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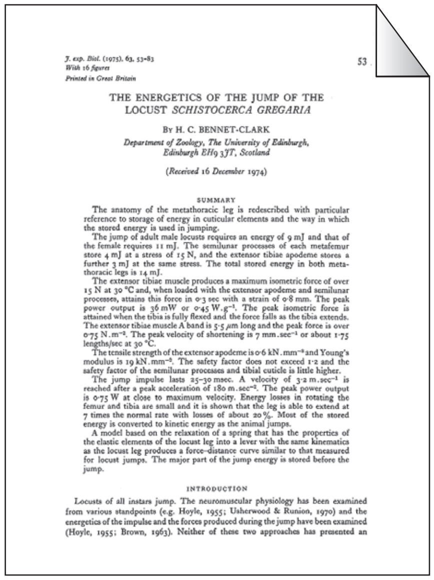
AN EXEMPLAR OF ENERGY ACCOUNTING: THE ENERGETICS OF THE LOCUST JUMP



J. exp. Biol. (1975), 63, 53-83
With 16 figures
Printed in Great Britain

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THE ENERGETICS OF THE JUMP OF THE LOCUST *SCHISTOCERCA GREGARIA*

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(Received 16 December 1974)

SUMMARY

The anatomy of the metathoracic leg is redescribed with particular reference to storage of energy in cuticular elements and the way in which the stored energy is used in jumping.

The jump of adult male locusts requires an energy of 9 mJ and that of the female requires 11 mJ. The semilunar processes of each metafemur store 4 mJ at a stress of 15 N, and the extensor tibiae apodeme stores a further 3 mJ at the same stress. The total stored energy in both metathoracic legs is 14 mJ.

The extensor tibiae muscle produces a maximum isometric force of over 15 N at 30 °C and, when loaded with the extensor apodeme and semilunar processes, attains this force in 0·3 sec with a strain of 0·8 mm. The peak power output is 36 mW or 0·45 $W.g^{-1}$. The peak isometric force is attained when the tibia is fully flexed and the force falls as the tibia extends. The extensor tibiae muscle A band is 5·5 μm long and the peak force is over 0·75 $N.m^{-2}$. The peak velocity of shortening is 7 $mm.sec^{-1}$ or about 1·75 lengths/sec at 30 °C.

The tensile strength of the extensor apodeme is 0·6 $kN.mm^{-2}$ and Young's modulus is 19 $kN.mm^{-2}$. The safety factor does not exceed 1·2 and the safety factor of the semilunar processes and tibial cuticle is little higher.

The jump impulse lasts 25–30 msec. A velocity of 3·2 $m.sec^{-1}$ is reached after a peak acceleration of 180 $m.sec^{-2}$. The peak power output is 0·75 W at close to maximum velocity. Energy losses in rotating the femur and tibia are small and it is shown that the leg is able to extend at 7 times the normal rate with losses of about 20%. Most of the stored energy is converted to kinetic energy as the animal jumps.

A model based on the relaxation of a spring that has the properties of the elastic elements of the locust leg into a lever with the same kinematics as the locust leg produces a force–distance curve similar to that measured for locust jumps. The major part of the jump energy is stored before the jump.

INTRODUCTION

Locusts of all instars jump. The neuromuscular physiology has been examined from various standpoints (e.g. Hoyle, 1955; Usherwood & Runion, 1970) and the energetics of the impulse and the forces produced during the jump have been examined (Hoyle, 1955; Brown, 1963). Neither of these two approaches has presented an

Gregory Sutton discusses Henry Bennet-Clark's 1975 paper entitled 'The energetics of the jump of the locust *Schistocerca gregaria*'.

A copy of the paper can be obtained from http://jeb.biologists.org/content/63/1/53.1.full.pdf

In 1974, the world of biomechanics had a problem resolving the physics of a most ubiquitous behaviour, the jump of an insect. It was well known that the faster a muscle shortens, the smaller the force it generates (Hill, 1938). This reduction in muscle force provides a hard limit to the amount of power that a mass of muscle can generate – a limit of approximately 100 W of power from 1 kg of muscle. As anyone who has tried to catch a jumping insect will note, however, jumping insects simultaneously generate both high forces and high speeds. When quantified, some of these behaviours require tens of thousands of watts from every kilogram of muscle, leading to the question, 'How are insects generating that much power?'

Examinations of jumping fleas (Bennet-Clark and Lucey, 1967; Rothschild et al., 1975) combined with research on jumping locusts (Brown, 1967; Heitler, 1974) showed that insects jump with a three-step process: first, insects lock their joints; second, they contract their muscles slowly to store energy in cuticular 'springs'; and third, insects unlock their joints, causing the recoil of the spring to catapult the insect into the air. The forces generated by the springs do not decrease with increasing velocity, thus allowing the spring to generate huge amounts of power. This reigning hypothesis did have a weakness: energy storage calculations were inexact and, until this point, based on indirect calculations from the movements of the insects. Nobody had yet been able to generate a detailed energy budget.

Henry Bennet-Clark sought to show exactly how much energy these springs could store by quantifying the energy budget of the jump of the locust (Bennet-Clark, 1975). The goal was a matter of accounting: show that the kinetic energy of the jump (energy output) matched the potential energy stored in the springs (energy input). By tracking every joule and watt, Bennet-Clark hoped to show that the idea of storing and releasing energy in a cuticular spring accounted for the entire energy budget.

He measured energy output by combining measurements of jump distance, high-speed video of the jump and estimates of wind drag. The result was 9 mJ in males and 11 mJ in females. He now knew the energy output. With that in hand, it then became a matter of finding which structures stored that energy.

To find the energy stores, Bennet-Clark first turned his attention to the leg muscles and the cuticular springs of the locust, structures at the femur–tibia joints called the semi-lunar processes (SLPs). To quantify the stored energy, he needed to know how much force the muscles in the leg apply to the SLPs and how much the SLPs deformed in reaction to those forces. He measured the forces in the muscles (between 12 and 15 N) and the amount of deformation in the SLPs in reaction to those forces (0.46 mm), resulting in SLPs that could store no more than 7 mJ of energy. He was between 2 and 4 mJ short!

Bennet-Clark struggled to determine where the last 2–4 mJ were stored until one morning, while cycling to lab, inspiration nearly caused him to lose control of his bicycle. Working to retain control, he thought, 'Could additional energy be stored in the apodemes (tendon-like structures) that were attached to the muscles?' By using a watch hairspring, he quantified the stiffness of the apodemes, and combined these measurements with the measurements of the forces in the muscles to quantify how much additional energy could be stored. The calculation showed that the apodemes could store an additional 6 mJ; more than enough to compensate for the energy shortage. The discovery of the second energy store allowed Bennet-Clark to account for the entire energy budget of the jump, with 60% of the energy stored in the SLPs and 40% of the energy stored in the apodemes.

Bennet-Clark had accounted for all of the energy, but he wasn't sure whether the mechanism he proposed could generate accelerations consistent with those seen in the biology. To test this, he built a kinetic model of his proposed mechanism and compared the predicted accelerations and power outputs with the accelerations and power outputs measured from the locust behaviour. The accelerations and power outputs matched almost exactly, providing the final piece of evidence. He had successfully shown that cuticular springs could account for all of the energy in a jump.

In the narrowest sense, Bennet-Clark had solved the problem of energy storage in the jump of the locust. He had shown how much energy was stored in the cuticular springs, and how much was stored in the apodemes. As the years went by, however, this idea of energy storage and release would be shown to apply much more widely. Many arthropods would be found to use similar structures whenever a behaviour required large amounts of power (for reviews see Gronenberg, 1996; Vogel, 2005; Patek et al., 2011). Outside of the idea of energy storage, Bennet-Clark's careful calculation of energy budgets followed by a synthetic kinetic model provided an excellent example of how biomechanical hypotheses should be tested. His 1975 paper not only demonstrated the veracity of a new idea, but also set a high standard for subsequent biomechanics work.

10.1242/jeb.056663

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