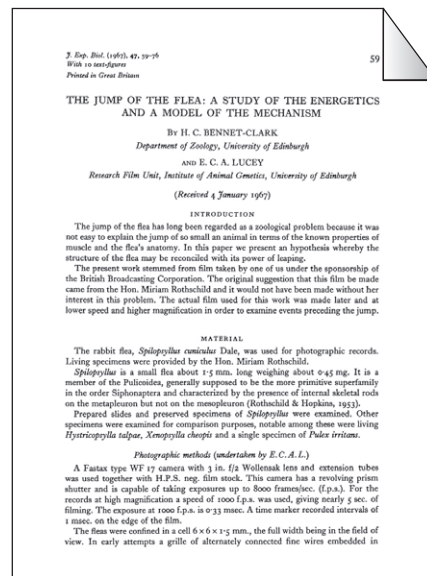


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# JEB CLASSICS

## HOW FLEAS JUMP



Malcolm Burrows discusses Henry Bennet-Clark and Eric Lucey's 1967 paper entitled: 'The jump of the flea: a study of the energetics and a model of the mechanism'

Copies of the paper can be obtained from <http://jeb.biologists.org/cgi/content/abstract/47/1/59>.

Our encounters with fleas are now thankfully limited to the unwanted infections of our pets, but for most mammals and birds they remain a continual annoyance. There are about 2000 species of fleas that suck the blood of a wide variety of hosts, each adapted to their own ecological niche. They belong to the order Siphonaptera but appear to be heading for reclassification with the Mecoptera, or scorpion flies.

The major problem a flea faces is to land on a moving host. It has solved this by a spectacular ability to jump, which so impresses us that it leads us unwisely to extrapolate to the size of buildings over which we might jump, if only length and mass scaled in the same way. How does such a small creature (a rabbit flea is only 1.5 mm long and weighs just 0.45 mg) jump huge distances with such speed and power?

A solution was proposed by Henry Bennet-Clark working with Eric Lucey in a paper (Bennet-Clark and Lucey, 1967) that for almost half a century has been an exemplar of a rare, multi-level analysis of complex behaviour. The paper shows how the interplay between mechanics, anatomy and physiology determine behaviour, and how this approach leads to a greater understanding of locomotion in general. Despite the explicit and careful separation of experimental data from the plausible

explanatory interpretation proposed, the two have become blurred over time into acceptance as established fact that flea jumping is understood.

To find out more about the mechanism of the flea jump, Bennet-Clark and Lucey used a film camera taking 1000 images  $s^{-1}$ , which enabled 20 jumps by an unstated number of fleas to be captured. Do not underestimate the difficulties here; in the mid 1960s these cameras took time to reach their true running speed yet it was impossible to predict when the fleas would jump. So the camera had to be started in the hope that a flea would jump before the film ran out. There was also a delicate trade-off between adequate lighting and frying the flea. Bennet-Clark and Lucey also supplemented this analysis with detailed mechanical modelling of the insect's anatomy.

The films showed that a flea first pulled the femora of its two hind legs forward so that they were almost vertical and they remained in this position without moving for about 100 ms (prolonged to a few seconds by cooling) in preparation for a jump. The hind trochantera and femora were then rapidly depressed and the tibiae extended propelling the flea upwards and forwards at variable body attitudes and take-off trajectories. The whole propulsive movement lasted less than 1 ms, or one frame of film.

Bennet-Clark and Lucey then calculated the insect's jumping performance. The hind legs propelled the flea to a take-off velocity of  $1 \text{ m s}^{-1}$  and to a measured and calculated height of 35 mm, or 23 times its body length. This is in the face of the considerable drag experienced on such a small body that reduces performance by 80% (Bennet-Clark and Alder, 1979). Some fleas have subsequently been shown to do better than this. From the blurred images it was estimated that the body was accelerated at  $1020\text{--}1330 \text{ m s}^{-2}$  (depending on whether the acceleration time is judged to be 0.75 or 1 ms), or  $100\text{--}130 \text{ g}$ . The energy output required was  $0.1 \mu\text{J}$ . The short legs allow little time for the body to be accelerated, so that to generate this energy would require a power output from the jumping muscles of some  $10,000 \text{ W kg}^{-1}$ ; that is, at least 25 times higher than could be produced by all known striated muscle (Alexander, 1995; Askew and Marsh, 2002; Vogel, 2005). In turn, this implies that direct muscle contractions could not generate the jump; power amplification and energy storage must occur.

So, where is the energy stored? In the direct line of action of the large trochanteral

depressor muscle in the thorax that powers a jump is a pad of resilin (Fig. 1A) [an almost perfect elastic protein – see the JEB Classic by Weis-Fogh (Weis-Fogh, 1960) and a review of it by Bennet-Clark (Bennet-Clark, 2007)]. Each pad has a volume of  $1.4 \times 10^{-4} \text{ mm}^3$  at the articulation between stiff structural elements of the thoracic exoskeleton. If stretched by 100% then the resilin pads of both hind legs were estimated to store almost twice the required energy for a jump. But in preparation for jumping the resilin is compressed, and its recoil delivers the energy for a jump. In froghopper insects (Hemiptera, Cercopidae), a 10% change in length occurs in their storage devices, indicating that only a small percentage of total energy needs can be provided by resilin alone (Burrows et al., 2008). It would seem that in fleas, as in froghoppers, a combination of soft, elastic resilin and hard, stiff cuticle store the energy.

To find out how the stored energy is released, Bennet-Clark and Lucey built a mechanical model 400 times larger than a

flea to illustrate the actions of the muscles, tendons and joints, which led them to the following interpretation of how the jump is generated (Fig. 1B,C).

An initial contraction of the trochanteral levator muscle lifts the trochanter and femur of each hind leg, and in so doing moves the tendon of the trochanteral depressor over the centre of the pivot of the coxo-trochanteral joint (Fig. 1B). A contraction of the main part of the depressor in the thorax is thus unable to depress the trochanter, but instead rotates the coxa so that a catch between a cuticular hook on its dorsal surface engages with a thoracic ridge. The energy generated by the continuing contraction of the main depressor muscle is stored in compression of the resilin. A small part of the depressor muscle within the coxa then contracts (Fig. 1C). Its fibres attach at almost right angles to the same tendon, which is thus moved forward so that its line of action is now on the appropriate side of the pivot for the stored energy to bring about depression of a

hind leg. The thrust of both hind legs is applied to the ground through their tarsi. The mechanical model works suggesting that it is ‘an adequate model of the jump of the flea’ (Bennet-Clark and Lucey, 1967).

However, is this the answer to how fleas jump? From similar data, another interpretation was proposed later by Miriam Rothschild, which differs in the following ways (Rothschild and Schlein, 1975; Rothschild et al., 1975; Rothschild et al., 1973; Rothschild et al., 1972). First, the initial contraction of the levator lifts the trochanter, but the tendon of the depressor is specifically prevented from going over-centre by a slot in the cuticle as it enters the coxa, and by an internal protrusion from the trochanter close to the pivot. Second, two different mechanical catches are invoked; first, an anterior catch between the mesothorax and metathorax and second, a posterior catch between the coxa and the first abdominal segment. The thoracic segments are thus locked together and the coxa is fixed to the abdomen whilst the depressor contracts slowly. Third, as a result of the levator contraction the hind trochantera rest on the ground. Fourth, the jump occurs when the levator relaxes and other thoracic muscles disengage the cuticular locks. Fifth, the energy stored is then delivered along the same line that the depressor tendon has adopted throughout the preparations for a jump, and surprisingly through the trochanter to the ground.

There is, however, no experimental evidence, such as recordings to reveal the real actions of the various muscles, or detailed mechanics to show the effects of the locks and potential changes in the lines of actions of tendons, that could distinguish between the two interpretations. Furthermore, neither interpretation explains how the movements of the two hind legs are synchronised. Modern high speed, and high resolution imaging could determine whether the trochantera or tarsi deliver the force to the ground. Even were such images to become available, will it still take us another half century to resolve the remaining puzzling mechanisms of jumping in fleas, or will we have to rely on extrapolations from larger and therefore more tractable insect jumpers to understand the flea’s jump?

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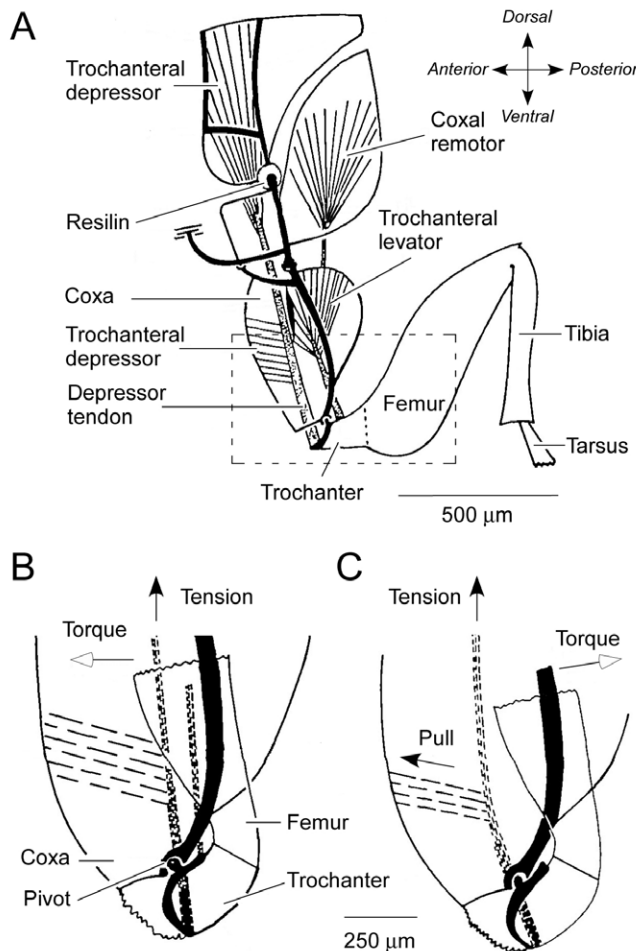


Fig. 1. A combination of figures 5A and 6B and C from Bennet-Clark and Lucey (Bennet-Clark and Lucey, 1967), after re-labelling, to show the key structures of the left hind leg involved in jumping by a flea. The dashed box in A indicates the area enlarged in B,C.

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