment with appropriate movements and behavior (Montgomery and Macdonald, 1990) and the ability to modulate performance during movement through feedback control may be impacted by the reduced ability of sensory cells and neurons to sense, process and respond to external stimuli at colder temperatures (Hodgkin and Katz, 1949). Finally, temperature effects on movement performance in animals have long been linked to the thermal sensitivity of muscle shortening, the source of mechanical work in many movements (e.g. Else and Bennett, 1987; Swoap et al., 1993).

Despite these physiological limitations, movement performance is maintained across temperature ranges from nearly 0 to 30°C in numerous ectotherms (Box 1). This performance is said to be thermally robust and includes both impressively high performance

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Box 1. Evidence for thermal robustness using elastic recoil

Thermally robust performance has been observed in several disparate taxa that are hypothesized to use elastic recoil to power movement. Movement velocity that is thought to be driven by elastic recoil (mean \pm s.e.m., blue) is less sensitive to changes in temperature compared with muscle-powered movements in the same species (red). Ballistic tongue projection in plethodontid salamanders is robust to changing temperatures (Deban et al., 2020). For example, peak tongue projection velocity is independent of a 2–24°C temperature change in *Hydromantes platycephalus* (Deban and Richardson, 2011), is unaffected by temperature from 9 to 24°C in *Eurycea guttolineata* (Anderson et al., 2014) and shows only a minor decrease from 1.73 m s⁻¹ at 25°C to 0.96 m s⁻¹ at 5°C (45% drop) in *Ensatina eschscholtzii* (Deban and Scales, 2016) and from 2.34 m s⁻¹ at 25°C to 1.61 m s⁻¹ at 5°C (32% drop) in *Bolitoglossa franklini* (Scales et al., 2016). In chameleons (*Chamaeleo calypttratus*), tongue projection velocity decreases by only 23% with a 20°C decrease in body temperature (Anderson and Deban, 2010). In toads (*Bufo terrestris*), peak velocity of ballistic mouth opening and tongue projection do not change significantly from 20 to 35°C (Deban and Lappin, 2011), and a similar pattern is seen in frogs (*Rana pipiens*) (Sandusky and Deban, 2012). For *C. calypttratus*, *B. franklini*, *Thorius maddougalli*, *H. platycephalus*, *E. eschscholtzii* and *E. guttolineata*, peak tongue projection velocity (blue) is compared with peak tongue retraction velocity (red). For *B. terrestris* and *R. pipiens*, ballistic mouth opening velocity (blue) is compared with jaw closing velocity (red).

For many of these thermally robust movements, power that exceeds what has been measured from isolated muscle tissue under ideal conditions (300–900 W kg⁻¹ muscle) (Askew et al., 2001; Curtin et al., 2005; Lutz and Rome, 1996; Olberding and Deban, 2017) points to a more powerful actuator of movement, such as a recoiling spring. Thermally robust salamander tongue projection has a muscle mass-specific power output ranging from 1284 to 6765 W kg⁻¹, although salamander tongue projector muscles have contractile properties similar to those of other vertebrate muscles (Deban et al., 2007, 2020; Olberding et al., 2018). Similarly high peak power outputs are seen in chameleon (2900 W kg⁻¹) and toad feeding mechanisms (9600 W kg⁻¹) (Anderson and Deban, 2010; Lappin et al., 2006). For tongue projection in salamanders, chameleons and toads, electromyography recordings reveal muscle activity hundreds of milliseconds prior to any external movement, indicating the stretching of elastic structures (Anderson and Deban, 2012; Anderson et al., 2014; Deban and Dicke, 1999, 2004; Deban and Lappin, 2011; Lappin et al., 2006; Roberts and Marsh, 2003; Scales et al., 2017). Finally, in all of these cases, structures have been identified that could serve as springs and latches (Astley and Roberts, 2012; Bennet-Clark and Lucey, 1967; Deban et al., 1997; de Groot and van Leeuwen, 2004; Scales et al., 2016, 2020).

and relatively mundane performance that can be reproduced reliably under different temperature conditions. This movement performance is not maintained by elevation of body temperature via endothermy or behavioral thermoregulation and there is no evidence of adaptations in the chemical processes underlying muscle shortening to alter the effects of temperature. Instead, these movements are powered by recoiling elastic structures rather than muscle shortening, removing direct influences of some muscle contractile properties by shifting power demands from muscle shortening to elastic recoil (Deban et al., 2007; Longo et al., 2019; Roberts and Azizi, 2011).

Here, we argue that thermally robust performance is not a unique feature of elastic recoil, but is instead a widespread

phenomenon that emerges when a mechanical process replaces or augments a chemical process (Fig. 1). We first define the principle of thermal robustness and describe a general analytical framework for identifying thermally robust performance by comparing temperature effects on whole-system function with those of underlying physiological processes. We then highlight a number of biomechanical systems with diverse functions in which thermal robustness that is conferred by mechanical processes may be revealed when this framework is applied.

What is thermal robustness?

Thermal robustness of performance is distinct from simply producing high performance at challenging temperatures; it is a reduced response

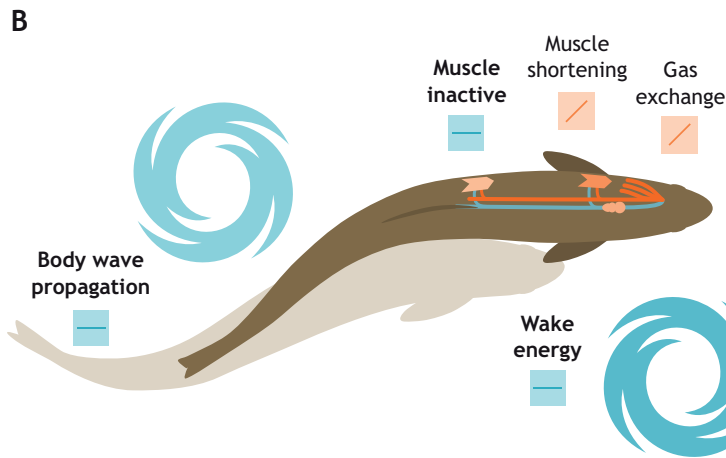
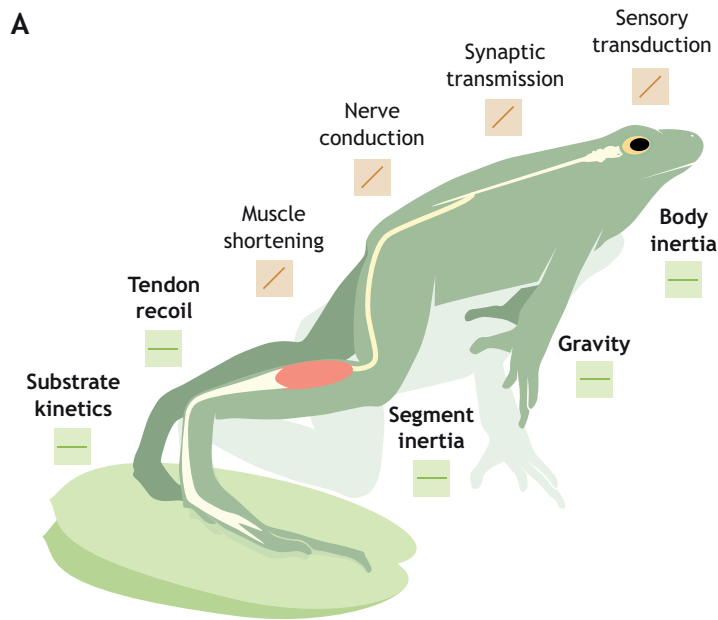


Fig. 1. Thermally robust mechanical processes can replace or augment temperature-sensitive chemical processes. Thermal robustness schemata for the examples of a frog jumping from a compliant substrate (A) and a fish swimming in a Kármán vortex street (B). Chemical processes, such as sensory transduction, synaptic transmission, nerve conduction, gas exchange, circulation and muscle shortening are sensitive to temperature. Mechanical processes, such as inertia and viscoelastic properties of tissues, body parts and the substrate, fluid energy and gravitational acceleration are less thermally sensitive. By storing energy in elastic structures, a jumping frog (A) may temporarily redistribute work done by muscles so performance depends on the temperature-insensitive rate of elastic recoil rather than the temperature-sensitive rate of muscle shortening. A swimming fish (B) can exploit the energy contained in vortices to reduce muscle activity and shift to mechanical processes, such as force transmission by inactive muscle and connective tissue, which may provide thermal robustness to endurance if gas exchange, circulation or metabolism is thermally sensitive. Small graphs depict the approximate thermal dependence of each process (performance versus temperature) with blue/green graphs representing thermally robust processes and red graphs representing relatively strong effects of temperature on the processes.

to changes in temperature (Fig. 2). For example, adding muscle mass or increasing the energy density of muscle could improve the performance of a muscle-driven movement, but not confer thermal robustness (Fig. 2, compare lines A and C). Alternatively, a movement may have thermally robust performance across a range of temperatures, yet still have lower performance compared with another movement at any one temperature (Fig. 2, compare lines B and C). The potential benefit of thermal robustness is the ability to produce consistent output in the face of changing temperatures, but not necessarily elevated performance at all temperatures.

Identifying thermal robustness requires quantifying movement performance across an ecologically relevant range of temperatures. By definition, temperature-independent performance can be identified statistically by finding no significant effects of temperature. However, even when effects of temperature are significant, a movement may still be described as thermally robust if the strength of the temperature effect is less than would be expected if it were driven by chemical processes. In animal movements, this often involves a comparison of temperature effects on movement performance with those on muscle-driven movement (Box 1). However, other physiological processes, such as oxygen delivery or metabolic rate, could be limiting factors expected to determine temperature effects on performance depending on the temporal and spatial complexity of a movement. For organisms

that lack muscle, such as plants, temperature effects on movement performance can be compared with cellular mechanisms of motion, such as active solute transport.

A customary way to represent effects of temperature on a biological process is the temperature coefficient, or Q_{10} . This expresses the factor by which a rate property changes across a 10°C temperature increase, and can be calculated over any temperature increase. A Q_{10} value can be calculated via linear regression of \log_{10} -transformed variables in order to obtain a significance level associated with temperature effects using 10 times the base-10 antilogarithm of the partial regression coefficient (PRC) of the temperature effect on the dynamic variable of interest: $Q_{10} = 10^{(10 \times \text{PRC})}$ (Deban and Richardson, 2011). A biological response to a broad range of temperatures is complex; therefore, it is important to measure responses at a number of different temperatures and calculate Q_{10} values across multiple temperature intervals to reveal the shape of this relationship. Reporting a single Q_{10} value for a wide range of temperatures may conceal this shape (Deban and Lappin, 2011; Deban and Richardson, 2011; Oertli, 1989), which is typically non-linear and has a plateau of performance at medium-high temperatures in muscle-driven movements and other chemical processes (Huey and Kingsolver, 2011).

The use of Q_{10} values to identify thermal robustness relies on the choice of an appropriate comparison to measured performance.

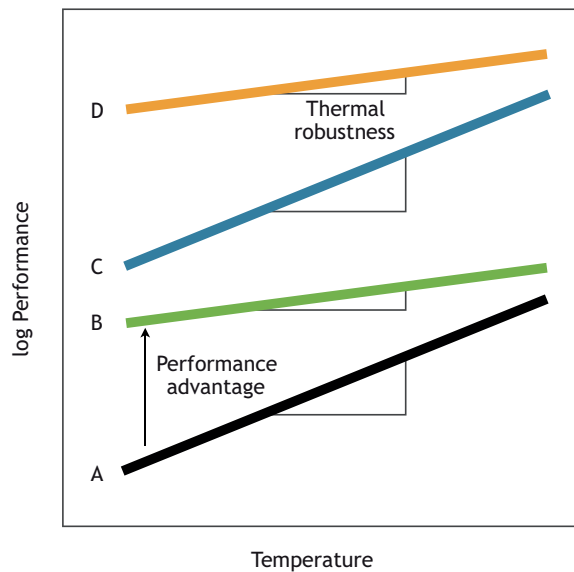


Fig. 2. Thermal robustness is distinct from absolute performance advantage. Compared with a condition (A) that shows both low performance and high thermal sensitivity of that performance, a system may have (B) greater thermal robustness and a modest performance advantage, (C) a large performance advantage but high thermal sensitivity or (D) a dramatic performance advantage with a high degree of thermal robustness. Condition D characterizes many organisms that make use of elastic recoil (Box 1).

To avoid spurious conclusions, comparisons should ideally differ in only the presence or absence of the mechanical process of interest. Therefore, the mechanism under study must be well understood to arrive at the best comparison for experimentally derived Q_{10} values. Predicted temperature effects on movement performance may not simply be effects of temperature on underlying chemical properties, which may be measured under laboratory conditions that do not accurately replicate *in vivo* use. For example, muscle contractile properties are usually quantified under conditions of fixed length (isometric) or constant force (isotonic) during *in vitro* or *in situ* experiments, but muscles rarely experience these simple mechanical conditions *in vivo*. Therefore, temperature effects on *in vitro* muscle contractile properties do not necessarily represent temperature effects on muscle-driven movement performance, and can show different Q_{10} values from movements powered by these muscles *in vivo*.

A useful approach to identify thermally robust performance is to compare performance between systems that differ in the presence of the mechanical process of interest. For example, thermal robustness conferred by elastically powered tongue projection in some plethodontid salamanders is clearly demonstrated through comparisons with closely related species that lack sufficient elastic structures in their tongue apparatus (Deban et al., 2020). Alternatively, thermal robustness can be identified by comparing the Q_{10} values of different phases of movement in the same behavior, such as elastically powered tongue projection versus muscle-powered tongue retraction in chameleons and salamanders (Box 1) (Anderson and Deban, 2010; Deban and Richardson, 2011). When such comparisons are difficult to find, an alternative or complementary approach would be to construct a model of the mechanism (physical, computational or analytical) with underlying physiological parameters modeled with values appropriate for the temperature conditions of interest. Such models can be used to generate predicted temperature effects on movement performance without the presence of a mitigating mechanical process.

It is critical to recognize that comparison of measured Q_{10} values with predictions is most useful when coupled with consideration of the ecological consequences of a change in the performance measure of interest. When measured Q_{10} values are lower than predictions based on chemical processes, yet not thermally independent ($Q_{10}=1$), we would need to understand the relationship between performance and ecology to interpret the functional significance of the temperature effect. For example, relatively low Q_{10} values may not indicate thermally robust performance if the resulting change in performance would still impact fitness in an ecological setting.

Where do we find thermal robustness?

Thermally robust performance is a consequence of any system that replaces a temperature-sensitive chemical process with a mechanical process less sensitive to changes in temperature. This phenomenon has been observed primarily in small ectothermic animals using stored elastic energy to actuate burst acceleratory movements when facing below-optimal temperatures, but the principles of thermal robustness are not exclusive to organisms meeting this description. Numerous organisms rely on mechanical processes to effect movement and any of these have the potential to show movement performance that is robust to changes in temperature in an ecologically beneficial way. These may not be adaptations for thermally robust performance; other possible benefits, such as an absolute performance advantage, simplified control requirements or decreased risk of injury, could conceivably drive the evolutionary elaboration of mechanical processes in movement systems. Nonetheless, thermal robustness may be ecologically important once the mechanism is in place, expanding niche breadth through expanded active temperatures, geographical ranges and access to microhabitat and novel resources. Thermally robust movement could also reduce the need for thermoregulation and its associated costs, such as water loss, high metabolic rate or exposure to predators (Feder, 1983; Huey, 1974).

Although most research has focused on performance that is robust to decreasing temperatures, the same principles may apply to movement performance that is compromised by warmer temperatures. The mechanisms by which lower temperature affects the physiology of movement are clearer than those determining the effects of warmer temperatures. For example, muscle power decreases at lower temperatures because rates of actin–myosin cross-bridge formation in sarcomeres are slower (Wang and Kawai, 2001) and these cross-bridges are less likely to form in a high-force generating state (Bershtitsky and Tsureyan, 2002; Decostre et al., 2005; Piazzesi et al., 2003); however, it is not clear why muscle power may decrease at temperatures above optimal. Performance may be reduced not through a single rate-limiting chemical process at higher temperatures but rather through a mismatch of rates in a network of many temperature-sensitive processes (Vornanen, 2020). Mechanical processes could possibly ameliorate performance decreases by replacing one or more of these temperature-sensitive chemical processes. However, some decreases in performance at warmer temperatures may result from structural changes in tissues, which could also affect mechanical processes.

Thermal robustness is also not limited to small ectotherms. Endothermy may be an important adaptation for reducing the effect of temperature on chemical processes, but many endotherms are in fact regionally heterothermic. For example, circulatory heat exchangers keep blood temperature low in extremities to avoid heat loss to the environment and reduce the metabolic costs of maintaining core body temperature (Midtgard, 1981; Scholander and Schevill, 1955). The extremities of some endotherms match environmental

temperature despite a relatively constant core body temperature (Irving and Krog, 1955; Midtgard, 1981; Rummel et al., 2019; Scholander and Krog, 1957; Scholander and Schevill, 1955). Because these extremities are often the structures interacting with the environment to produce motion, thermally robust mechanisms may be ecologically important even in large endotherms.

Finally, evidence for thermally robust performance is currently focused on measures of peak capacity during burst acceleratory movements, where mechanisms are relatively easy to understand and the thermal sensitivity of all relevant processes can be explored. However, sub-maximal movements and those with more spatial and temporal complexity, like cyclical locomotion, which rely on multiple physiological processes, could still benefit from the principles of thermal robustness. When organisms are not moving at peak capacity, greater exertion could potentially offset negative effects of temperature (e.g. by recruiting a greater proportion of muscle fibers at lower temperatures). For submaximal performance during burst-acceleratory movements, like jumping or striking speed, the ability to increase effort at challenging temperatures could preclude the need for or importance of mechanisms that confer thermal robustness. However, increased exertion at lower temperature would require greater energetic expenditure, which could decrease performance in repeated or sustained performance, like cyclical locomotion. Therefore, mechanical processes that confer thermal robustness may be important even for non-peak activity because of the potential to reduce energy costs incurred by greater effort at challenging temperatures.

Consideration of the influence of temperature on the processes underlying a wide variety of movements may reveal surprising thermal effects on performance. Below, we present some mechanical processes that may confer thermal robustness to biological movements in a wide variety of organisms with many different performance goals.

Elastic recoil

Thermally robust performance is likely to be found in organisms that rely on latch-mediated spring actuation to power movement, other than those described above (Box 1). Elastic recoil bypasses temperature effects on muscle power because energy is loaded before external motion with reduced time restrictions (Deban et al., 2007; de Groot and van Leeuwen, 2004). The power of recoiling biological springs is expected to be relatively unaffected by temperature because the change in mechanical performance of viscoelastic materials is negligible across a biologically relevant range of 0 to 40°C (Alexander, 1966; Denny and Miller, 2006; Gosline, 2018; Rigby et al., 1959), in contrast to the strong effects of temperature on muscle power (Bennett, 1984; James, 2013). For example, frog jumping is a well-studied model for elastically powered movement. Frog hindlimb muscles load energy into their tendons and aponeuroses while motion of the body is prevented by a combination of inertia of the body and poor muscle mechanical advantage (Astley and Roberts, 2012, 2014); therefore, their jump performance may be expected to be relatively robust to changes in temperature (Fig. 1A). However, the prediction of thermally robust performance from latch-mediated spring actuation requires that the function of the latch, preventing motion during spring loading and releasing to mediate spring recoil, is unaffected by temperature. It is also important to note that temperature effects on other muscle properties, including force generation and net mechanical work, may still impact movement performance in these systems (Olberding and Deban, 2017). Nonetheless, muscles that deform elastic elements can, in some cases, do more mechanical work than

when acting directly against an inertial load (Olberding et al., 2019), thus potentially offsetting temperature effects on muscle work (Olberding and Deban, 2017).

Minimal temperature effects on performance have been described in some movements thought to be driven by springs, even if not explicitly labeled as thermal robustness. Jumping fleas load a pad made of the elastic protein resilin using the femoral depressor muscle during the preparatory phase prior to the jump, and allow the pad to recoil against isometric muscle contraction to extend the legs and launch them into the air (Bennet-Clark and Lucey, 1967). As temperature drops, fleas extend the period of loading of elastic structures before the jump, but jumping performance is reported to be undiminished: velocity does not change significantly from 10 to 21.5°C (Bennet-Clark and Lucey, 1967; Rothschild and Schlein, 1975; Rothschild et al., 1972). Flea beetles can jump when cold by virtue of a possible spring mechanism in the hindlimb (Heinrich, 1993). Snow fleas show no effect of temperature on jumping velocity at less than 10°C compared with 21.5°C, and their muscle mass-specific power is estimated to be up to 740 W kg⁻¹, indicating elastic recoil is at work (Burrows, 2011). In vocalizing frogs, temperature has far less influence on call frequency properties than on other call parameters; frequency properties are governed by isometric muscle tension and mass and spring constants of laryngeal structures, none of which have high thermal dependence (Gerhardt and Mudry, 1980; McLister, 2001). Similarly, temperature shows little or no effect on wingbeat frequency during takeoff in beetles; frequency is determined by the resonant properties of the thorax and not directly by muscle shortening velocity (Oertli, 1989). Finally, the velocity of defensive strikes in two rattlesnake species has relatively low Q_{10} values ($Q_{10}=1.19-1.00$ from 15 to 35°C) compared with vertebrate muscle contractile properties (Whitford et al., 2020), and EMG evidence in some vipers suggests the loading of elastic structures prior to striking (Young, 2010).

Other movements hypothesized to be spring actuated have not been studied in the context of temperature, but may yet be revealed as thermally robust. For example, recoiling elastic structures power prey capture and processing in numerous aquatic invertebrates and vertebrates (Longo et al., 2018; Patek et al., 2004; Van Wassenbergh et al., 2008) as well as terrestrial animals (Gibson et al., 2018; Han et al., 2019; Kaji et al., 2018; Patek et al., 2006; Wood, 2020; Wood et al., 2016). Moreover, they enable jumping in several insect species (Burrows, 2003; Sutton and Burrows, 2018) and sound production in some insects (Bennet-Clark and Daws, 1999; Davranoglou et al., 2019).

Elastic recoil is often studied in animals where muscles load energy into springs, but diverse ectothermic organisms, from cnidarians to plants and fungi, use rapid release of energy that was stored slowly in tissues or fluid to fire nematocysts, seeds and spores, respectively, or to capture prey (Berg et al., 2019; de Rooter et al., 2019; Edwards et al., 2005; Hayashi et al., 2010; Holstein and Tardent, 1984; Poppinga et al., 2016; Vincent et al., 2011). In cases where muscle cannot be described as a default motor for comparison, temperature effects on alternative physiological motors can be used to assess thermal robustness. For example, spring actuation is likely more robust to changing temperature in bladderwort prey capture than the molecular pumps used to establish the pressure differentials that store energy during trap loading (Sasago and Sibaoka, 1985).

Mechanisms that recover energy during cyclical movements using springs also likely have thermally robust performance. When springs store and release energy during cyclical movement with high efficiency, muscle may be able to contract nearly isometrically

and do very little work per cycle (Biewener and Roberts, 2000; Blickhan, 1989; Dickinson et al., 2000; Roberts et al., 1997). Temperature effects on muscle force production are relatively low compared with effects on power generation (Olberding and Deban, 2017), so cyclical movements using elastic energy recovery may be more robust to changes in temperature than movements generating muscle power during every cycle. During cyclical running, springs can also allow for more work to be done per cycle by effectively increasing average power (Lichtwark, 2014; Lichtwark and Wilson, 2005). Even when positive work is being done during cyclical movements, any energy that can be recovered from the previous cycle using springs will be robust to changes in temperature compared with work done directly by the muscle, in addition to this energy contributing to higher power per cycle.

Gravity

Movements taking advantage of gravitational potential energy could have thermally robust performance. Falling with gravity is an effective means of accelerating a mass and is used by plants for dispersal and by animals for escape behaviors or prey capture (Cuadrado et al., 2001; Losey and Denno, 1998; Tucker, 1998). Many plants can take advantage of sloped terrain with round fruits or seeds that roll once they contact the ground. Even some animals adopt round body postures that allow them to roll down slopes as a means of predator escape, including some salamanders, frogs and pangolins (García-París and Deban, 1995; McDiarmid and Gorzula, 1989; Tenaza, 1975). Organisms that glide use airfoils to translate downward acceleration due to gravity into horizontal movement as seen in a variety of animals (e.g. Bishop, 2007; McCay, 2001; McGuire and Dudley, 2011; Socha et al., 2005; Yanoviak et al., 2010) and the seeds of many plants (Greene and Johnson, 1993; Lentink et al., 2009; Norberg, 1973). Even insects, birds and bats capable of powered flapping flight use gliding gaits under some circumstances (Blake, 1983; Lindhe-Norberg et al., 2000; Okamoto et al., 2009; Wakeling and Ellington, 1997). For all of these examples, performance may only be affected by temperature via changes in take-off movements and steering adjustments, air density or substrate properties.

Gravitational potential energy is also found in the pendular dynamics of limbed locomotion and some flying gaits that incorporate gliding or bounding phases (Bertram and Chang, 2001; Cavagna et al., 1977; Rayner, 1985; Ward-Smith, 1984). Rates of energy recovery in these systems are low, given that acceleration due to gravity is slow relative to muscle-powered accelerations, so thermal robustness from the recovery of gravitational potential energy may be most prevalent in relatively slow movements and large animals. However, any gait that can decrease the proportion of the stride cycle in which the foot is in contact with the substrate by adding or lengthening a recovery phase (without an associated decrease in active phase duration) may avoid some detrimental effects of temperature by decreasing the required frequency of muscle contraction for a given speed; temperature effects on rate properties of muscle contraction are generally greater than those on force and work production (Olberding and Deban, 2017).

Fluid energy

Movements may be more thermally robust if they take advantage of the inertia of a fluid medium. Organisms that passively rely on fluid motion for movement will be subject only to temperature effects on the density of that fluid (Andersen, 1993; Bell et al., 2005; Scheltema, 1968). Burst and coast swimming may be less thermally sensitive, similar to ambulatory or volant locomotion that takes advantage of gravitational

potential energy (Gleiss et al., 2011). Undulatory swimming shows curiously low Q_{10} values (Marvin and Beaupre, 2003), perhaps because attached vortices may store energy that is recaptured (Gemmell et al., 2015, 2018). Many flocking and schooling animals can ‘wake surf’ (Alexander, 2004; Fish, 1994; Liao, 2007; Newbolt et al., 2019) for a variety of energetic and performance benefits, such as enhanced lift or reduced drag. Similarly, the gait used by fish swimming in the wake of an object in the flow (Kármán gait) (Fig. 1B) is kinematically distinct and shows reduced muscle activity compared with the swimming gait used in open flow (Liao, 2007; Liao et al., 2003).

Force-based behaviors

Force generation in behaviors like clinging or climbing can be accomplished by suction, adhesion or interlocking mechanisms (Ditsche et al., 2014; Labonte et al., 2016), and this performance may be more thermally robust than mechanisms using muscle, such as gripping. However, even behaviors that rely on muscle force generation may be thermally robust compared with muscles that depend more on muscle rate properties. For example, some animals rely on biting rather than fleeing as an anti-predator behavior at low body temperatures, presumably because bite force is determined by muscle force generation which has a relatively low Q_{10} compared with the strong thermal effects on muscle power generation during running (Herrel et al., 2007; Hertz et al., 1982). Muscle rates that rely on physical properties, such as breaking cross-bridge bonds or stretching titin proteins within sarcomeres during eccentric activity (Holt, 2020; Lindstedt and Nishikawa, 2017), should be robust, whereas chemical processes that convert chemical to mechanical energy will be more thermally sensitive. Relatively low effects of temperature on isometric muscle force production (Berman, 1979) may also mean that behaviors that require muscle to act as a cable (Dickinson et al., 2000) are thermally robust.

Neuromechanical control

Mechanisms that bypass or augment the need for active neural control can also confer thermal robustness to movement performance. Performance may be limited not just by temperature effects on processes that transform and deliver energy but also by the ability to effectively sense and respond to external conditions or body position. Sensory, nervous and endocrine systems rely on chemical processes that are sensitive to changes in temperature. Therefore, the ability to coordinate responsive movement in complex environments or rapidly changing conditions may be difficult at lower temperatures even if other processes can still function effectively (Montgomery and Macdonald, 1990). Over longer time scales, increases in neuronal signal travel and processing time with lower temperature can be accommodated by shifting signal initiation earlier. However, shifts in the timing of control signals cannot satisfy the need for responses to real-time changes or perturbations when facing slower signals at lower temperatures. In contrast, responses that rely upon either the physical properties of segments that are accelerated by external forces or the intrinsic mechanical properties of muscle tissue (Daley et al., 2007, 2009; Lindstedt et al., 2002; Nishikawa et al., 2007; Pearson et al., 2006) should be thermally robust, even if the configuration of the system is established by neuromuscular processes. Nervous systems and musculature set up the mechanical system and even if neural control and muscle activation are slowed down in cold conditions, the mechanical system can still respond quickly and be thermally robust.

Conclusions

Despite appearing exceptional, movement performance that is robust to changing temperature can be explained by replacing thermally

sensitive chemical processes with mechanical processes that are less sensitive to temperature. Thermal robustness may be more widespread than previously appreciated. The broadly applicable theoretical and analytical framework developed from the investigation of a handful of extraordinary organisms that we present here can inform further investigations into the thermal biomechanics of organismal movement. Additionally, the study of thermal biomechanics can inform the design and use of bio-inspired machines operating under diverse or challenging temperature conditions, because the principles of thermally robust performance understood from biology also apply to manufactured systems. Even if temperature is not the primary selective pressure shaping a particular biomechanical system, nearly all organisms must reckon with variable temperature. Investigating biomechanics in the context of changing temperature can reveal informative patterns and consequences for performance. Inversely, identifying thermally robust performance can generate testable predictions about the importance of mechanical processes in movement mechanisms. In either case, the thermal ecology of some organisms may be clarified through the mechanistic understanding of temperature effects on movement.

Acknowledgements

We are grateful to the Azizi and Daley lab groups at UC Irvine for feedback on earlier versions of the manuscript. We also thank three anonymous referees for suggestions that improved this work.

Competing interests

The authors declare no competing or financial interests.

Funding

This work was supported by The National Science Foundation (IOS-0842626 and IOS-1350929 to S.M.D.).

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