Invited reply

A force–speed trade-off is not absolute

In the pages of *Biology Letters*, McHenry [1] recently described a mathematical model of the biomechanics of a locust leg as it kicks. The author concluded that this lever system exhibits no trade-off between its abilities to generate force and to move quickly. This interpretation was challenged by Arnold *et al.* [2], who asserted that a force–speed trade-off exists in all rigid lever systems, including a locust leg. Here we distinguish the arguments behind these two diametrically opposed interpretations.

The lever systems within a skeleton transmit force like the gears on a bicycle. Most bikes have high and low gears that are affixed to the pedals by a crank arm. When starting from a standstill, a cyclist will get the bike moving by standing up and applying their full body weight to a pedal. The low gear is the smart choice in this situation because it offers a superior mechanical advantage to accelerate the mass of the bike and the rider. Similarly, a higher mechanical advantage in a skeleton will move the mass of a limb with greater acceleration. This principle is well articulated by Arnold *et al.* and not challenged by McHenry. Therefore, the ‘force’ component of the debated ‘force–speed trade-off’ is not in dispute.

Speed is the point on which these authors disagree. The high gear on a bike offers a low mechanical advantage, but is the better choice for cruising at high speed. This is because its ratio of wheel speed to pedal speed is higher than that of the low gear. This ratio, a measure of relative speed, is equivalent to the inverse of mechanical advantage for both bike gears and lever systems. Therefore, it is true that there is always a trade-off between force and relative speed. This is the argument offered by Arnold *et al.* However, McHenry’s analysis focused on the maximum absolute speed of a lever system. This speed was shown to be unaffected by differences in mechanical advantage among simulations where the system was driven by an equivalent amount of stored elastic energy.

This result demonstrates that a trade-off between force and absolute speed is not universal. Only if an actuator (muscle or biological spring) can provide a fixed rate of shortening, can the speed output decrease with an increase in mechanical advantage. However, muscles and springs generally do not apply a speed that can be arbitrarily set. Instead, shortening speed is determined both by the actuator’s

ability to generate force and the load which it encounters. A fixed rate of shortening is only possible under special cases, such as in a system that may be treated as massless, or where a viscous load is independent of differences in geometry. Therefore, a trade-off between force and absolute speed is not a general law.

This result is not disputed by Arnold *et al.* and is a simple consequence of conservation of energy, yet it is a big revelation to many biologists. This is because of a long-standing [3] and wide-spread practice (e.g. [4–6]) of inferring how fast a lever system can move (i.e. absolute speed) from a measurement of its mechanical advantage. As stated by Smith & Savage [7], high mechanical advantage ‘is only an advantage for strong but slow movements’, whereas low mechanical advantage ‘is an advantage for fast movements’. This interpretation pervades an enormous body of research that uses mechanical advantage as a metric of a species’ capacity to move quickly. The McHenry model challenges this interpretation.

Inferring speed from animal skeletons is like predicting the winner of a bike race from the gears chosen by the cyclists. In reality, the winner of a race will be determined by one’s ability to handle the loads imposed by the terrain, the weight of the bike, and the wind. Depending on the nature of these dynamics, the winner could be either the rider using the highest or the lowest gears. Similarly, one cannot predict the faster species from measurements of mechanical advantage alone. A predictive understanding of speed also requires a consideration of the dynamics of a lever’s actuators and sources of resistance.

The geometry of a skeleton does dictate its range of displacement. Actuators have a limited range of shortening and this displacement is amplified by the motion of the appendage. A high displacement is one benefit for a species that possesses a low mechanical advantage. The McHenry study is consistent with this view—locust legs modelled with lower mechanical advantage achieved the same maximum speed, but they achieve this with a longer displacement over more time.

This debate is more than a minor quibble about semantics. While the McHenry study proposed no new physics, it conveys an important message to the biomechanics field: speed cannot be inferred from geometry alone. This is a message, which agrees with the Arnold *et al.*’s commentary, that challenges an assumption implicit in a century of literature.

Matthew McHenry^{1,*} and Adam Summers²

¹*Ecology and Evolutionary Biology, UC Irvine, Irvine, CA, USA*

²*Friday Harbor Laboratories, University of Washington, Friday Harbor, WA, USA*

*mmchenry@uci.edu

- McHenry, M. J. 2011 There is no trade-off between speed and force in a dynamic lever system. *Biol. Lett.* 7, 384–386. (doi:10.1098/rsbl.2010.1029)
- Arnold, A. S., Richards, C. T., Ros, I. G. & Biewener, A. A. 2011 There is always a trade-off between speed and force in a lever system: comment on McHenry (2010). *Biol. Lett.* 7, 878–879. (doi:10.1098/rsbl.2011.0431)

- 3 Gregory, W. K. 1912 Notes on the principles of quadrupedal locomotion. *Ann. NY Acad. Sci.* **22**, 267–326. (doi:10.1111/j.1749-6632.1912.tb55164.x)
- 4 Westneat, M. 1994 Transmission of force and velocity in the feeding mechanisms of labrid fishes (Teleostei, Perciformes). *Zoomorphology* **114**, 103–118. (doi:10.1007/BF00396643)
- 5 Kier, W. M. & Smith, K. K. 1985 Tongues, tentacles and trunks: the biomechanics of movement in muscular-hydrostats. *Zool. J. Linn. Soc.* **83**, 307–324. (doi:10.1111/j.1096-3642.1985.tb01178.x)
- 6 Sakamoto, M. 2010 Jaw biomechanics and the evolution of biting performance in theropod dinosaurs. *Proc. R. Soc. B* **277**, 3327–3333. (doi:10.1098/rspb.2010.0794)
- 7 Smith, J. M. & Savage, R. J. G. 1956 Some locomotory adaptations in mammals. *Zool. J. Linn. Soc. Lond.* **42**, 603–622. (doi:10.1111/j.1096-3642.1956.tb02220.x)