

RESEARCH ARTICLE

Biomechanics of jumping in the flea

Gregory P. Sutton* and Malcolm Burrows

Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

*Author for correspondence (RScealai@gmail.com)

Accepted 16 November 2010

SUMMARY

It has long been established that fleas jump by storing and releasing energy in a cuticular spring, but it is not known how forces from that spring are transmitted to the ground. One hypothesis is that the recoil of the spring pushes the trochanter onto the ground, thereby generating the jump. A second hypothesis is that the recoil of the spring acts through a lever system to push the tibia and tarsus onto the ground. To decide which of these two hypotheses is correct, we built a kinetic model to simulate the different possible velocities and accelerations produced by each proposed process and compared those simulations with the kinematics measured from high-speed images of natural jumping. The *in vivo* velocity and acceleration kinematics are consistent with the model that directs ground forces through the tibia and tarsus. Moreover, in some natural jumps there was no contact between the trochanter and the ground. There were also no observable differences between the kinematics of jumps that began with the trochanter on the ground and jumps that did not. Scanning electron microscopy showed that the tibia and tarsus have spines appropriate for applying forces to the ground, whereas no such structures were seen on the trochanter. Based on these observations, we discount the hypothesis that fleas use their trochanters to apply forces to the ground and conclude that fleas jump by applying forces to the ground through the end of the tibiae.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/214/5/836/DC1>

Key words: trajectory control, kinematics, Siphonaptera.

INTRODUCTION

For almost one hundred years the mechanisms of how fleas jump has continued to be a challenging biological problem (Russel, 1913; Snodgrass, 1946; Rothschild, 1965). The jumps were known to be quick and energetic, so that the power requirements were beyond what a muscle could produce by a direct contraction (Askew and Marsh, 2002; Roberts and Marsh, 2003; Vogel, 2005). A series of studies then used anatomical and engineering analyses, together with high-speed films to show that fleas propel their jumping by the storage and release of elastic energy. They first lock the thoraco-coxal joints of the two hindlegs and then contract two large dorsoventral muscles to compress part of the skeletal structure of the thorax that contains the elastic protein resilin, so that it acts as a tensed spring (Bennet-Clark and Lucey, 1967; Rothschild et al., 1972; Rothschild et al., 1973; Rothschild and Schlein, 1975; Rothschild et al., 1975). The lock on the hindlegs is then released and the rapid expansion of the spring releases the stored energy, which propels the jump (Bennet-Clark and Lucey, 1967; Rothschild et al., 1972; Rothschild et al., 1973; Rothschild and Schlein, 1975; Rothschild et al., 1975). These studies were in agreement about how fleas stored energy for a jump, but provided two different hypotheses for how the force was transmitted to the ground. The hypothesis put forward by Rothschild et al. (Rothschild et al., 1972; Rothschild et al., 1973; Rothschild and Schlein, 1975; Rothschild et al., 1975), henceforth called the Rothschild hypothesis, argued that the expansion of the spring pushed the hind trochanter onto the ground to transmit the force. This argument was based on two observations: first, in the preparatory phase of the jump, fleas placed their hind trochanters on the ground; second, amputation of the hind tarsi had only a small effect on the frequency of jumping. By contrast, the

hypothesis proposed by Bennet-Clark and Lucey (Bennet-Clark and Lucey, 1967), henceforth called the Bennet-Clark hypothesis, argued that expansion of the spring applied a torque about the coxo-trochanteral joint that was carried through the femur and tibia, and finally resulted in a force applied to the ground by the hind tibia and tarsus. This argument was based on the observation that the average acceleration during a jump was consistent with the spring expansion having a significant mechanical disadvantage; the ground forces were approximately a factor of ten fewer than the forces present in the spring.

The ability of a flea to control the direction of its jump is determined by how the forces from the spring reach the ground. If forces were channelled directly to the ground through the hind trochanter, as proposed by the Rothschild hypothesis, then recoil of the spring would push the trochanter straight down, propelling the animal vertically. Generating jumps with a large component in the horizontal direction would thus be difficult. If, however, forces were directed through the hind tibia and tarsus, as proposed by the Bennet-Clark hypothesis, then the tibia could be rotated about the femoro-tibial joint to direct the forces and generate jumps with a more horizontal trajectory.

To distinguish between these two hypotheses, we have used scanning electron microscopy and ultraviolet microscopy to reveal relevant structures on the hind trochanters and tarsi, high-speed video to analyse the joint movements of the legs during natural jumping, and kinetic modelling. Analysis of natural jumping shows that fleas do not have to place the hind trochanters on the ground to jump and that even when they do, there is no reduction of the acceleration when the trochanters leave the ground before take-off. Jump trajectories also had large horizontal

components and were never in the vertical direction. To determine whether the observed accelerations were consistent with the Rothschild or Bennet-Clark hypotheses, we developed two mathematical models to predict the velocities and accelerations that would result from each hypothesis. We then compared the model predictions with the data from natural jumping. Modelling indicates that both hypotheses can generate take-off velocities that are consistent with those observed in nature. If forces were transmitted through the trochanter, however, accelerations should be higher and briefer than those observed in natural jumping. If forces were transmitted through the end of the tibia and the tarsus, the model predicted accelerations that were consistent with those observed in natural jumping. These experimental and theoretical analyses support the hypothesis that fleas jump by transmitting forces from a spring in their thorax through a lever system to their tarsi and thus to the ground.

MATERIALS AND METHODS

Ten adult hedgehog fleas, *Archaeopsyllus erinacei* (Bouc  1835), taken from hedgehogs were kindly supplied by staff at St Tiggywinkles Wildlife Hospital Trust, Aylesbury, Bucks., UK. To determine leg movements and jump trajectory, sequential images of jumps were captured at rates of 5000 frames⁻¹ and with an exposure time of 0.067 ms with a single Photron Fastcam 1024 PCI camera [Photron (Europe) Ltd, West Wycombe, Bucks, UK] that fed images directly to a computer. 51 jumps by 10 adult fleas were analysed. Each flea jumped between three and nine times (median five). Jumps occurred in a chamber of optical quality glass 80 mm wide, 80 mm tall and 10 mm deep at its base expanding to 25 mm at the top, in which the temperature was 20–25°C. All analyses of the kinematics were based on the two-dimensional images provided by the single camera. The flat body plan of the body of a flea and the orientation of the chamber made it possible determine which jumps were within 20 deg of the sagittal plane. Within this 20 deg arc, errors in the calculation of jump velocity and jump trajectory will be small (a maximum 6% underestimate of velocity and a maximum 2 deg error in the elevation of the jump).

Jumps were either spontaneous, elicited by a light touch of a paintbrush, or in reaction to turning on lights. The fleas jumped from a high-density Styrofoam floor, which was flat and stable, but allowed them to grip the substrate firmly. The motion of the flea over the first four frames after take-off was used to calculate the take-off velocity and elevation of the jump. When analysing the sequences of images of a jump, a line was drawn through the body to represent its transverse axis and its orientation with respect to the ground. If the centre of this line does not represent the true centre of mass of the flea, there will be an error in the estimation of the velocity and trajectory of the centre of mass that is proportional to the flea's rotation rate multiplied by the distance between the centre of the measurement line and the real centre of mass. Fleas do not, however, rotate at sufficiently high rates for this error to be large. For example, even if it is assumed that the centre of a line drawn through the flea is as much as half a body length away from the true centre of mass then the error will be only 8% and thus negligible for all reasonable estimates of the centre of mass.

Jump trajectory, linear velocity and angular velocity were measured. For statistical analyses, one jump was taken randomly from each flea and data were compared with the data on locusts from Sutton and Burrows (Sutton and Burrows, 2008) using an *F*-test (the var.test function) in the software package R (R Foundation for Statistical Computing). Data are presented as means ± standard deviation unless otherwise stated.

The morphology of the hindlegs was photographed and drawn using a Leica stereomicroscope fitted with a drawing tube, or with a Nikon DXM 1200 camera. The presence of the elastic protein resilin was revealed by its characteristic fluorescence (Weiss-Fogh, 1960; Andersen, 1963) established using an Olympus BX51WI compound microscope with OlympusMPlan ×10/0.25 NA and LUCPlanFLN ×20/0.45 NA objective lenses, under ultraviolet (UV) or white epi-illumination. Images were captured with a Q-imaging Micropublisher 5.0 digital camera (Marlow, Bucks., UK) as colour (RGB) TIFF files. The UV light was provided by an X-cite series 120 metal halide light source, conditioned by a Semrock DAPI-5060B Brightline series UV filter set (Semrock, Rochester, NY, USA) with a sharp-edged (1% transmission limits) band from 350 nm to 407 nm. The resulting blue fluorescence emission was collected in a similarly sharp-edged band at wavelengths from 413 nm to 483 nm through a dichromatic beam splitter. Images captured at the same focal planes under UV and visible light were superimposed in Canvas X (ACD Systems of America, Miami, FL, USA). To look for structures on the hind tarsus and trochanter that might be associated with improving traction with the ground, dried specimens were sputter-coated with gold and images were taken with a Phillips XL-30 scanning electron microscope.

Two kinetic models were used to calculate the kinematics predicted by the Rothschild and the Bennet-Clark hypotheses. The equations of motion for both models were written and implemented in Mathematica 5.0 (Wolfram Research, Champaign, IL, USA) (Appendix 1, 2). The parameters for each model are based on the data presented for *Xenopsylla cheopis* in (Bennet-Clark and Lucey, 1967; Rothschild and Schlein, 1975; Rothschild et al., 1975).

RESULTS

Anatomy

Hedgehog fleas have a body mass of 0.7±0.16 mg (*N*=10) and a body length of 1.8±0.19 mm (*N*=10). The body is flattened laterally and is dominated by large hindlegs that rotate in the sagittal plane (Fig. 1A,B). A hindleg is 2.8 mm long, with the coxa, femur and tibia all of similar lengths (0.5–0.6 mm), the trochanter is smaller (0.2 mm) and the tarsus is longer (1.0 mm; Table 1). The ratio of leg lengths is 1:1.3:1.9 (front:middle:hind). The hindlegs have a ratio of 3.1 relative to the cube root of the body mass and are 154% of the body length, compared with 83% for the front legs and 110% for the middle legs.

Table 1. Body form of the flea *Archaeopsyllus erinacei*

Parameter	Value
Body mass (mg)	0.7±0.16
Body length (mm)	1.8±0.19
Hindleg length (mm)	
Coxa	0.5±0.06
Trochanter	0.2±0.04
Femur	0.5±0.03
Tibia	0.6±0.04
Tarsus	1.0±0.06
Ratio of leg lengths	
Front	1
Middle	1.3
Hind	1.9
Leg length (% body length)	
Front	83
Middle	110
Hind	154
Hindleg length (mm)/mass (mg) ^{0.33}	3.1

Values are means ± s.d., *N*=10.

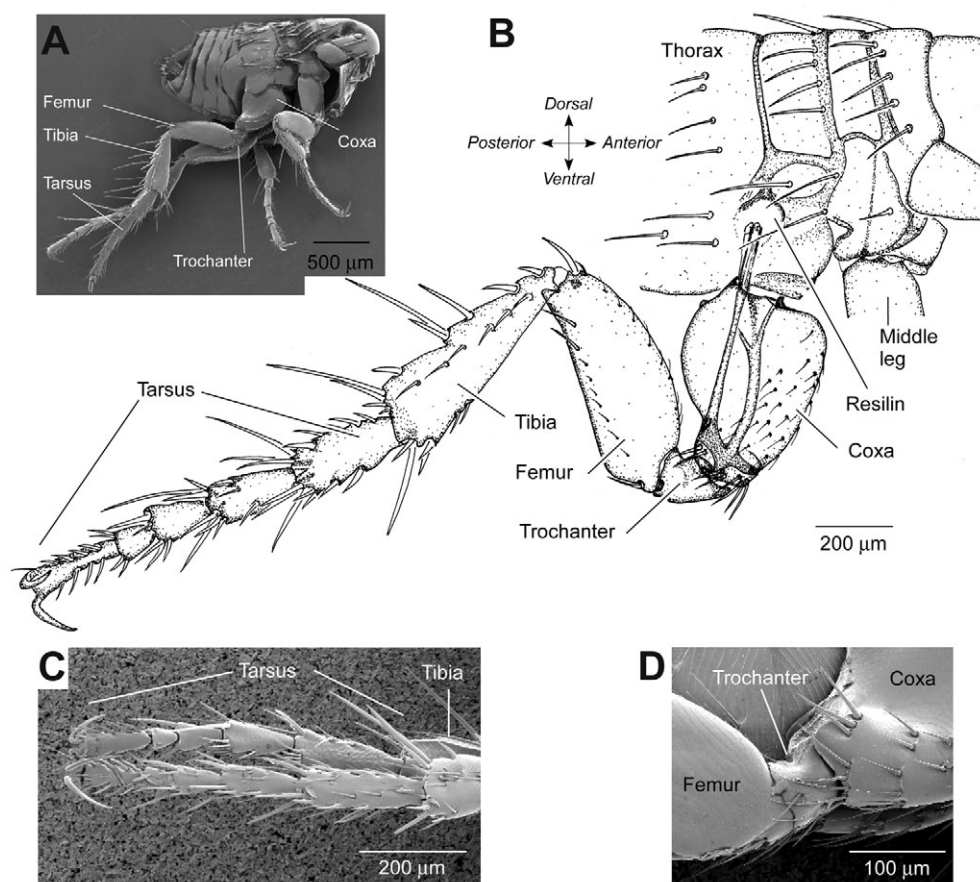


Fig. 1. Anatomical features of the flea *Archaeopsyllus erinacei* involved in jumping. (A) Scanning electron micrograph of the whole flea with the hindlegs outstretched. (B) Drawing of the right hindleg and part of the thorax to show the joints and the skeletal reinforcements in the coxa and thorax. (C) Scanning electron micrograph of the tibio-tarsal joints and the tarsi of the hindlegs in another flea to show the spines and claws that make contact with the ground when jumping. (D) The hind trochanter of a third flea showing that there are few structures that could aid traction with the ground.

Consistent with extensive previous findings, the scanning electron micrographs of the hindlegs showed that the five segments of the hind tarsus and the distal end of the tibia have a number of prominent bristles and spines that would normally contact the ground and thus improve traction (Fig. 1C). Moreover, the distal end of the most distal tarsal segment has two large hook-like cuticular spines, which could also be used to gain traction on a substrate. The trochanter has a series of hairs but these are much smaller than the spines and claws present on the tarsus (Fig. 1D).

The hind coxae pivot with the thorax so that the whole hindleg can be rotated through 15 deg in a plane parallel to the long axis of the body (Fig. 2A,B). Each coxa is reinforced by sclerotised struts and a distal sclerotised rim at the joint with the trochanter. The trochanter itself can rotate through 100 deg in the same plane but moves little relative to the femur, so that both can be treated as a single element in modelling the movements of a hindleg. Rotation of the trochanter about the coxa is key to jumping; levation of this joint moves the whole hindleg forwards into a cocked position ready for jumping so that the femur fits into a lateral indentation of the coxa (Fig. 2). The tibia can rotate through 130 deg about the femur, again in the same plane as the more proximal joints. The long tarsus can bend at the various joints between its five segments.

When the hindlegs were examined under UV light a consistent patch of blue fluorescence was seen in the thorax (Fig. 3A,B). With the specific wavelengths used this blue fluorescence is a characteristic signature of the elastic protein resilin (Weis-Fogh, 1960; Andersen, 1963). The fluorescence was associated with sclerotised elements of the internal thoracic skeleton (Fig. 3A,C). The metathorax has two symmetrically arranged areas of resilin associated with each hindleg (Fig. 3C), but no resilin could be

detected associated with the front and middle legs at the equivalent sites. Bennet-Clark and Lucey suggested that this lump of resilin was the energy store for the flea, based on a calculation that stated that a lump of resilin this size could, in theory, store the necessary energy (Bennet-Clark and Lucey, 1967). In froghoppers and locusts, however, a significant amount of energy is stored not only in resilin lumps, but also in the bending of sclerotised cuticle (Bennet-Clark, 1975; Burrows et al., 2008), thus pointing to the possibility that the flea may also store energy by bending the reinforced cuticle surrounding the resilin lump. There is agreement, however, that the recoil of the energy storage applies a force at the coxo-trochanteral joint (Bennet-Clark and Lucey, 1967; Rothschild and Schlein, 1975).

Table 2. Jumping performance of the flea, *Archaeopsyllus erinacei*

Parameter	Formula	Mean (N=10)	Fastest jump
Body mass (M ; mg)		0.7 ± 0.16	1
Body length (L ; mm)		1.8 ± 0.19	2
Time to take off (t ; ms)		1.4 ± 0.25	1.2
Take-off velocity (v ; $m\ s^{-1}$)		1.3 ± 0.21	1.9
Take-off angle (deg)		39 ± 5.7	45
Body angle at take-off (deg)		23 ± 8.7	39
Acceleration (a ; $m\ s^{-2}$)	$a = v/t$	960 ± 233	1600
g force (g)	$g = f/9.86$	98 ± 23.7	160
Energy (e ; μJ)	$e = 0.5Mv^2$	0.6 ± 0.28	1.8
Power (p ; mW)	$p = e/t$	0.43 ± 0.19	1.5
Force (F ; mN)	$F = ma$	98 ± 23.7	160
Power/muscle mass* ($W\ kg^{-1}$)	$p/(0.11M)$	6000 ± 2100	14,000

*This assumes that fleas have the same percentage of their body mass devoted to jumping (11%) as locusts do (Bennet-Clark, 1975).

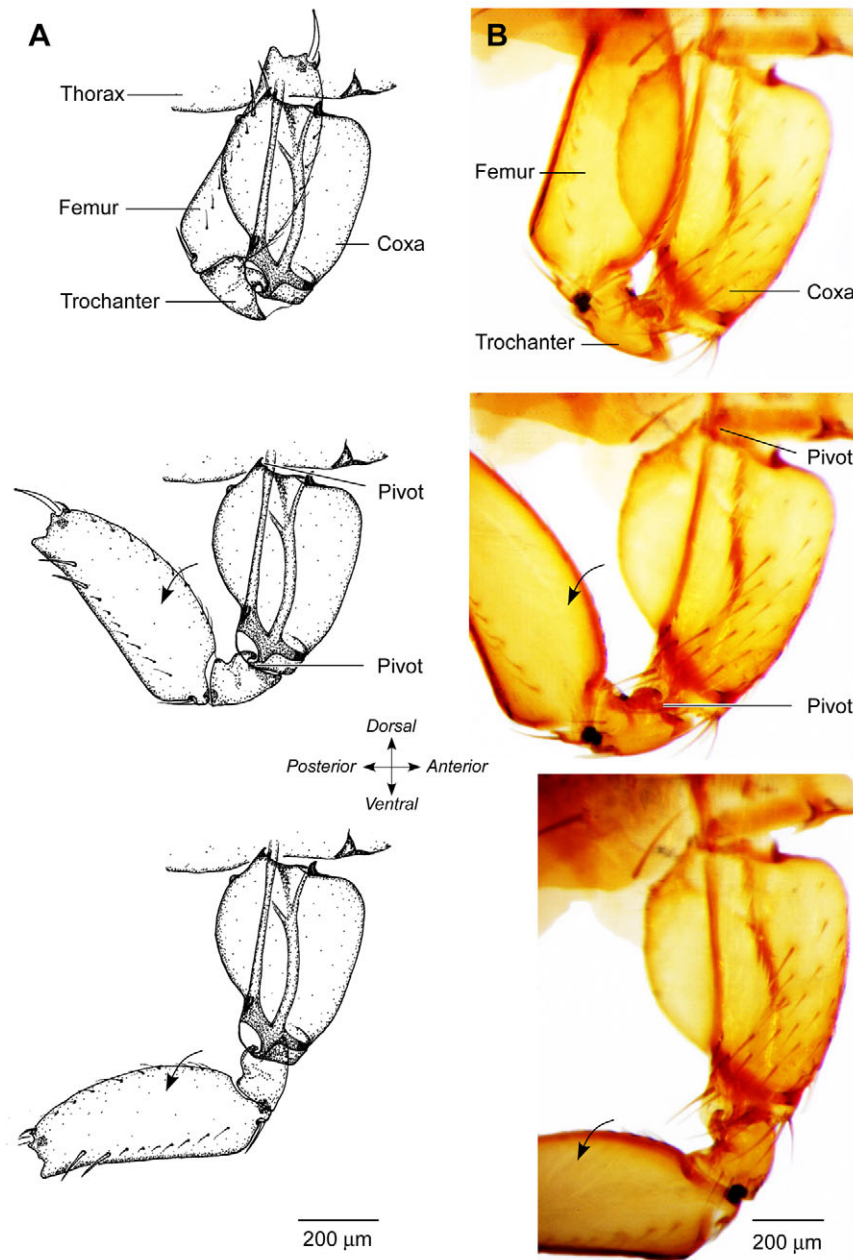


Fig. 2. Drawings (A) and photographs (B) of the proximal joints of a right hindleg of a flea to show the rotation of the coxa about the thorax, and of the depression of the trochanter and femur about the coxa in movements that are used during a jump. The top row shows the hindleg in the fully cocked position that it adopts before a jump. The next two rows show the progressive depression of the trochanter about the coxa. The femur and trochanter do not move much relative to each other so that they can be modelled as one link.

Kinematics of natural jumps

The jump of a flea was propelled by the rapid and simultaneous movements of the two hindlegs (Table 2). Preparation for a jump began with an initial phase where the body was rotated largely by the action of the front and middle legs thus setting the different attitudes of the body from which the rapid, propulsive movements of the legs could be delivered (Figs 4 and 5). The hind trochanters were then levated, moving the more distal segments of the hindlegs forwards so that the femur fitted into an indentation of the coxa. The legs then depressed at the coxo-trochanteral and extended at the femoro-tibial joints propelling the flea forwards.

In 45 of the 51 jumps (88%), the first propulsive movements of the hindlegs in a jump began from a position in which both hind tarsi were on the ground and both hind trochanters were close to or touching the ground (Fig. 5 and supplementary material Movie 1), confirming the observations made by Rothschild et al. (Rothschild et al., 1975). The initial depression of the trochanters

thus occurred while they were either directly in contact with the ground, or very close to it. Despite this initial contact or closeness to the ground, the trochanters were obviously clear of the ground approximately 0.6 ms after their initial movement. This would indicate that if the forces were applied to the ground by the trochanters, the acceleration of the body would drop once they left the ground. In fact, the acceleration did not decrease when the trochanters left the ground, but, instead, the body continued to be accelerated until take-off approximately 0.6 ms later.

In six of the 51 jumps (12%) by *A. erinacei* the two hind trochanters were both clear of the ground at the time the hindlegs first began their propulsive movements. In the examples shown, the gap from the ventral surface of the trochanter and the ground ranged from 200–520 μm (Fig. 4A–D). The sequence of joint movements during these jumps was the same as when the trochanters were in contact with the ground initially. The first propulsive movements of the hindlegs were a depression of the trochanter about the coxa

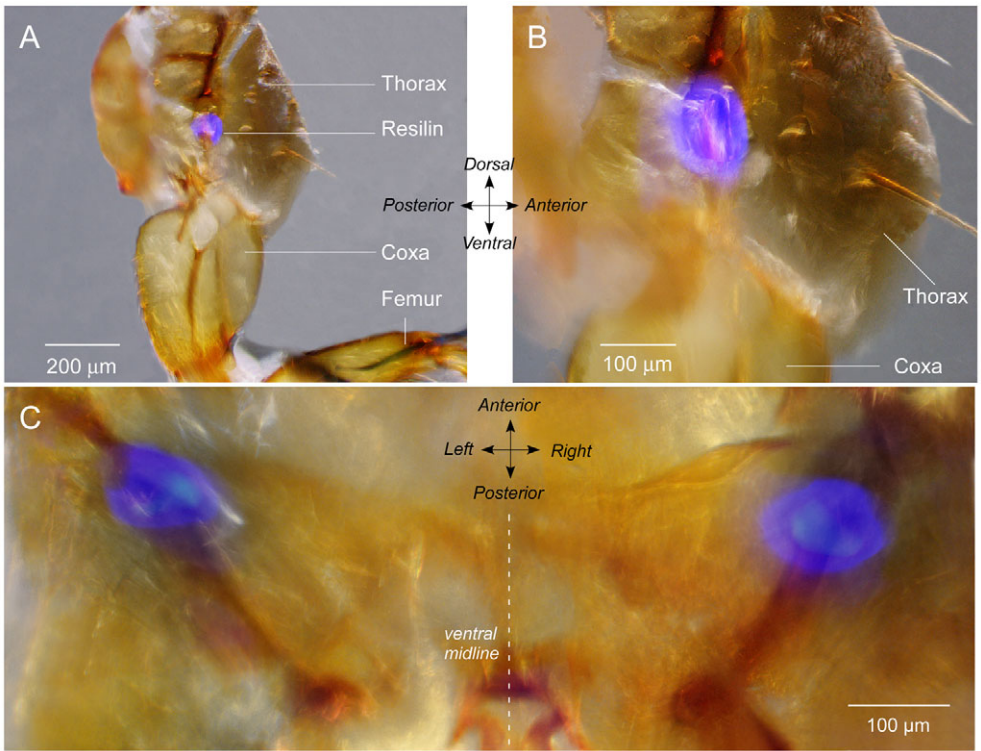


Fig. 3. Photographs showing the regions of blue fluorescence under UV illumination that indicate the presence of resilin. (A) View of the right hindleg and metathorax from inside. A single patch of blue fluorescence is present in the thorax. (B) The same region at higher magnification. (C) View of the ventral metathorax viewed from inside with the ventral midline at the centre (dashed line) and patches of blue fluorescence associated with the left and right hindlegs.

that was progressively accompanied by an extension of the tibia about the femur (Fig. 6, supplementary material Movie 2). The effect of these movements was to raise the body, accelerate it forwards and to cause both the front and middle legs to lose contact with the ground before take-off. The time when these legs left the ground depended on the initial attitude of the body relative to the ground, but could occur as much as 1 ms before take-off. By the point of take-off, the hind coxa had rotated backwards relative to the thorax, the trochanter had rotated through 100 deg so that it was at its most depressed position, the tibia was extended by an angle of 130 deg about the femur and the tarsus was depressed about the tibia with

all its segments aligned. After take-off, the hindlegs remained outstretched and trailed underneath and behind the body.

If the initial thrust for a jump was delivered through the trochanter, then beginning with the trochanter off the ground would reduce the initial thrust so that the flea should take longer to reach take-off and there would be a differently shaped relationship between velocity and time than if the trochanter began in contact with the ground (Fig. 7). No differences, however, were seen in the acceleration times whether jumping occurred with the trochanter initially on or off the ground. The acceleration time was 1.4 ± 0.20 ms for jumps starting with the hind trochantera off the ground (one

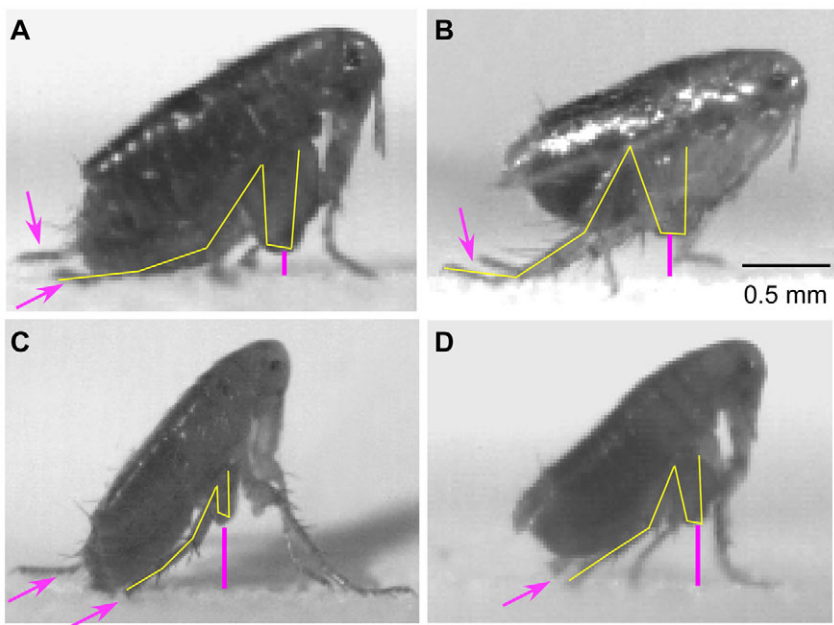


Fig. 4. Images of four *A. erinacei* (A–D) captured at 5000 frames s⁻¹ during natural jumping and at the moment when their hindlegs first began to move to propel a jump. The thick vertical magenta bar shows that the trochanter was not in contact with the ground in any of these jumps. The hind tarsus (magenta arrows) was in contact with the ground in each jump. The position of the segments of the hindlegs are indicated by thin yellow lines.

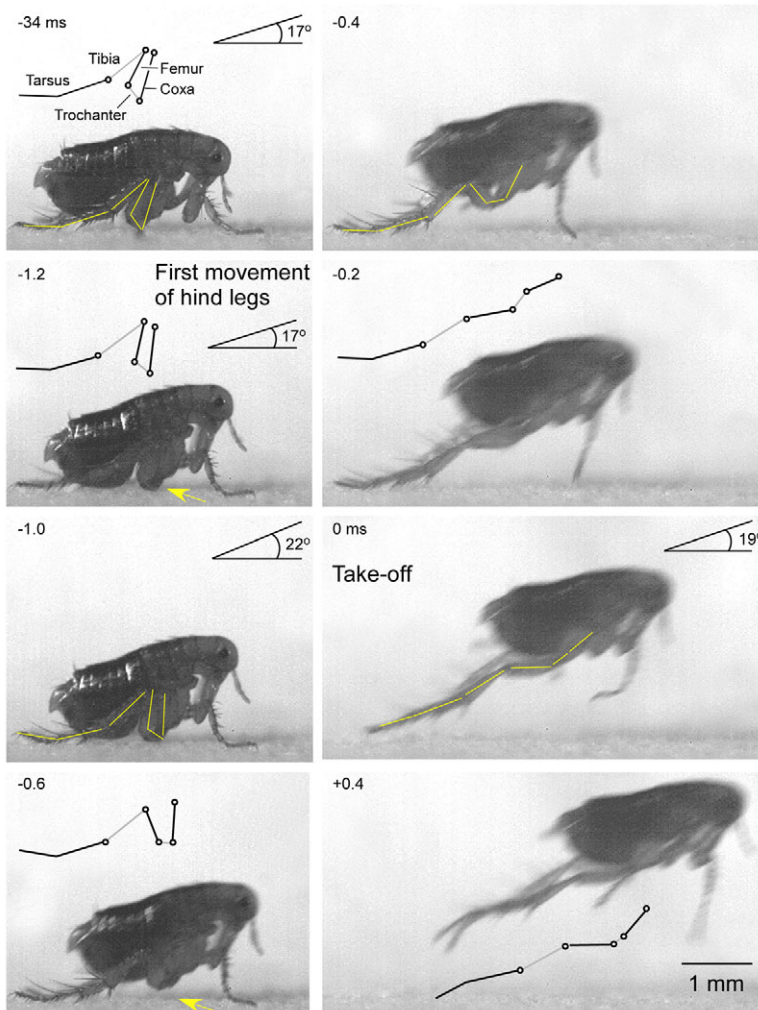


Fig. 5. Photographs of a natural jump of *A. erinacei* in which the trochanter began close to the ground. The yellow arrow indicates the position of the hind coxa at the point when the hindlegs first move to propel a jump. Selected images at the times indicated are arranged in two columns with the bottom left hand corner as a constant point of reference. The positions of the segments of the right hindleg are shown above each image and are superimposed in yellow on the first image. The angle of the body relative to the ground is shown for four images. The yellow arrows in the images at -0.6 and -1.2 ms indicate that the trochanter was clear of the ground before and at the first movement of a hindleg. Take-off occurred at 0 ms. Images in this and Fig. 6 were captured at $5000 \text{ frames s}^{-1}$.

jump randomly taken from each of five fleas) and $1.4 \pm 0.24 \text{ ms}$ for jumps starting with them on the ground (one jump randomly taken from each of ten fleas). The values are not significantly different ($P=0.86$, $t=0.18$, $d.f.=10.3$, Welch two-sample t -test).

The take-off velocity for jumps that began with the trochanters off the ground was $1.3 \pm 0.25 \text{ m s}^{-1}$ ($N=5$), whereas the velocity for jumps that began with the trochanters on the ground was $1.3 \pm 0.22 \text{ m s}^{-1}$ ($N=10$). The values were again not significantly different ($P=0.67$, $t=0.44$, $d.f.=6.5$, Welch two-sample t -test).

The shape of the relationship between velocity and time for jumps that started with the trochanters off the ground (Fig. 7A) was qualitatively similar to that for jumps starting with the trochanters on the ground (Fig. 7B). Both velocity curves are S-shaped, rising to a peak just before take-off and falling when the hind tarsi had left the ground, at which point force could no longer be delivered through them to the ground. Acceleration times were also comparable. Moreover, in those jumps where the trochanters were initially on the ground, there was no decrease in acceleration when they left the ground before take-off (Fig. 7B). If force were applied through the trochanters, the velocity should fall at the time when they lost contact with the ground. Instead, in all 51 jumps the flea continued to accelerate from the first depression of the trochanters until take-off, regardless of whether the starting position of the trochanters was on or off the ground, indicating that force was transmitted through the tibiae and tarsi, and not through the trochanters.

Take-off elevation

The elevation trajectories at take-off for 51 jumps by 10 fleas were all within a narrow 24 deg window (Fig. 8A). The minimum angle was 28 deg and the maximum was 52 deg, with a mean of 39 ± 6.1 deg. A histogram of the jump elevations (Fig. 8B) shows that *A. erinacei* most commonly took-off with an elevation of 36 deg. No jumps had the trajectories close to vertical as predicted by the Rothschild model. In this model, the trochanter would be pushed downward onto the ground and therefore the resulting ground reaction force would be vertical. By contrast, the observed range of low elevation angles in natural jumping were consistent with the Bennet-Clark model and could easily be directed if forces were directed to the ground through the tibia and tarsus.

The narrow 24 deg range of elevation angles used by fleas contrasts with the much wider 80 deg range used by locusts when jumping [fig. 9A in Sutton and Burrows (Sutton and Burrows, 2008)]. The ranges are significantly different ($P=0.0011$, ratio of variances=0.093, $d.f.=9$; R var.test function). Data on take-off velocity and elevation are not available for other species of fleas, but the horizontal distance that seven species jump has been reported (Krasnov et al., 2003). For these fleas, the minimum distance of a jump was between 39 and 73% (Fig. 8C) of the maximum jumping distance (Krasnov et al., 2003). Although we did not directly measure the distance jumped by the fleas in our experiments, we have used the physics of a ballistic projectile to answer the following question: does the restricted elevation of *A.*

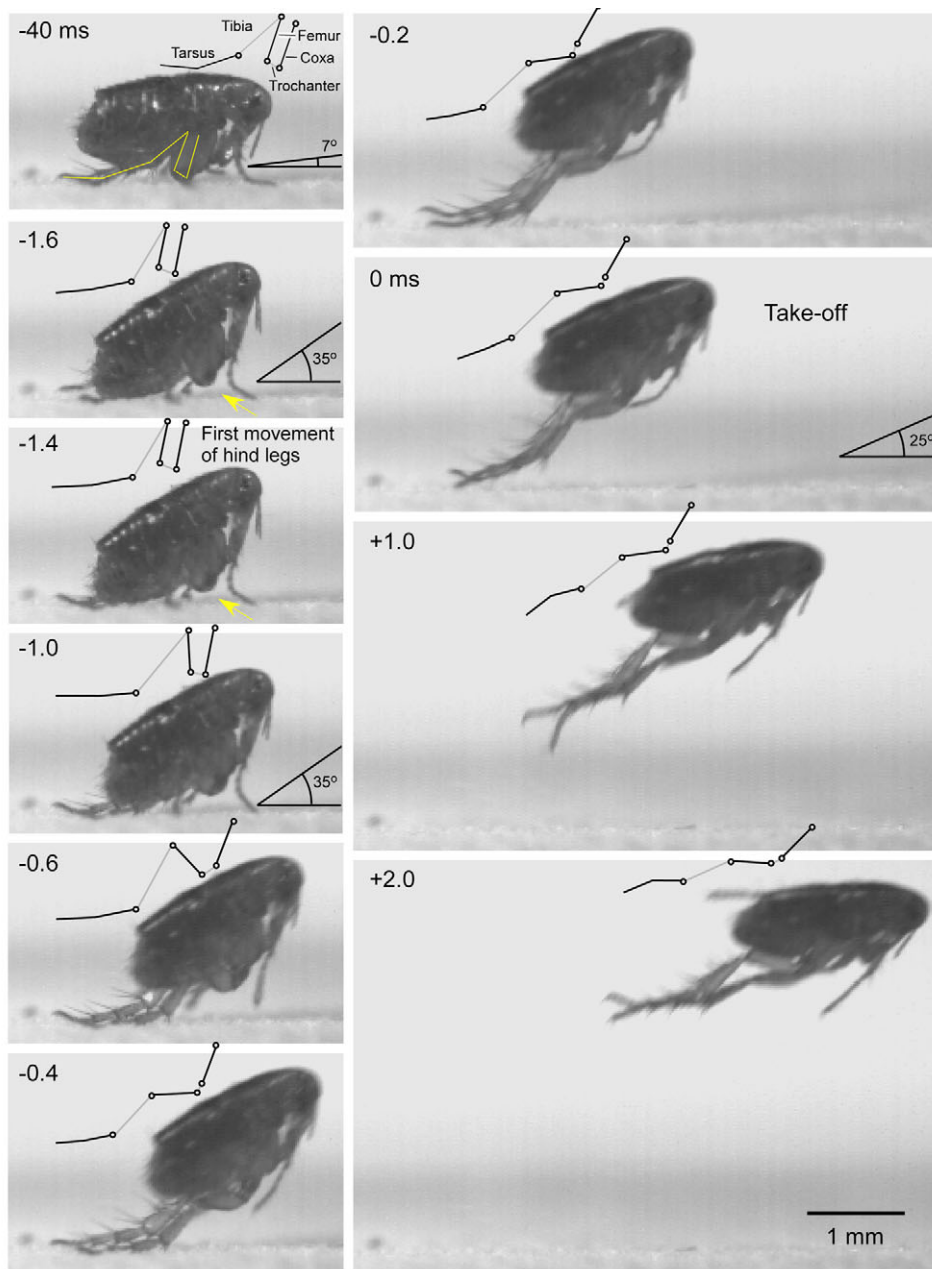


Fig. 6. Photographs of a natural jump of *A. erinacei* in which the trochanter began off the ground. Selected images are annotated as in Fig. 5.

erinacei result in restricted variation in possible jump distance? The jumping distance of *A. erinacei* can be estimated from Eqn 1:

$$D = 2V^2 \sin(\theta) \cos(\theta) / g, \quad (1)$$

where D is distance, V is velocity, θ is the angle of elevation at take-off and g is the acceleration due to gravity.

From our measurements, an *A. erinacei* jumping with a constant velocity would have a minimum jump distance (at 28 deg elevation) that is 83% of the maximum distance (at 45 deg) (Fig. 8C). The window for jump elevation in *A. erinacei* is thus insufficient to generate jump distances that are as variable as those in other species of flea. If velocity is taken into consideration, however, *A. erinacei* will have variations in jump distance that are similar to those of other fleas. The window of jump velocities for *A. erinacei* ranges between 0.9 and 1.85 m s^{-1} (Fig. 9A), which means that the minimum jump distance will be 25% that of the maximum (Fig. 9B). This suggests that jump distances in *A. erinacei* are a little more variable

than those in other species of flea [Fig. 10B, compare lines i and iii (Krasnov et al., 2003)] and that it generates these differences more by altering its take-off velocity than its angle of elevation. It is not known which of these two parameters determine jump distances in other fleas.

Kinetic modelling

To model the Rothschild hypothesis, which proposed that ground forces are directed through the trochanter, the flea was considered as a mass with a spring that applies its force through the coxa and trochanter directly to the ground (Fig. 10A). This model has similar dynamics to a mass-spring system. To model the Bennet-Clark hypothesis, which proposed that ground forces are directed through the hind tibia and tarsus, the flea was considered as a three-link mechanical system (Fig. 10B): one link represented the coxa, the second the femur and trochanter (Fig. 2) and the third the tibia. The first question was to determine if either model could duplicate the

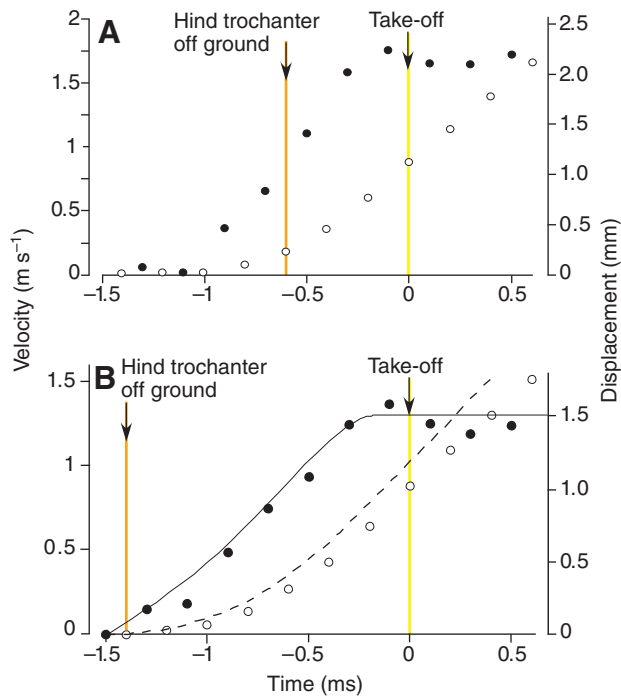


Fig. 7. Graphs of the displacement (unfilled circles) and velocity (filled circles) of the centre of mass of the body for the jumps shown in Fig. 5 when the hind trochanter was close to the ground at the start and left the ground at -0.6 ms (A, orange vertical line) and Fig. 6 when the trochanter started off of the ground (B, orange vertical line). The solid line in B shows the velocity kinematics for *A. erinacei* derived from the Bennet-Clark model and the dashed line shows the position kinematics. The profiles of each parameter are the same for each jump.

kinematics observed by Rothschild et al. (Rothschild et al., 1975). We chose this kinematic data in an effort to give the Rothschild hypothesis every advantage over the Bennet-Clark hypothesis.

The kinetic model of the Rothschild hypothesis (Fig. 10A) predicted a final velocity that was identical to that observed in natural jumping (Fig. 11B). First, the displacement of the centre of mass of the body predicted by the model described well the trajectory of a natural jump (Fig. 11A). Second, the velocity at take-off predicted by this model was also consistent with the observed velocity (both are 1.35 ms^{-1}). The time course by which this end result was achieved was very different between the Rothschild model and the kinematics observed in a natural jump (Fig. 11B). The model predicted that there was a very fast change from stationary to the final take-off velocity, whereas in natural jumping the velocity increased over an acceleration period of approximately 1 ms. The model predicted that the acceleration should peak rapidly at the high value of $22,000\text{ ms}^{-2}$, when the hindlegs first moved, and should then decrement to zero 0.7 ms before take-off (Fig. 11C). In natural jumps, however, the initial acceleration as the hindlegs started to move was much smaller, at 500 ms^{-2} , rose steadily to 1500 ms^{-2} , but then dropped to zero at take-off (Fig. 11C). This model therefore failed to predict the time course of velocity and acceleration of a natural jump.

The kinetic model of the Bennet-Clark hypothesis (Fig. 10B), in contrast, predicted displacements, velocities and accelerations that were similar to those observed during natural jumps (Fig. 11A–C). First, the displacement of the centre of mass of the body predicted

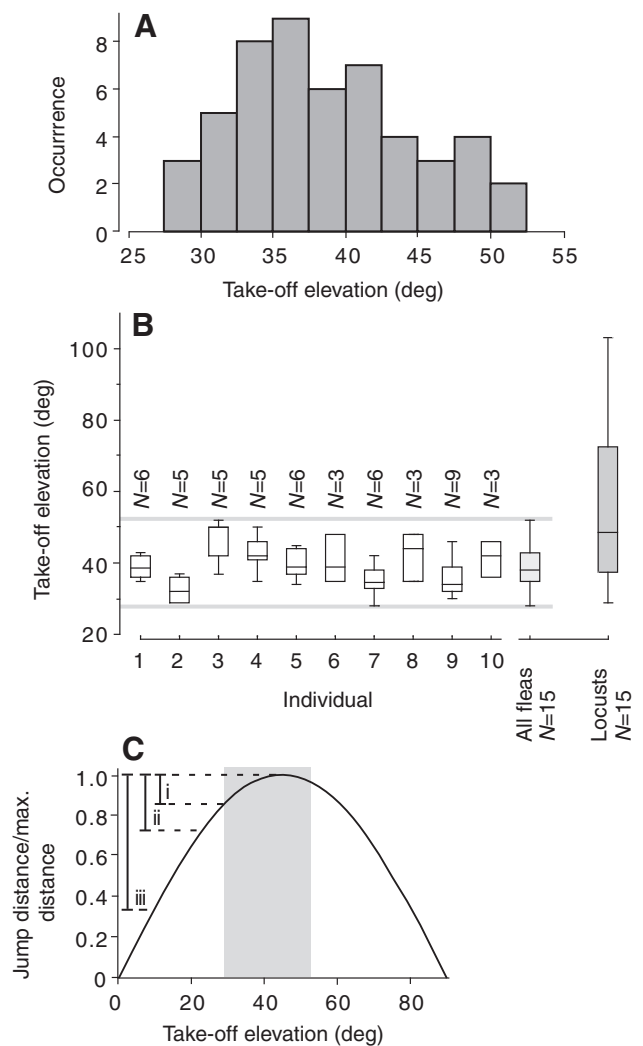


Fig. 8. Control of jump elevation. (A) Histogram to show the distribution of take-off angles in the 51 jumps by 10 *A. erinacei*. (B) Box plot of the jump elevations for all the fleas in this study, shown individually (1–10) and together (all fleas). The horizontal grey lines define the upper and lower limits of the 24 deg window of take-off angles. For comparison, the box plot on the right shows the larger range of take-off angles for locusts (Sutton and Burrows, 2008). (C) Projected distances of jumps by fleas. The vertical bars show the minimum and maximum distances that *A. erinacei* would jump using: (i) the range of take-off angles in A and assuming a constant take-off velocity, (ii) the minimum and (iii) maximum distances jumped by some other fleas based on data from Krasnov et al. (Krasnov et al., 2003). The shaded area of the graph marks the area of jump elevations observed for *A. erinacei*.

by the model described the trajectory of a natural jump well (Fig. 11A). Second, the model accurately predicted both the time course and the final take-off velocity (Fig. 11B). The model accurately predicted the time course of acceleration; it predicted an acceleration of 450 ms^{-2} when the hindlegs first moved, a peak at 1800 ms^{-2} , and then a return to zero just before take-off (Fig. 11C). This form of acceleration resulted in an S-shaped curve for velocity (Fig. 11B), in good agreement with the data from natural jumps (Rothschild et al., 1975) and our data (Fig. 7A).

The gradually rising and rapidly falling shape of the acceleration curve predicted by the Bennet-Clark model is a direct consequence

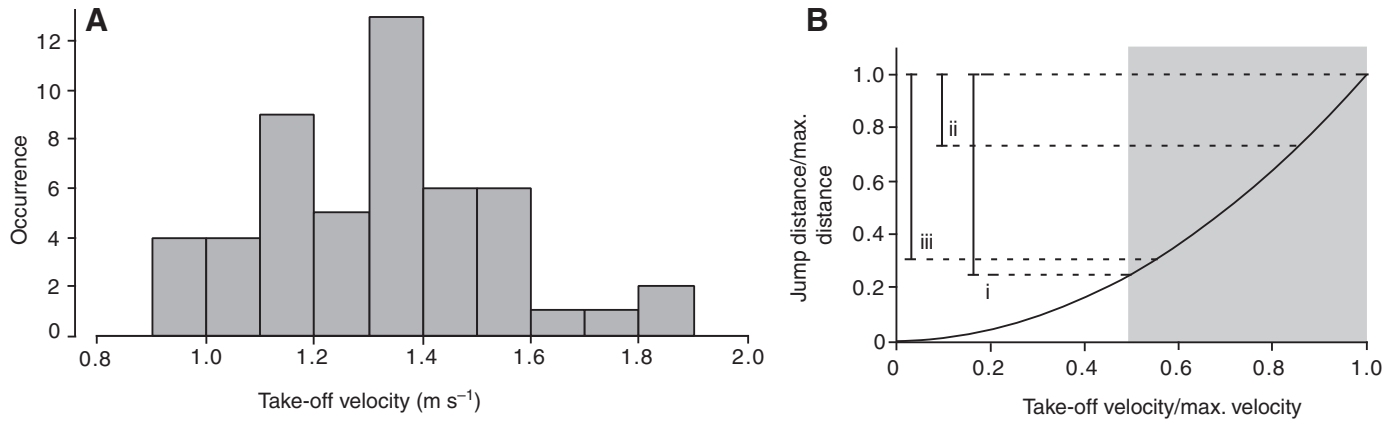


Fig. 9. Jump velocity. (A) Histogram of the take-off velocities that ranged between 0.9 and 1.85 m s^{-1} in 51 jumps by 10 *A. erinacei*. (B) Projected distances that fleas would jump with a constant elevation of 39 deg. (i) Ratio of minimum and maximum distance predicted by fleas jumping with a constant elevation. (ii) Minimum and (iii) maximum ratio for the data of Krasnov et al. (Krasnov et al., 2003). The shaded area of the graph marks the area of jump velocities observed for *A. erinacei*.

of the mechanics of a spring–moment arm system. At the start of a jump, the force in the spring will be high, but the moment arm is small, thus the product of the force and the moment arm starts small. This results in a small ground reaction force. Because the coxo-trochanteral joint depresses to propel the jump, the force in the spring will decrease linearly, but the moment arm will increase as a sine wave function. The moment arm initially increases faster than the force decreases, so that the product of the two increases (Fig. 11C). Finally, as the sine wave function of the moment arm reaches a maximum, the spring force decreases faster than the moment arm increases, so that the product of the two decreases (Fig. 11C). The initial rise and subsequent fall of the acceleration curve is consistent with a combination of an elastic mechanism and a rotating lever arm system.

Parameters of the Bennet-Clark model were varied to reflect the morphology of *A. erinacei* (Fig. 7A) and other possible morphologies (data not shown). Take-off velocity and take-off times could be changed by altering the model parameters. The qualitative shape of the acceleration curve, however, was insensitive to changes in the model parameters, because the basic geometry of a moment arm combined with an elastic mechanism constrains the acceleration time curve to have this form. In particular, the shape of the acceleration curve was insensitive to the stiffness of the spring. The model was re-run with a series of linear springs, which all stored sufficient kinetic energy to achieve a take-off velocity of 1.3 m s^{-1} , and all of these springs returned an acceleration vs time curve that had an initial rise followed by a fall. The Rothschild model, however, was unable to generate time courses of acceleration that were similar to our kinematic analysis of *A. erinacei*. This leads us to the conclusion that the Bennet-Clark model is more able to duplicate the *in vivo* kinematics than the Rothschild model.

DISCUSSION

This paper has provided five lines of evidence to support the hypothesis proposed by Bennet-Clark and Lucey (Bennet-Clark and Lucey, 1967) that fleas jump by transmitting force developed by muscles in the thorax through their hind tibiae and tarsi to the ground: (1) extensive structures are present on the tarsus and the end of the tibia, but not on the trochanter, which could be used to grip a substrate; (2) fleas can jump even when the trochantera are not in contact with the ground; (3) the acceleration of a jump does not

decrease when the trochantera lose any contact they may have with the ground; (4) jumps have large horizontal components; and (5) the acceleration of a jump is consistent with a kinetic model that applies force to the ground through the tarsus and tibia but is not consistent with a model that applies force through the trochanter.

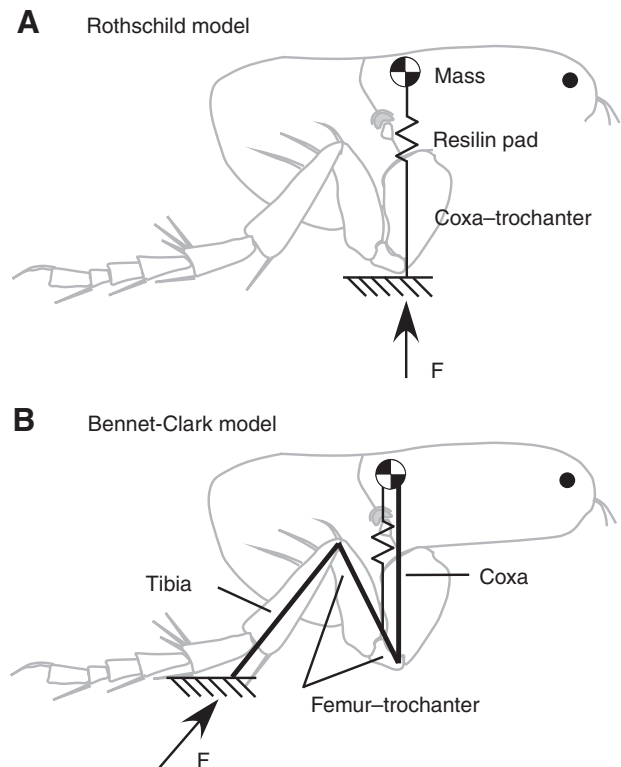


Fig. 10. (A) Mechanical model for the hypothesis that a flea directs forces to the ground with the trochanter (Rothschild model). The resilin pad is modelled as a spring between the ground and the centre of mass. (B) Mechanical model for the hypothesis that a flea directs forces to the ground with the tibia and tarsus (Bennet-Clark model). The leg is modelled as a three link system; tibia, femur–trochanter and coxa, with the resilin pad acting as a spring that generates a torque about the coxo-trochanteral joint. In both models, the centre of mass was placed at the end of the coxa.

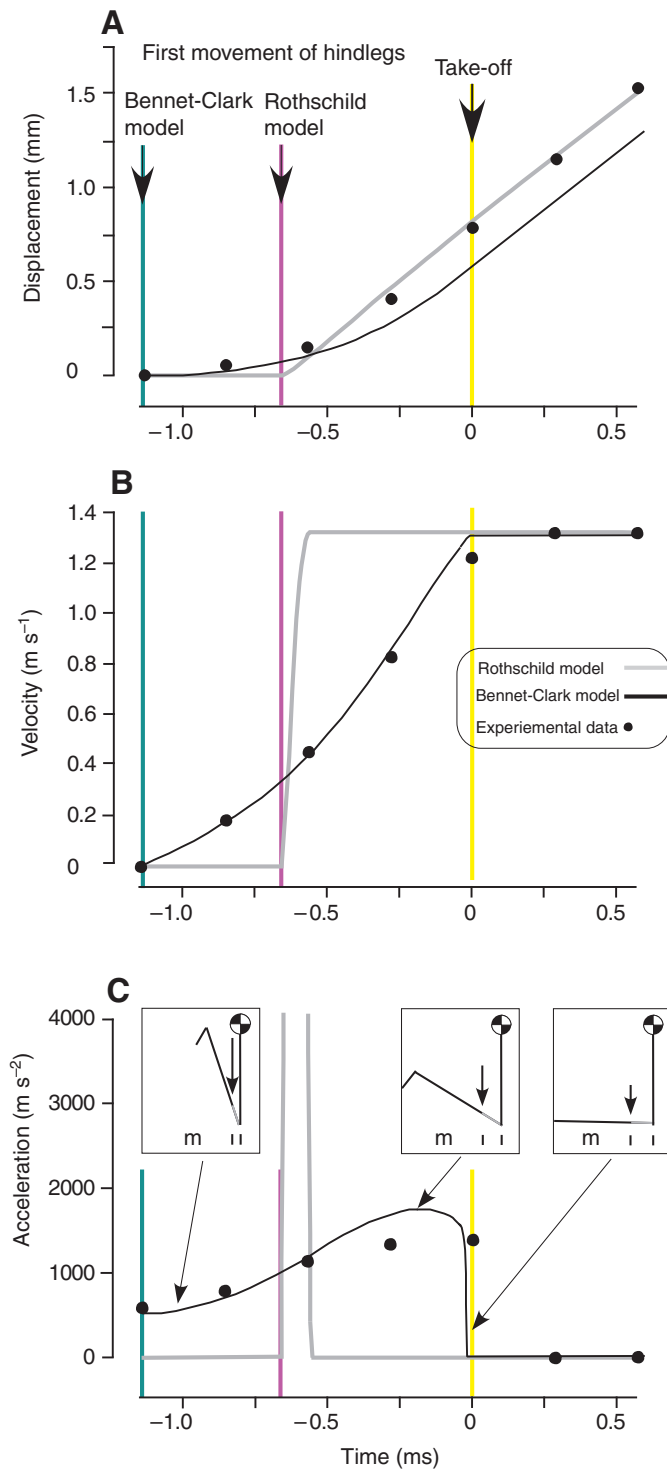


Fig. 11. Comparison of the outcomes of the Rothschild model for jumping (grey line), and the Bennet-Clark model (black line) with data from natural jumps of *Xenopsylla cheopis* (Rothschild et al., 1975) (black dots). The displacement (A), velocity (B) and acceleration (C) of the centre of mass are shown. Take-off occurred at time zero (vertical yellow line) with the first movement of the hindlegs occurring at different times (vertical teal and magenta lines) for the two models. In the Rothschild model, the predicted acceleration extended above the y -axis to $22,000 \text{ m s}^{-2}$. Insets in C show the positions of the femur and coxa in the Bennet-Clark model illustrating that the rise and fall in acceleration (black line) is caused by a combination of a decreasing spring force (downward pointing arrows) and an increasing moment arm (marked by 'm'). See text for details.

The only evidence to support the hypothesis of Rothschild and Schlein (Rothschild and Schlein, 1975) that the force is transmitted to the ground by the hind trochantera is that: (1) during a majority of jumps the trochantera start in close proximity to the ground; and (2) there are short hairs on the trochantera that could possibly be used to grip the ground. Although both the Bennet-Clark and the Rothschild models propose viable mechanisms to propel a jump, only the Bennet-Clark model proposes a mechanism that is consistent with the accelerations, velocities, initial position kinematics, take-off trajectories and the attachment mechanisms observed *in vivo*. Moreover, the kinematic data presented here and the data presented by Rothschild et al. are both consistent with the Bennet-Clark hypothesis (Rothschild et al., 1975).

From the data presented here it is not possible to differentiate between the hypotheses stated by Bennet-Clark and by Rothschild about the locking mechanisms for the leg joints. Bennet-Clark hypothesized that the joints were locked by the moment arm of the trochanteral depressor muscle going 'over centre', and thus the resilin 'spring' would act initially as a trochanteral levator [a similar mechanism has been proposed for the claw snap of an alpheid shrimp (Ritzmann, 1974) and for the femoro-tibial joint of the locust hindleg (Cofer et al., 2010)]. Subsequently, activation of another muscle pulls the apodeme over so that the spring acts as a depressor, thus triggering the jump (Bennet-Clark and Lucey, 1967). Rothschild hypothesized that the joints were locked *via* a series of cuticular 'catches' along the hindlegs and the body, and that the release of these locks triggered the jump (Rothschild and Schlein, 1975). To distinguish between this aspect of the two hypotheses requires a different sets of experiments that we have not attempted, and thus the release mechanism remains unresolved.

Control of jump direction and distance

The fact that the flea exerts force to the ground through the tibia means that its leg mechanics are very similar to those of the froghopper (Hemiptera, Auchenorrhyncha, Cercopidae) (Burrows, 2006a; Sutton and Burrows, 2010). Froghoppers and fleas both have an elastic storage mechanism that applies a large torque about the coxo-trochanteral joint, a trochanter that is mechanically linked closely to the femur, and very little torque is applied about their femoro-tibial joints. These insects do differ in that the legs of a flea are orientated in the sagittal plane of the animal, in contrast to the legs of a froghopper that are orientated in the coronal plane. The mechanics predict that the legs of both froghoppers and fleas generate forces that are parallel to their hind tibiae. From this, it follows that the mechanisms that froghoppers use to control jump azimuth could be used by fleas to control jump elevation. *A. erinacei*, however, does not vary greatly the elevation of its jumps. The 51 jumps analysed here were all within a 24 deg window of elevation. By contrast, the jumps of locusts (*Schistocerca*) and flea beetles (*Alticinae*) both have almost a 90 deg window of elevation (Brackenbury and Wang, 1995; Sutton and Burrows, 2010), and the jumps of froghoppers have a 72 deg window of elevation (Burrows, 2006b).

The small window of jump elevations used by fleas is puzzling because it would seem to be in its best interest to jump in a wide range unpredictable directions. It has been observed that some invertebrates have a limited number of preferred escape trajectories (Domenici et al., 2008), but *A. erinacei* appears to be different in that it has only one small window of escape trajectories. *A. erinacei* can vary its jumping distance, and it does so not by adjusting its take-off elevation, but by adjusting its take-off velocity. This variation in jump distance is consistent with the variation in jump

distance seen in other species of flea (Krasnov et al., 2003) and strongly suggests that fleas in general vary the distance they jump by changing jump velocity and not jump elevation. This makes the amount of energy stored before a jump a crucial control parameter for flea jumps. Although it is possible that the high-density foam platform used here restricts the directions in which the flea is able to jump, we do not think this is probable, because other species of insect have had little difficulty generating different jump trajectories from this surface (Burrows, 2010; Burrows, 2009; Burrows, 2003).

It is ironic that a famous jumper like a flea has such a restricted jump direction relative to insects less renowned for their jumping prowess, such as locusts (Bennet-Clark, 1975; Santer et al., 2005; Sutton and Burrows, 2008), froghoppers (Burrows, 2003; Sutton and Burrows, 2010), flies (*Drosophila*) (Card and Dickinson, 2008) or flea beetles (*Alticinae*) (Brackenbury and Wang, 1995). Because fleas also use jumps to reach prey, it is also reasonable to compare restricted jump trajectory to fast predatory strikes. The flea jump is more constrained in direction than frog tongue strikes (Mallet et al., 2001; Monroy and Nishikawa, 2009), squid tentacle strikes (Van Leeuwen and Kier, 1997) or spider predatory jumps (Weihmann et al., 2010). Applying force to the ground *via* the tibia gives the flea a theoretical ability to control its take-off elevation, but it does not use this mechanism.

Generality of proposed mechanisms in other fleas

Are the mechanisms that we report for *A. erinacei* representative of other species of flea such as *Xenopsylla cheops* (Rothschild and Schlein, 1975), *Spilopsyllus cuniculus* (Bennet-Clark and Lucey, 1967) and several species examined by Krasnov et al., including *Xenopsylla conformis* (Krasnov et al., 2003)? The average velocity at take-off ($1.3 \pm 0.22 \text{ m s}^{-1}$) in *A. erinacei* is slightly faster the average for *Spilopsyllus cuniculus* [1.0 m s^{-1} (Bennet-Clark and Lucey, 1967)]. The average jumping range from this take-off velocity, 169 mm (from Eqn 1, at an elevation of 39 deg), places *A. erinacei* in the upper range of performance for the flea species measured by Krasnov (Krasnov et al., 2003). *A. erinacei* also has a similar variability in the range of its jumps compared with other flea species (Fig. 9). *A. erinacei* also begins a jump with an initial position indistinguishable from the initial position taken by *Xenopsylla cheops* (Fig. 4) (Rothschild et al., 1975). Finally, the body plan of *A. erinacei* is very similar to the body plan of other fleas (Grimaldi and Engel, 2005). Based on these data, we suggest that the mechanical conclusions about flea jumping based on jumps by *A. erinacei* are applicable to other species of flea.

APPENDIX 1

The equations of motion for the Rothschild model of flea jumping were developed based on the hypothesis that the cuticular ‘spring’ applied forces directly to the ground through the hind trochanter. In this model, the recoil of the spring pushes directly down on the trochanter and onto the ground.

The equation of motion is thus:

$$M_{\text{COM}} \ddot{Y} = -K_{\text{Spring}} Y, \quad (\text{A1})$$

where M_{COM} is the mass of the flea, \ddot{Y} is the vertical acceleration of the flea, K_{Spring} is the spring stiffness and Y is the vertical position of the flea. The spring is constrained only to be able to provide positive forces. Take-off is when the spring displacement=0. Parameters for the model are presented in Table A1.

Table A1. Model parameters for the Rothschild and Bennet-Clark models, based on *Xenopsylla cheops*

Parameter	Value	Units	Source*
M_{COM}	0.2	mg	a
I_{COM}	0.144	mg mm ²	b
M_{Coxa}	0.004	mg	c
I_{Coxa}	5.3×10^{-5}	mg mm ²	d
L_{Coxa}	0.4	mm	a
M_{Femur}	0.04	mg	c
I_{Femur}	5.3×10^{-5}	mg mm ²	d
L_{Femur}	0.4	mm	a
M_{Tibia}	0.004	mg	c
I_{Tibia}	1.2×10^{-4}	mg mm ²	d
L_{Tibia}	0.6	mm	a
K_{Spring}	55.0	N m ⁻¹	e
L_{Initial}	0.35	mm	e
L_{M}	0.055	mm	a
Initial θ_{Coxa}	80.0	deg	f
Initial θ_{Femur}	-90.0	deg	f
Initial θ_{Tibia}	30.0	deg	f
Initial $\dot{\theta}_{\text{Coxa}}$	0	deg s ⁻¹	f
Initial $\dot{\theta}_{\text{Femur}}$	0	deg s ⁻¹	f
Initial $\dot{\theta}_{\text{Tibia}}$	0	deg s ⁻¹	f

I , inertia; K , stiffness; L , length; M , mass; θ , angle of elevation at take-off; $\dot{\theta}$, y .

*Sources: a, Bennet-Clark and Lucey (Bennet-Clark and Lucey, 1967) and Rothschild and Schlein (Rothschild and Schlein, 1975). b, The moment of inertia of the center of mass was estimated by approximating the flea’s body as a uniform disc. c, The mass of the coxa, tibia and femur were estimated, but had little affect on the output of the simulation. They were given mass because modelling the legs as massless resulted in equations of motion that were unstable (see Appendix 2). d, Moments of inertia for the coxa, femur and tibia were estimated by approximating the legs as uniform rods. e, The stiffness and resting length of the spring were estimated by assuming that the initial energy stored in the spring ($1/2 \text{ stiffness} \times \text{spring compression}^2$) was equal to the final kinetic energy of the jump ($1/2 \text{ mass} \times \text{velocity}^2$). Many values of spring stiffness and initial spring length were modelled, but the qualitative shape of the output was not dependent on this parameter. f, The starting leg angles were determined from the leg kinematics of *A. erinacei* because starting leg kinematics were hard to determine from the photos in Rothschild et al. (Rothschild et al., 1975).

APPENDIX 2

The equations of motion for the Bennet-Clark model of flea jumping were developed based on the hypothesis that the cuticular ‘spring’ applied forces through the hindlegs as a system of lever arms, with the final ground reaction forces being directed through the tibia. This model has a larger set of parameters, based on the properties of the spring and on the properties of the leg segments. These parameters are presented in Table A1. The model output was almost completely insensitive to the mass and moment of inertia of the leg segments, but these values were included because running the model with massless leg segments created numerical instability in the simulation.

Equations of motion for each segment were generated using a Lagrangian formulation (Greenwood, 1988), which derives the equations of motion for the torques on each link (T_{Tibia} , T_{Femur} , T_{Coxa}) by differentiating the energy (E) of the system by the angle of each link (θ_{Tibia} , θ_{Femur} , θ_{Coxa}).

The kinetic energy of the system was then calculated in terms of the masses of the body, coxa, femur and tibia (M_{COM} , M_{Coxa} , M_{Femur} and M_{Tibia} , respectively), the velocities of the body, coxa, femur and tibia (V_{COM} , V_{Coxa} , V_{Femur} and V_{Tibia} , respectively), the moments of inertia of the body, coxa, femur and tibia (I_{COM} , I_{Coxa} , I_{Femur} and

I_{Tibia} , respectively) and the angular velocities of the coxa, femur and tibia ($\dot{\theta}_{Coxa}$, $\dot{\theta}_{Femur}$ and $\dot{\theta}_{Tibia}$, respectively). The model's centre of mass was rigidly attached to the coxa and thus had the same angular velocity as the coxa:

$$E = \frac{1}{2} (M_{COM} V_{COM}^2 + M_{Coxa} V_{Coxa}^2 + M_{Femur} V_{Femur}^2 + M_{Tibia} V_{Tibia}^2 + I_{COM} \dot{\theta}_{Coxa}^2 + I_{Coxa} \dot{\theta}_{Coxa}^2 + I_{Femur} \dot{\theta}_{Femur}^2 + I_{Tibia} \dot{\theta}_{Tibia}^2) \quad (A2)$$

The equations of motion in terms of the torques (T_{Femur} , T_{Tibia} , T_{Coxa}) on the links were generated using Lagrange's equations (Greenwood, 1988):

$$T_{Femur} = \frac{D}{Dt} \left(\frac{\partial E}{\partial \dot{\theta}_{Femur}} \right), \quad (A3)$$

$$T_{Tibia} = \frac{D}{Dt} \left(\frac{\partial E}{\partial \dot{\theta}_{Tibia}} \right), \quad (A4)$$

$$T_{Coxa} = \frac{D}{Dt} \left(\frac{\partial E}{\partial \dot{\theta}_{Coxa}} \right). \quad (A5)$$

For small insects, the gravity terms are negligible and thus were omitted (Scholz et al., 2006).

The torques were calculated by modelling the resilin lump as a spring connecting the centre of mass with the end of a moment arm (L_M) on the trochanter–femur link. This produced equal and opposite torques on the femur and the coxa, which generated an expression for T_{Coxa} and T_{Femur} : in terms of the stiffness of the spring (K_{Spring}), the length of the spring (L_{Spring}) and the moment arm of the trochanter (Arm_{Spring}):

$$T_{Coxa} = -T_{Femur} = K_{Spring} L_{Spring} Arm_{Spring} \quad (A6)$$

(K_{Spring} is identical to the stiffness for the Rothschild model). L_{Spring} is the distance between the attachment point of the spring and the centre of mass minus the resting length of the spring in terms of the geometry of the leg. As the legs rotate, this distance changes with the function:

$$L_{Spring} = \sqrt{L_{Coxa}^2 + L_M^2 - 2L_{Coxa} L_M \cos(\theta_{Coxa} - \theta_{Femur})} - L_{initial}, \quad (A7)$$

where L_{Coxa} and L_M are the lengths of the coxa and the trochanteral moment arm for the spring, respectively. θ_{Coxa} and θ_{Femur} are the angles of the coxa and femur. $L_{initial}$ is the resting length of the spring.

Arm_{Spring} is the component of the moment arm perpendicular to the force applied by the spring:

$$Arm_{Spring} = \frac{L_{Coxa} L_M}{\sqrt{L_{Coxa}^2 + L_M^2 - 2L_{Coxa} L_M \cos(\theta_{Coxa} - \theta_{Femur})} \sin(\theta_{Femur} - \theta_{Coxa})}. \quad (A8)$$

Lastly, we assumed that the small musculature connecting the femur to the tibia allowed no torques to be applied at that joint, i.e. $T_{Tibia}=0$.

At each timestep the ten equations were solved for the angular accelerations of the links ($\ddot{\theta}_{Coxa}$, $\ddot{\theta}_{Femur}$ and $\ddot{\theta}_{Tibia}$). The equations were solved with the Mathematica 5.2 NDSolve function. The model parameters are shown in Table A1.

ACKNOWLEDGEMENTS

G.P.S. was funded by the Marshall Sheffield Commission and the Human Frontiers Research Program. We thank Cambridge colleagues for their many helpful suggestions during the course of this work and for their comments on the draft manuscript.

REFERENCES

- Andersen, S. (1963). Characterization of a new type of cross-linkage in resilin, a rubber-like protein. *Biochim. Biophys. Acta* **69**, 249-262.
- Askew, G. N. and Marsh, R. L. (2002). Muscle designed for maximum short-term power output: quail flight muscle. *J. Exp. Biol.* **205**, 2153-2160.
- Bennet-Clark, H. C. (1975). The energetics of the jump of the locust *Schistocerca gregaria*. *J. Exp. Biol.* **63**, 53-83.
- Bennet-Clark, H. C. and Lucey, E. C. A. (1967). The jump of the flea: a study of the energetics and a model of the mechanism. *J. Exp. Biol.* **47**, 59-76.
- Brackenbury, J. and Wang, R. (1995). Ballistics and visual targeting in flea-beetles (Alticinae). *J. Exp. Biol.* **198**, 1931-1942.
- Burrows, M. (2003). Froghopper insects leap to new heights. *Nature* **424**, 509.
- Burrows, M. (2006a). Morphology and action of the hind leg joints controlling jumping in froghopper insects. *J. Exp. Biol.* **209**, 4622-4637.
- Burrows, M. (2006b). Jumping performance of froghopper insects. *J. Exp. Biol.* **209**, 4607-4621.
- Burrows, M. (2009). Jumping strategies and performance in shore bugs (hemiptera, heteroptera, saltididae). *J. Exp. Biol.* **212**, 106-115.
- Burrows, M. (2010). Jumping mechanisms and performance of pygmy mole crickets (Orthoptera, Tridacylidae). *J. Exp. Biol.* **213**, 2386-2398.
- Burrows, M., Shaw, S. R. and Sutton, G. P. (2008). Resilin and chitinous cuticle form a composite structure for energy storage in jumping by froghopper insects. *BMC Biol.* **6**, 41.
- Card, G. C. and Dickinson, M. H. (2008). Visually mediated motor planning in the escape response of *Drosophila*. *Curr. Biol.* **18**, 1300-1307.
- Cofer, D., Cymbalyuk, G., Heitler, W. J. and Edwards, D. H. (2010). Neuromechanical simulation of the locust jump. *J. Exp. Biol.* **213**, 1060-1068.
- Domenici, P., Booth, D., Blagburn, J. M. and Bacon, J. P. (2008). Cockroaches keep predators guessing by using preferred escape trajectories. *Curr. Biol.* **18**, 1792-1796.
- Greenwood, D. T. (1988). *Principles of Dynamics*. Englewood Cliffs, NJ, USA: Prentice-Hall, Inc.
- Grimaldi, D. A. and Engel, M. S. (2005). *Evolution of the Insects*. Cambridge: Cambridge University Press.
- Krasnov, B. R., Burdelov, S. A., Khokhlova, I. S. and Burdelova, N. V. (2003). Sexual size dimorphism, morphological traits and jump performance in seven species of desert fleas (Siphonaptera). *J. Zool. (Lond.)* **261**, 181-189.
- Mallett, E. S., Yamaguchi, G. T., Birch, J. M. and Nishikawa, K. C. (2001). Feeding motor patterns in anurans: insights from biomechanical modeling. *Am. Zool.* **41**, 1364-1374.
- Monroy, J. A. and Nishikawa, K. C. (2009). Prey location, biomechanical constraints, and motor program choice during prey capture in the tomato frog, *Dyscophus guineti*. *J. Comp. Physiol. A* **195**, 843-852.
- Ritzmann, R. E. (1974). Mechanisms for snapping behaviour of 2 alpheid shrimp, *Alpheus californiensis* and *Alpheus heterochelis*. *J. Comp. Physiol.* **95**, 217-236.
- Roberts, T. J. and Marsh, R. L. (2003). Probing the limits to muscle-powered accelerations: lessons from jumping bullfrogs. *J. Exp. Biol.* **206**, 2567-2580.
- Rothschild, M. (1965). Fleas. *Sci. Am.* **213**, 44-53.
- Rothschild, M. and Schlein, J. (1975). The jumping mechanism of *Xenopsylla cheopis* I. Exoskeletal structures and musculature. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **271**, 457-490.
- Rothschild, M., Schlein, Y., Parker, K. and Sternberg, S. (1972). Jump of the oriental rat flea. *Xenopsylla cheopis* (Roths.). *Nature* **239**, 45-47.
- Rothschild, M., Schlein, Y., Parker, K., Neville, C. and Sternberg, S. (1973). The flying leap of the flea. *Sci. Am.* **146**, 92-98, 100.
- Rothschild, M., Schlein, J., Parker, K., Neville, C. and Sternberg, S. (1975). The jumping mechanism of *Xenopsylla cheopis*. III. Execution of the jump and activity. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **271**, 499-515.
- Russel, H. (1913). *The Flea*. Cambridge, UK: Cambridge University Press.
- Santer, R. D., Yamawaki, Y., Rind, C. F. and Simmons, P. J. (2005). Motor activity and trajectory control during escape jumping in the locust *Locusta migratoria*. *J. Comp. Physiol. A* **191**, 965-975.
- Scholz, M. N., Bobbert, M. F. and Knoek van Soest, A. J. (2006). Scaling and jumping: Gravity loses grip on small jumpers. *J. Theor. Biol.* **240**, 554-561.
- Snodgrass, R. E. (1946). The skeletal anatomy of fleas (Siphonaptera). *Smithsonian Misc. Collections* **104**, 1-89.
- Sutton, G. P. and Burrows, M. (2008). The mechanics of elevation control in locust jumping. *J. Comp. Physiol. A* **194**, 557-563.
- Sutton, G. P. and Burrows, M. (2010). The mechanics of azimuth control in jumping by froghopper insects. *J. Exp. Biol.* **213**, 1406-1416.
- Van Leeuwen, J. L. and Kier, W. M. (1997). Functional design of tentacles in squid: linking sarcomere ultrastructure to gross morphological dynamics. *Philos. Trans. R. Soc. Lond. B, Biol. Sci.* **352**, 551-571.
- Vogel, S. (2005). Living in a physical world. III. Getting up to speed. *J. Biosci.* **30**, 303-312.
- Weihmann, T., Karner, M., Full, R.J. and Blickhan, R. (2010). Jumping kinematics in the wandering spider *Cupiennius salei*. *J. Comp. Physiol. A* **196**, 421-438.
- Weis-Fogh, T. (1960). A rubber-like protein in insect cuticle. *J. Exp. Biol.* **37**, 889-907.