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Animals prefer leg stiffness values that may reduce the energetic cost of locomotion

ZhuoHua Shen, Justin Seipel*

School of Mechanical Engineering, Purdue University, 585 Purdue Mall, West Lafayette, IN 47906, USA

HIGHLIGHTS

- Here we study a theoretical relationship between the cost of transport of running and leg stiffness.
- The theoretical model predicts that the leg stiffness preferred by human runners minimizes the cost of transport, reaching a value consistent with human experiments.
- The biologically observed range of preferred relative leg stiffness, between 7 and 27, studied over a range of system parameters representing most animal runners, yields a generally lower mechanical cost of transport.
- These results strongly imply that animals, across species, select relative leg stiffness in part to reduce energetic cost.

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ABSTRACT

Despite the neuromechanical complexity and wide diversity of running animals, most run with a center-of-mass motion that is similar to a simple mass bouncing on a spring. Further, when animals' effective leg stiffness is measured and normalized for size and weight, the resulting relative leg stiffness that most animals prefer lies in a narrow range between 7 and 27. Understanding why this nearly universal preference exists could shed light on how whole animal behaviors are organized. Here we show that the biologically preferred values of relative leg stiffness coincide with a theoretical minimal energetic cost of locomotion. This result strongly implies that animals select and regulate leg stiffness in order to reduce the energy required to move, thus providing animals an energetic advantage. This result also helps explain how high level control targets such as energy efficiency might influence overall physiological parameters and the underlying neuromechanics that produce it. Overall, the theory presented here provides an explanation for the existence of a nearly universal preferred leg stiffness. Also, the results of this work are beneficial for understanding the principles underlying human and animal locomotion, as well as for the development of prosthetic, orthotic and robotic devices.

1. Introduction

Running is a fundamental behavior of legged animals arising from complex interactions of neurons, muscles, and the skeletal system (Dickinson et al., 2000; Holmes et al., 2006). Despite the inherent neuromechanical complexity of running, some surprising and nearly universal patterns of behavior have been observed. Legged animals, across many species, exhibit whole-body center-of-mass motion during running that is similar to a pogo-stick (spring-mass) model where the leg is represented as an effective spring (Blickhan and Full, 1993; Full and Koditschek, 1999). See Fig. 1(a)–(b). The effective leg spring stiffness k is empirically determined as the ratio of peak ground reaction force F to peak leg compression Δl (Blickhan and Full, 1993), and expressed as $k := F/\Delta l$. To compare leg stiffness across species, the effective stiffness is nondimensionalized relative to body weight mg and resting leg length l_0, yielding the *relative leg stiffness*:

$$k_{rel} := \frac{F/mg}{\Delta l / l_0} = \frac{k l_0}{mg}. \quad (1)$$

Despite significant differences in size, morphology, and physiology, most animals prefer a relative leg stiffness between 7 and 27 (Blickhan and Full, 1993; Holmes et al., 2006). See Fig. 1(c). Why does this nearly universal pattern exist?

In related studies, it was discovered that humans actively change the overall properties of the leg to accommodate for varying terrain stiffness (Ferris et al., 1998; Bishop et al., 2006), thus maintaining an effective leg stiffness (a combination of leg and terrain stiffness in

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* Corresponding author. Tel.: +1 609 647 7972 (mobile).
E-mail address: jseipel@purdue.edu (J. Seipel).

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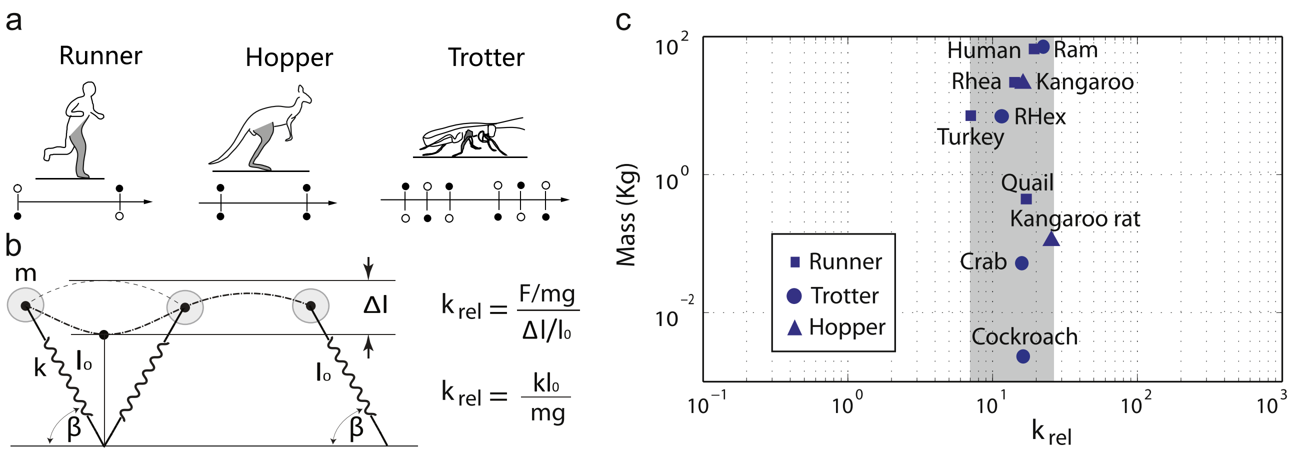

Fig. 1. Spring mass running and animal relative stiffness. (a) Many animals produce similar whole body motion and ground reaction forces similar to a pogo-stick. (b) A pogo-stick or Spring-Loaded Inverted Pendulum (SLIP) model (Schwind, 1988) is shown, where a mass atop a springy leg generates ground reaction forces similar to those found for animals during stance. In the SLIP model, the foot lifts off when the normal ground reaction force reaches zero and during flight resets to a landing angle β until the next touchdown, when the foot reaches ground. The spring leg in the model represents the effective stiffness of an animal's leg. The effective stiffness is nondimensionalized by body weight and leg length to yield a relative stiffness. (c) The relative leg stiffness of different animals was found experimentally. The shaded region stands for the *biologically preferred region* of relative leg stiffness. For multi-legged runners, the relative leg stiffness represents the collective effect of all legs sharing the same stance phase.

these cases) near a constant level, with an effective dimensionless relative stiffness in the same range preferred by other legged animals. However, it is not known why maintaining an effective relative leg stiffness between 7 and 27 is beneficial.

Energetic cost of transport may be one reason for animals to exhibit preferred relative leg stiffness. It has been demonstrated that animals generally utilize energy efficiently when undergoing steady sustained locomotion (Bejan, 2006). For flying and swimming, animals prefer Strouhal numbers that have been associated with higher energy efficiency (Taylor et al., 2003). Humans and other animals also tend to choose a walking speed that can minimize energy expenditure (Hoyt and Taylor, 1981; Hoyt et al., 2000; Alexander, 2002; Ralston, 1958). Further, the adjustment of kinematic gait determinants such as step length, frequency and step width in humans and other animals is associated with reduced energetic cost (Bertram and Ruina, 2001; Donelan et al., 2001; Kuo, 2001; Kuo et al., 2005; Alexander, 1989; Srinivasan and Ruina, 2005).

Could the preferred relative leg stiffness exhibited and regulated by animals exist in order to reduce the energetic cost of legged locomotion? If so, this would directly connect a high level goal such as energy efficiency with the regulation of a whole limb physiological property, leg stiffness. Given that the preferred leg stiffness is known to be actively regulated, we could then understand better how high level targets such as energy efficiency directly relate to the physiology and control of the neuro-musculo-skeletal system of animals. Knowledge of why and how leg stiffness is regulated during locomotion could also enable advancements for a range of applications including medical treatment of locomotion, orthoses, prostheses, legged robots, and wearable technology.

2. Methods

Our *objective* is to determine the relationship between relative leg stiffness and the energetic cost of motion. Our *overall approach* is to use a physics-based model of legged locomotion to calculate the minimum attainable mechanical cost of transport over a range of relative stiffness values from 1 to 100.

It is known that animals actively maintain overall effective leg stiffness (Bishop et al., 2006; Ferris et al., 1998) during locomotion. Therefore, it is not trivial to independently vary effective leg stiffness in living animals, and this currently prohibits a study of this scope from being conducted experimentally. A physics-based mathematical model and simulation approach allows for direct and accurate control of the relative leg stiffness value during simulation.

We therefore construct a physics-based mathematical model of locomotion that depends on the relative leg stiffness and is capable of predicting a mechanical cost of transport, which can be directly compared with experimentally calculated values of the mechanical cost of transport. We developed a locomotion model based upon the canonical Spring-Loaded Inverted Pendulum (SLIP) model (Schwind, 1988; Seyfarth et al., 2002; Ghigliazza et al., 2003). Previous research about SLIP has shown that there exists a certain relationship between relative stiffness and leg landing angle for periodic solutions (Seyfarth et al., 2002). However, SLIP is energy conserving and cannot predict net energetic cost of locomotion. We therefore extended it to include a mathematically simple actuation and damping so that energetic cost predictions can be made. The governing equations of the model are derived and nondimensionalized to simplify analysis and comparison across many species of legged animals.

2.1. The actuated spring-mass model

As shown in Fig. 2, an established physics-based model of locomotion is used for this study, based upon the canonical Spring-Loaded-Inverted-Pendulum model (Shen and Seipel, 2012). It includes actuation which is capable of representing the combined effects of both hip and ankle torque during locomotion, and the effective action of the knee is represented as a spring along the leg in order to agree with the established spring-mass modeling framework that has been used to analyze and compare experimental data collected from species across the animal kingdom. The governing equations of the actuated SLIP model in terms of center-of-mass position x and y are described as

$$m\ddot{x} = -F_l \cos\phi + F_\tau \sin\phi, \tag{2}$$

$$m\ddot{y} = F_l \sin\phi + F_\tau \cos\phi - mg. \tag{3}$$

where F_l and F_τ denote the force acting on the center-of-mass along and perpendicular to the leg, while ϕ is the leg angle measured from the ground to the leg in a clockwise direction. The magnitude of F_l is given by $F_l = k(l_0 - l) - cl^{-1}[(x - x_f)\dot{x} + y\dot{y}]$. k,