A quick guide to the use of springs in insect jumping

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How do some insects jump so quickly?

As anyone who has tried to catch a grasshopper or a planthopper knows, many insects can jump very rapidly. A planthopper can accelerate in less than 1 ms to take-off velocities of 5 m s^{-1} requiring a power output (energy per given time) of tens of thousands of Watts kg^{-1} of muscle. To do this jumping insects have to overcome two mechanical limitations. First, the maximum mechanical power a muscle can produce is only approximately 300 W kg^{-1} and furthermore, the faster a muscle contracts, the less force it can generate, exacerbating the problem. Second, a jumping animal can only accelerate while it remains in contact with the ground. In most small insects, the length of the propulsive legs therefore determines the time available to reach a given take-off velocity. Some larger insects, like katydids, use the leverage provided by their disproportionately long legs to multiply the power produced by direct muscle contraction to propel jumps. If the legs are short, however, alternative mechanisms must be used to generate the necessary mechanical power. How do these insects do it? They jump by using springs; devices that allow energy to be stored gradually in mechanical deformations and then released abruptly.

How do springs enable quick jumps?

In insects that use springs to jump, the legs are first moved into the same cocked position and the joints locked. The power-producing muscles then contract slowly over periods of 100 ms to a few seconds without moving the legs. Instead, the force generated distorts parts of the skeleton, which store mechanical energy. The sudden release of these loaded skeletal springs then powers the rapid propulsive movements of the legs. The elastic recoil of the spring returns the stored energy very quickly. The power is amplified because almost all the energy produced by the slow contraction of muscle is returned to the leg in a much shorter time, delivering the thousands of W kg^{-1} of mechanical power required for jumping. The principle is the same as that of an archery bow. Archers first slowly contract their arm muscles to bend the bow and store energy, and then when they let go the recoil of the bow returns energy quickly to the arrow; compare how far you can throw an arrow with how far you can fire it with a bow.

Which insects use these springs?

Spring-assisted jumping mechanisms were first discovered in fleas (*Siphonaptera*) and grasshoppers (*Acrididoidea: Orthoptera*). Springs have since been found in froghoppers and planthoppers (*Auchenorrhyncha: Hemiptera*), flea beetles (*Alticini: Coleoptera*), and even in a cockroach (*Blattodea*). This list is not exhaustive, however, and there are surely more to be discovered. A good rule of thumb for determining whether jumping requires a spring, or some other energy storage mechanism, is to calculate the mechanical power or mass specific power (total kinetic energy / (jumping muscle mass * acceleration time)). If more than 300 W kg^{-1} of muscle is needed, then a spring is likely being used.

Where are the springs?

Grasshoppers have springs which are visible externally at the distal end of each hind femur and are called 'semi-lunar processes' after their shape. The contractions of large femoral extensor muscles store energy for the jump by bending the semi-lunar processes and by stretching their apodemes (called tendons in vertebrates). Recoil of these two springs then causes the rapid extension of the knee (femoro-tibial) joints, thus powering the jump. In froghoppers and planthoppers, the springs are highly elaborated parts of the internal, thoracic skeleton called 'pleural arches' (Figure 1). Energy for the jump is generated by a pair of huge trochanteral depressor muscles in the thorax, which bend the pleural arches in a similar way to the bending of the semi-lunar processes in grasshoppers. Recoil of the pleural arches then depresses the hind legs, powering the jump. Similarly, fleas also use recoil of their springs to propel a jump.

What are the springs made of?

The detailed construction and component materials of the springs have been analysed in froghoppers, planthoppers, grasshoppers, and, to a lesser extent, fleas. These springs are a composite of hard, highly-sclerotized cuticle and the highly-elastic protein resilin. A hard material such as sclerotized cuticle can store considerable energy even if deformed by only a small amount, but is susceptible to fracture. Resilin, on the other hand, is much softer stores much less energy when deformed a similar amount, but is resilient and able to strain large amounts if necessary. It returns quickly and reliably to its original shape upon repeated deformations.

What are the shapes of the springs?

The detailed morphology of the springs in different insects is both complex and intricate. In froghoppers (Figure 1A) the soft resilin-containing region are sandwiched between hard cuticle with an air-filled tunnel penetrating from outside the body (Figure 1B). In grasshoppers, the resilin-containing region is bonded to an outer layer of hard cuticle. In fleas, the resilin is in a pad linked to the exoskeleton by hard cuticular struts. The principles by which these springs act, however, are the same; all, with the exception of muscle apodemes, have a curved shape in which energy is stored by bending as in an archery bow. Recoil of the bow-like springs then power the final propulsive leg movements.

Open questions on these springs.

The shape and material composition of these biological springs is very different from man-made springs. If we wish to apply biological lessons to modern spring design we need to address three outstanding questions. First, how does the geometry of the biological springs affect their ability to bend, store and release energy? How are the different springs adapted to meet the specific needs of different insects? Finally, what contributions do the hard and soft component materials make to the properties of the springs that enable such reliable storage and release of energy?

Where can I find out more?

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Figure 1 Legend:

Springs used by jumping froghoppers. **A:** The froghopper, *Philaenus spumarius*. **B:** Scanning confocal image to show the arrangement of resilin (blue) and hard cuticle (grey) in a spring (a pleural arch. B: In sections, the resilin and hard cuticle form a sandwich.