

# There is no trade-off between speed and force in a dynamic lever system

Matthew J. McHenry

*Biol. Lett.* 2011 **7**, 384-386 first published online 8 December 2010  
doi: 10.1098/rsbl.2010.1029

---

## References

**This article cites 7 articles, 1 of which can be accessed free**  
<http://rsbl.royalsocietypublishing.org/content/7/3/384.full.html#ref-list-1>

**Article cited in:**  
<http://rsbl.royalsocietypublishing.org/content/7/3/384.full.html#related-urls>

## Subject collections

Articles on similar topics can be found in the following collections

[biomechanics](#) (41 articles)

## Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

# There is no trade-off between speed and force in a dynamic lever system

Matthew J. McHenry\*

Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697, USA

\*mmchenry@uci.edu

**Lever systems within a skeleton transmit force with a capacity determined by the mechanical advantage,  $A$ .  $A$  is the distance from input force to a joint, divided by the distance from the joint to the output force. A lever with a relatively high  $A$  in static equilibrium has a great capacity to generate force but moves a load over a small distance. Therefore, the geometry of a skeletal lever presents a trade-off between force and speed under quasi-static conditions. The present study considers skeletal dynamics that do not assume static equilibrium by modelling kicking by a locust leg, which is powered by stored elastic energy. This model predicts that the output force of this lever is proportional to  $A$ , but its maximum speed is independent of  $A$ . Therefore, no trade-off between force and velocity exists in a lever system with spring-mass dynamics. This demonstrates that the motion of a skeleton depends on the major forces that govern its dynamics and cannot be inferred from skeletal geometry alone.**

**Keywords:** functional morphology; biomechanics; skeleton; locomotion

## 1. INTRODUCTION

The geometry of a skeleton affects an animal's ability to generate force and move quickly [1]. The mechanical advantage ( $A$ ) measures the leverage about a joint and, therefore, provides an index of biomechanical performance.  $A$  is the distance from an input force to the joint, divided by the distance from the joint to an output force (figure 1*a*). Under static equilibrium, the force output by the lever is equal to the product of input force and  $A$ . The output velocity is equal to the input velocity, divided by  $A$  (figure 1*b*). Therefore,  $A$  indicates whether a skeleton is endowed with the capacity for high force or rapid speed under quasi-static conditions [1–3].

It is less clear if there exists a trade-off between force and velocity under dynamic conditions. For example, the resistance generated by a mass at the output end of a lever depends on the rate at which it is accelerated. If the input force is constant, a low- $A$  lever will accelerate more slowly than a high- $A$  lever because of its relatively poor leverage. In contrast to the quasi-static case, this dynamic condition suggests that levers with relatively high  $A$  both generate more force and achieve high speed more quickly.

The present study considers the relationship between the velocity and  $A$  in a dynamic lever system. In

particular, I have modelled kicking by the metathoracic leg of the locust, which is powered by stored elastic energy and resisted primarily by the mass of the leg [4]. Unlike a muscle, the force and energy generated by an elastic system are independent of the rate of contraction. This relative simplicity allows for a focused consideration of the effects of skeletal geometry on biomechanical performance. Furthermore, this classic system has a morphology, mechanical properties and kinematics that have been well-characterized [5–7], which provides a basis for model verification.

## 2. MATERIAL AND METHODS

The kick of a locust leg was mathematically modelled by considering the torque generated at the joint between the femur and tibia (figure 1*c*) using previously measured parameter values [5–7]. This torque is generated by a spring force ( $F_{\text{spring}}$ ) created by elastic structures within the leg:

$$F_{\text{spring}} = kL, \quad (2.1)$$

where  $k$  is spring stiffness and  $L$  is the distance the spring has been stretched beyond its resting length. The component of this force normal to the lever ( $F_{\text{spring}} \sin \theta$ , where  $\theta$  is the leg angle) creates torque that depends on the distance between force application and the joint ( $l_{\text{in}}$ ). This torque drives acceleration of the leg mass, as determined by the governing equation:

$$I\ddot{\theta} = l_{\text{in}}F_{\text{spring}} \sin \theta, \quad (2.2)$$

where  $I$  is the leg moment of inertia ( $I = 6.3 \text{ g mm}^2$ , modelled as a cylinder with the size and mass of the tibia and tarsus,  $m = 21 \text{ mg}$ ) and  $\ddot{\theta}$  is the acceleration of rotation by the tibia. Although this equation may be solved analytically for small deflections, I found it necessary to use a numerical solver for the large excursions achieved during a kick. Simulations were performed with an explicit fourth-order Runge–Kutta method [8] in MATLAB (v. 2009a, Mathworks, Natick, MA, USA) to find the position and velocity ( $\dot{\theta}$ ) of leg angle with the following initial conditions:  $\theta_0 = 6^\circ$ ,  $\dot{\theta}_0 = 0^\circ \text{ s}^{-1}$ . These kinematics were tested against previous measurements [6] and provided the basis for energetic calculations. The elastic energy of the leg spring ( $E_{\text{elastic}}$ ) and the kinetic energy ( $E_{\text{kinetic}}$ ) of the leg were calculated as follows:

$$E_{\text{elastic}} = \frac{1}{2}kL^2 \quad (2.3)$$

and

$$E_{\text{kinetic}} = \frac{1}{2}I\dot{\theta}^2. \quad (2.4)$$

The effect of  $A$  on leg kinematics was considered by a series of simulations.  $A$  was defined by treating the moment of inertia as a point mass at a fixed distance ( $l_{\text{out}}$ ) from the joint:

$$l_{\text{out}} = \sqrt{\frac{I}{m}}. \quad (2.5)$$

The acceleration at this point ( $\dot{v} = l_{\text{out}}\ddot{\theta}$ ) is proportional to mechanical advantage ( $A = l_{\text{in}}/l_{\text{out}}$ ), as shown by an alternative form of the governing equation (2):

$$\dot{v} = \frac{k}{m}AL \sin \theta. \quad (2.6)$$

$A$  was varied between simulations by individually altering  $l_{\text{out}}$  ( $11.7 < l_{\text{out}} < 50.7$ , with  $l_{\text{in}} = 0.76 \text{ mm}$ ) and  $l_{\text{in}}$  ( $0.87 \text{ mm} < l_{\text{in}} < 1.73 \text{ mm}$ , with  $l_{\text{out}} = 17.3 \text{ mm}$ ) at regular intervals. For each simulation, the maximum velocity of the point mass ( $v_{\text{max}}$ ) and the time to reach this maximum ( $\lambda$ ) were recorded.

## 3. RESULTS

The model predicts that the velocity of the leg increases as a sigmoid-shaped function of time (figure 2*a*), as the elastic energy of the leg spring is transferred into the kinetic energy of the tibia and tarsus (figure 2*b*). The model predicts  $v_{\text{max}} = 59.3^\circ \text{ m s}^{-1}$  (achieved within 6.7 ms, where  $L_0 = 1.5 \text{ mm}$ ,  $k = 0.3 \text{ N mm}^{-1}$ ); this is similar to previous

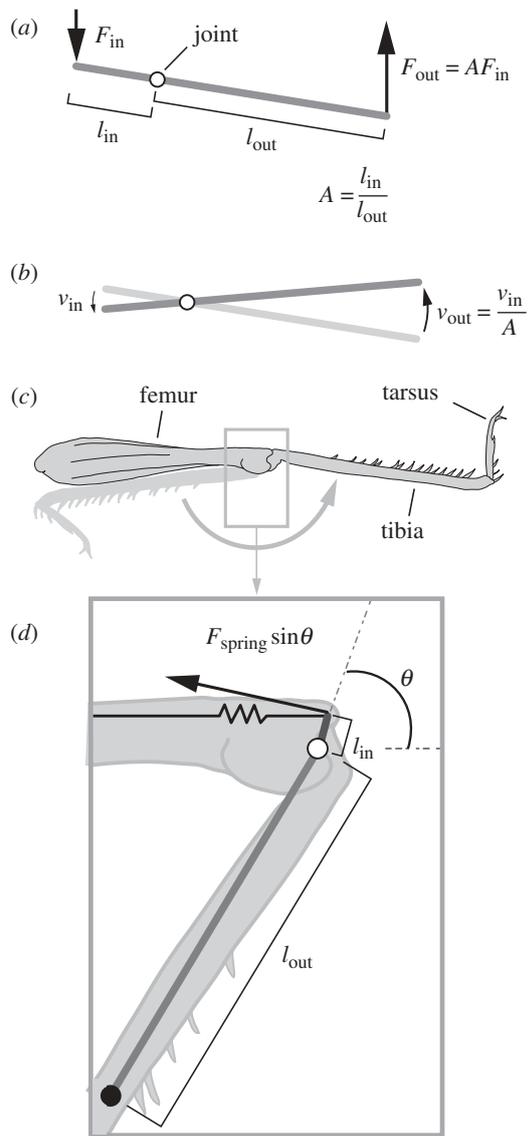


Figure 1. Models of lever systems. (a) Under static equilibrium, the output force ( $F_{\text{out}}$ ) is proportional to the mechanical advantage ( $A$ ), but (b) the output velocity ( $v_{\text{out}}$ ) is inversely proportional to  $A$ , assuming a fixed input velocity ( $v_{\text{in}}$ ). (c) The metathoracic leg of a locust can rapidly kick owing to a lever powered by stored elastic energy. (d) In a dynamic model of this kick, the normal component of force generated by the leg spring ( $F_{\text{spring}} \sin \theta$ ) accelerates the mass of the leg, which is reflected in change in leg angle ( $\theta$ ) over time.

measurements (approx.  $55^\circ \text{ m s}^{-1}$  in approx. 6 ms; [6]). The ratio of maximum output force ( $F_{\text{out,max}}$ ) to maximum input force ( $F_{\text{in,max}}$ ) was found to be equivalent to  $A$  (figure 2c). The maximum speed was independent of  $A$  and exactly predicted by equating the maximum kinetic energy to the maximum elastic energy (equations (2.3) and (2.4), where  $v = l_{\text{out}} \dot{\theta}$ ):

$$v_{\text{max}} = \sqrt{\frac{k}{m}} L_0. \quad (3.1)$$

The time to reach maximum velocity was inversely proportional to  $A$  in simulations where  $l_{\text{out}}$  was varied, but scaled with  $A$  to the power of  $-0.74$  when altering  $l_{\text{in}}$  (figure 2d).

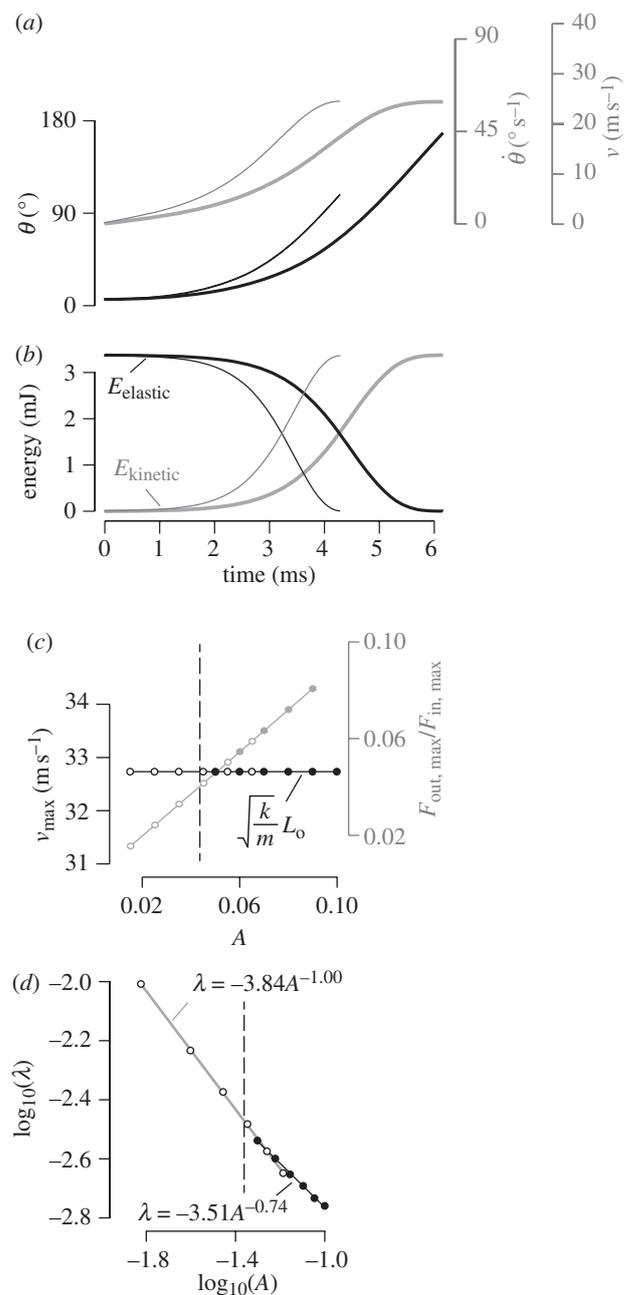


Figure 2. Simulated kinematics of kicking in the locust leg. (a–b) Predicted kinematics and energetics for simulations of a locust (where  $A = 0.044$ , thick lines) and with 50% greater  $A$  ( $A = 0.066$ , thin lines). In these simulations, (a) change in leg angle ( $\theta$ , black lines) and velocity (rotation:  $\dot{\theta}$  and translation:  $v$ , grey lines) is created by (b) the conversion of elastic energy ( $E_{\text{elastic}}$ , black lines) into kinetic energy ( $E_{\text{kinetic}}$ , grey lines). (c,d)  $A$  was varied around the value for a locust (dashed line) by altering  $l_{\text{out}}$  (open circles) and  $l_{\text{in}}$  (filled circles). (c) The maximum speed ( $v_{\text{max}}$ ) of a kick may be predicted (horizontal line, equation (3.1)) and does not vary with  $A$ . The ratio of maximum output to maximum input force (grey symbols) is equal to  $A$  (grey line). (d) Log-transformed values for the time ( $\lambda$ ) to  $v_{\text{max}}$  and  $A$  reveals the scaling relationships between these variables.

#### 4. DISCUSSION

The present model offers an interpretation of skeletal geometry, which is a contrast with the current theory. In the kicking of a locust leg, a large value of  $A$  produces greater force and achieves high speed more

quickly than a lever with a smaller  $A$  (equation (2.6), figure 2*c–d*). Furthermore,  $A$  does not affect the maximum speed of a kick, which may be predicted solely by the amount of stored elastic energy and the mass of the system (equation (3.1), figure 2*c*). Therefore, the geometry of a lever system with spring-mass dynamics does not present a trade-off between force and velocity. This finding is different from the predictions of the current theory (figure 1*a,b*) because the present model does not assume forces that operate in static equilibrium (as in [1,3]).

The present study is limited in its ability to offer a general model of skeletal dynamics. The locust leg model assumes conservation of energy, which is appropriate for a kicking locust leg because its mass provides the major source of resistance to motion, with little loss of energy [5,6]. However, this assumption would be violated in systems where significant energy is imparted to the surrounding environment or lost to internal dampening. Furthermore, the elastic energy storage that powers the motion of a locust leg operates differently from a muscle. A muscle, the more common source of mechanical power among animals, moves more slowly when encountering greater load [9]. Therefore, a nonlinear force–velocity trade-off is possible in muscle-powered levers. The locust leg does not include these dynamics and, therefore, does not model the relationship between  $A$  and speed for many muscle-powered systems.

Although it does not offer a general model of skeletal dynamics, the locust leg does illustrate some limitations of current theory. A force–velocity trade-off is predicted when the input velocity may be assumed to encounter mechanical resistance that is independent of the lever's motion (figure 1*b*). This quasi-static assumption is violated in the locust leg because the inertia of the leg creates resistance that depends on leg acceleration. This assumption is also

violated for swimming or flying animals, where fluid dynamic resistance varies with the speed, or the square of speed, of an appendage. Therefore, the relationship between the mechanical advantage of a lever system and its motion depends on the nature of mechanical resistance and the capacity of the muscle or spring that powers the system to overcome this resistance. Therefore, skeletal geometry provides a necessary, but insufficient, means to characterize the dynamic performance of a lever system.

This study evolved from conversations with S. Patek, M. Westneat, J. Strother and A. Summers, did not require institutional animal care approval, and was supported by the NSF (IOS-0952344).

- 1 Gregory, W. K. 1912 Notes on the principles of quadrupedal locomotion. *Ann. N. Y. Acad. Sci.* **22**, 267–326. (doi:10.1111/j.1749-6632.1912.tb55164.x)
- 2 Hildebrand, M. & Goslow, G. E. 2001 *Analysis of vertebrate structure*. New York, NY: John Wiley & Sons.
- 3 Maynard Smith, J. & Savage, R. J. G. 1956 Some locomotory adaptations in mammals. *J. Linn. Soc. Lond. Zool.* **42**, 603–622. (doi:10.1111/j.1096-3642.1956.tb02220.x)
- 4 Brown, R. H. J. 1967 Mechanism of locust jumping. *Nature* **214**, 939. (doi:10.1038/214939a0)
- 5 Bennet-Clark, H. 1975 Energetics of the jump of the locust *Schistocerca gregaria*. *J. Exp. Biol.* **63**, 53–83.
- 6 Burrows, M. & Morris, G. 2001 The kinematics and neural control of high-speed kicking movements in the locust. *J. Exp. Biol.* **204**, 3471–3481.
- 7 Heitler, W. 1974 The locust jump—specializations of the metathoracic femoral–tibial joint. *J. Comp. Physiol. A* **89**, 93–104. (doi:10.1007/BF00696166)
- 8 Dormand, J. R. & Prince, P. J. 1980 A family of embedded Runge–Kutta formulae. *J. Comp. Appl. Math.* **6**, 19–26. (doi:10.1016/0771-050X(80)90013-3)
- 9 Aidley, D. J. 1978 *The physiology of excitable cells*. New York, NY: Cambridge University Press.