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The jump of the click beetle (Coleoptera: Elateridae)—energetics and mechanics

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(With 5 figures in the text)

Some aspects of the energetics and mechanics of two jumps made by a single specimen of *Athous haemorrhoidalis* (Fab.) are considered. In the first jump, the 40 mg beetle had a take-off velocity of 2·4 m/s and the jumping action occurred in about 0·64 ms; in the second jump, the take/off velocity was 2·26 m/s and the jumping action took about 0·53 ms. Energy budgets have been constructed in two different ways for each jump, and the total energy involved in each case was estimated to lie between $1{\cdot}6 \times 10^{-4}$ J and $3{\cdot}8 \times 10^{-4}$ J. Power output during the jumping action (a "catapult") lay between 80×10^{3} W/kg muscle and 180×10^{3} W/kg muscle, whilst power output during the energy storing pre-jump period (of about 0·4 s) was at least 130 W/kg muscle (at over 25°C). Forces and tensile stresses in the jumping muscles and their apodemes have also been calculated. The method of jumping appears to be fairly inefficient in that only about 50–60% of the energy expended in the jumping action is energy of translation, which actually raises the beetle.

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Introduction

In the present paper, two jumps by a single specimen of *Athous haemorrhoidalis* (Fab.) will be considered. The two jumps were selected as being typical of several fairly high jumps which were recorded on 16 mm ciné film with a high speed camera. This method has been described in a previous paper (Evans, 1972). The first jump will be considered in some detail, and will be followed by a list of the equivalent figures derived from the second jump.

I. First jump

The beetle studied weighed 40 mg and had a take-off velocity of 2·4 m/s (averaged over the first 2 ms); the jumping action (jack-knifing) during which the beetle was accelerated from 0 to 2·4 m/s, took place in not more than 0·64 ms.

1. *Energetics*

It was noted (Evans, 1972) that the kinetic energy acquired in the jump described above was

$$\tfrac{1}{2} \times 40 \times 10^{-6} \times 2{\cdot}4^2 = 1{\cdot}15 \times 10^{-4}\,\mathrm{J}$$

This figure refers only to the translational energy. To obtain a more accurate estimate of the energy expended in jumping, the rotational energies of the two moving parts of the body must be considered. To calculate these energies, the angular velocities of the head plus prothorax (hereafter referred to as the prothorax) and the hind body were measured, and rough estimates were made of their moments of inertia.

a. Angular velocities

At the start of the jump, the prothorax moved through 41° and the hindbody through 12° in not less than 0·64 ms. Unfortunately, the acceleration involved is not constant, but if it is assumed to be constant over this period, a rough estimate of velocity can be made. Thus the terminal angular velocity of the prothorax, ω_p, was 2240 rad/s, and that of the hindbody, ω_h, was 650 rad/s.

b. Moments of inertia

To calculate these, both the prothorax and hindbody were considered as rigid bodies—prisms—which were related as shown in Fig. 1.

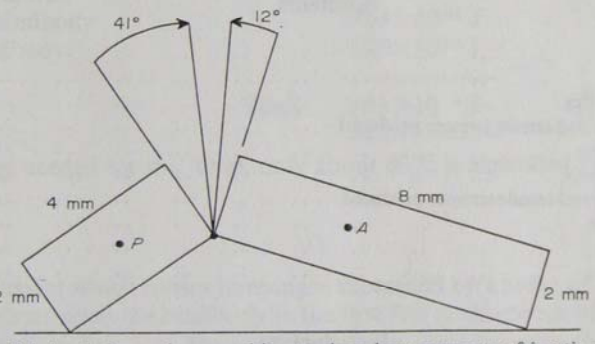

FIG. 1. Diagram of click beetle in pre-jump position to show how moments of inertia have been calculated. The angles of movement of the prothorax (10 mg) and the hindbody (30 mg) are shown for the first 0·64 ms. (For further explanation see text.)

The prisms have centres of gravity at P and A respectively. Then the moment of inertia, I_p, of the prothorax about P (following Prentis, 1970) is

$$\frac{10^{-5}}{12}\left[\,(4\times10^{-3})^2+(2\times10^{-3})^2\,\right] = 0{\cdot}17\times10^{-10}\ \mathrm{kg\ m^2}.$$

Similarly, the moment of inertia of the hindbody, I_h, about its centre of gravity A is

$$\frac{3\times10^{-5}}{12}\left[\,(8\times10^{-3})^2+(2\times10^{-3})^2\,\right] = 1{\cdot}7\times10^{-10}\ \mathrm{kg\ m^2}.$$

c. Kinetic energy of rotation

The K.E. of rotation of the prothorax is

$$\tfrac{1}{2}I_p.\ \omega_p{}^2 = \tfrac{1}{2}\times 0{\cdot}17\times 10^{-10}\times 2240^2 = 0{\cdot}43\times 10^{-4}\ \text{J}.$$

The K.E. of rotation of the hindbody is

$$\tfrac{1}{2}I_h.\ \omega_h{}^2 = \tfrac{1}{2}\times 1{\cdot}7\times 10^{-10}\times 650^2 = 0{\cdot}36\times 10^{-4}\ \text{J}.$$

d. Kinetic energy of translation

P moves 1·2 mm from rest in not more than 0·64 ms, so its terminal linear velocity is

$$\frac{12\times 10^{-4}\times 2}{6{\cdot}4\times 10^{-4}} = 3{\cdot}75\ \text{m/s}.$$

A moves 0·6 mm from rest in not more than 0·64 ms, so its terminal linear velocity is

$$\frac{6\times 10^{-4}\times 2}{6{\cdot}4\times 10^{-4}} = 1{\cdot}9\ \text{m/s}\ .$$

Thus the K.E. of translation of the prothorax is

$$\tfrac{1}{2}\times 10^{-5}\times 3{\cdot}75^2 = 0{\cdot}7\times 10^{-4}\ \text{J}\quad .$$

Similarly, the K.E. of translation of the hindbody is

$$\tfrac{1}{2}\times 3\times 10^{-5}\times 1{\cdot}9^2 = 0{\cdot}54\times 10^{-4}\ \text{J}.$$

e. Energy budget for the jump

K.E. of translation of prothorax	$0{\cdot}7\ \times 10^{-4}$ J
K.E. of rotation of prothorax	$0{\cdot}43\times 10^{-4}$ J
K.E. of translation of hindbody	$0{\cdot}54\times 10^{-4}$ J
K.E. of rotation of hindbody	$0{\cdot}36\times 10^{-4}$ J
Total:	$2{\cdot}03\times 10^{-4}$ J

Thus, of the total energy needed for the jump, only about 60 % is expended in raising the beetle.

f. Energy of vibration

The jack-knifing movement which causes jumping is succeeded by a series of "bouncing" movements of the prothorax upon the hindbody in the first few milliseconds of the beetle's trajectory (this can be seen in Fig. 3 of Evans, 1972). If the angle between the prothorax and the hindbody (measured between the lines mandibular apex to pivot, and pivot to apex of hindbody) is plotted against time, the graph seen in Fig. 2(a) is produced. These oscillations clearly resemble those of a lightly damped resonant system. They can be considered as representing the torsional vibration of two rotors of moments of inertia J_p and J_h mounted at opposite ends of a shaft of torsional stiffness S. The moments of inertia in this case are those with respect to the pivot—the hinge between the prothorax and hindbody. Thus the two prisms in Fig. 1 rotate about their corners. These are parallel axes to P and A, so

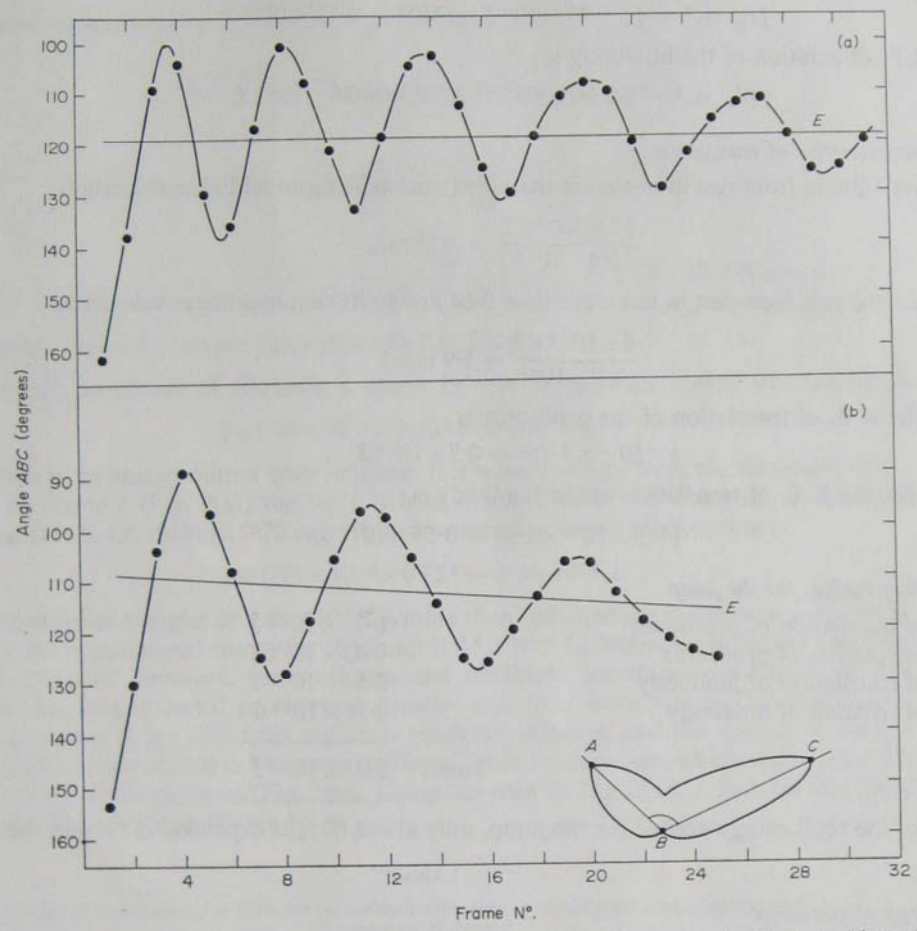

FIG. 2. Graphs to show the "bouncing" movement of the head and prothorax upon the hindbody. The angle in degrees (*ABC* on inset diagram) between the prothorax and hindbody is plotted against time (frame number). (a) Shows the first jump and (b) shows the second jump. In (a) frames are 0·32 ms apart, and in (b) are 0·27 ms apart. *E* Shows the equilibrium position on each graph.

$$J_p = \frac{10^{-5}}{12}\left[(4\times10^{-3})^2+(2\times10^{-3})^2\right]+10^{-5}\times(2{\cdot}2\times10^{-3})^2 = \underline{0{\cdot}65\times10^{-10}\ \text{kg m}^2}.$$

$$\text{and } J_h = \frac{3\times10^{-5}}{12}\left[(8\times10^{-3})^2+(2\times10^{-3})^2\right]+3\times10^{-5}\times(3{\cdot}5\times10^{-3})^2 = \underline{5{\cdot}38\times10^{-10}.\ \text{kg m}^2}.$$

The period of vibration of a two-rotor system with the above moments of inertia, (following Prentis, 1970), is

$$2\pi\left(\frac{S}{J_p}+\frac{S}{J_h}\right)^{-\frac{1}{2}}.$$

The initial vibration period is 1·4 ms (Fig. 2(a)), thus

$$1{\cdot}4\times10^{-3} = 2\pi\left(\frac{S}{0{\cdot}65\times10^{-10}}+\frac{S}{5{\cdot}38\times10^{-10}}\right)^{-\frac{1}{2}}$$

$$= 2\pi\left(\frac{5{\cdot}38\times10^{10}S+0{\cdot}65\times10^{10}S}{0{\cdot}65\times5{\cdot}38}\right)^{-\frac{1}{2}}$$

$$S = \frac{4\pi^2}{(1{\cdot}4\times10^{-3})^2\times1{\cdot}7\times10^{10}} = 1{\cdot}18\times10^{-3}\ \text{Nm/rad}\ .$$

The energy stored by torsion through angle θ is $\frac{1}{2}S\theta^2$.

If the initial amplitude of vibration is about 19° —0·33 rad—the energy of vibration is

$$\tfrac{1}{2}\times1{\cdot}18\times10^{-3}\times0{\cdot}33^2 = 0{\cdot}64\times10^{-4}\ \text{J}.$$

Since this is the energy output *after* jumping, it is wasted energy from the viewpoint of the jump. In frame 1 (Fig. 2(a)) the body is bent through about 43° from the equilibrium position (119°), i.e. through 0·75 rad. Thus the energy stored in this position is

$$\tfrac{1}{2}\times1{\cdot}18\times10^{-3}\times0{\cdot}75^2 = 3{\cdot}3\times10^{-4}\ \text{J}.$$

The difference in energies of $2{\cdot}66\times10^{-4}$J is more than sufficient for the amount required to provide the translational energy for the jump ($1{\cdot}15\times10^{-4}$ J). Immediately before the jump, the two "rotors" involved, the prothorax and hindbody, are flung together by the M4 muscle (the lateral dorsal prothoracic muscle) and then flung apart. This sequence is repeated several times whilst the muscle is gradually relaxing, and this relaxation may be responsible for the change in "torsional stiffness", S in the equation, which decreases as the period of vibration increases (Fig. 2(a)). Using the data in Fig. 2(a)), S may be calculated for successive vibrations (Table 1).

TABLE I

Change of S with period of vibration immediately after time indicated after start of jack-knifing movement at frame 1

Frame	time (ms)	Vibration period (ms)	S (Nm/rad × 10^{-3})
(1—) 2·5	0·5	1·4	1·18
7	1·9	1·6	0·91
12	3·5	1·9	0·64
18	5·4	2·1	0·53
24·5	7·5	2·3	0·46
(—31·5)			

If the decrease of S against time is graphed for the first 8 ms of the jump, the curve seen in Fig. 3 is obtained which enables a maximum value of S to be extrapolated. This is about $1{\cdot}35\times10^{-3}$ Nm/rad. This suggests that the maximum energy stored at the beginning of the jump was not $3{\cdot}3\times10^{-4}$ J, but $3{\cdot}8\times10^{-4}$ J.

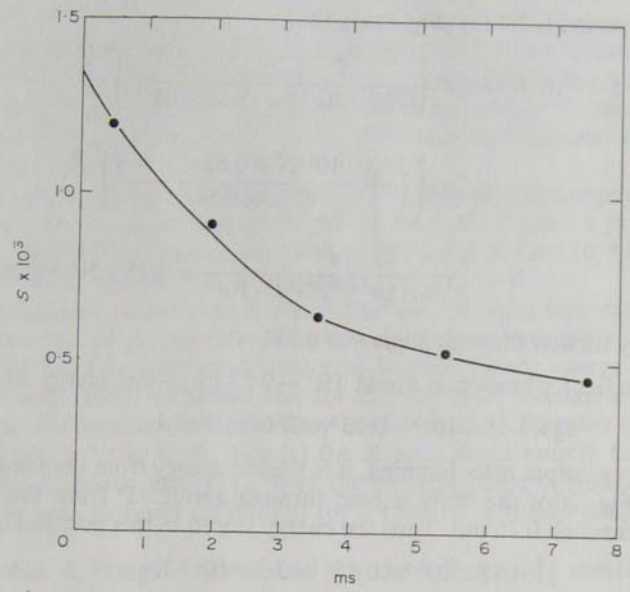

FIG. 3. For the first jump, the stiffness, S Nm/rad, of the jumping muscle (M4) has been plotted against time in milliseconds to obtain a maximum value of S. (For explanation see text.)

g. Alternative energy budget

The maximum energy stored at the beginning of the jump should be equal to the energy of vibration after take-off plus the energy of translation for the whole body plus the energy of rotation for the whole body. The latter figure must be included because the action of jumping imparts rotational energy to the whole beetle. In the jump considered, the 40 mg beetle rotated at 14·2 rev/s—89 rad/s.

If the beetle is considered as a rectangular prism 2 × 12 mm, rotating about its centre of gravity, then the energy of rotation is:

$$\tfrac{1}{2}\times\frac{40\times10^{-6}}{12}\left[(12\times10^{-3})^2+(2\times10^{-3})^2\right]\times89^2=0{\cdot}02\times10^{-4}\,\mathrm{J}.$$

Then the energy budget is

Energy of translation of whole body	$1{\cdot}15\times10^{-4}$ J
Energy of rotation of whole body	$0{\cdot}02\times10^{-4}$ J
Energy of vibration of whole body	$0{\cdot}64\times10^{-4}$ J
Total	$1{\cdot}81\times10^{-4}$ J

This figure is only about half the figure of $3{\cdot}8\times10^{-4}$ J for the maximum energy stored at the beginning of the jump. However, it is close to the previously calculated figure (e) of $2{\cdot}03\times10^{-4}$ J.

h. Power produced

The kinetic energy of translation of the whole body $1{\cdot}15\times10^{-4}$ J was used in a previous paper (Evans, 1972) to calculate a minimum power output during the jump of 54×10^{3} W/kg (54 W/g) muscle. In the jump considered the total energy estimates made were $2{\cdot}0\times10^{-4}$ J, $3{\cdot}8\times10^{-4}$ J and $1{\cdot}8\times10^{-4}$ J. In the following calculations the highest and lowest figures will be used.

The M4 muscle in the specimen studied weighed 3·36 mg, and the jumping action lasted not more than 0·64 ms. Thus, an energy output of $1{\cdot}8\times10^{-4}$ J gives a power output of 84×10^{3} W/kg muscle (84 W/g muscle), and an energy output of $3{\cdot}8\times10^{-4}$ J gives a power output of 177×10^{3} W/kg muscle (177 W/g muscle).

Of course, this immense power output merely reflects the short time during which the "catapult" operates. It is of greater interest to calculate the time over which the jumping muscle, M4, would have to contract in order to store sufficient energy for the jump. Bennet-Clark & Lucey (1967) estimated this for the depressor trochanter muscle of the hind leg of the flea, *Spilopsyllus cuniculus*. They used Machin & Pringle's (1959) figure of 6×10^{5} ergs.g. muscle^{-1}s^{-1} (60 W/kg muscle) for *Bombus* flight muscle to calculate the time needed by the depressor muscle to store the required energy. This time was 0·05 s, and as the flea was seen to build up tension for 0·1 to 0·25 s before jumping, this fitted nicely.

In *Athous*, Machin & Pringle's figure used for the 3·36 mg M4 muscle with a total energy output of

$$1{\cdot}8\times10^{-4}\text{ J gives } \frac{1{\cdot}8\times10^{-4}}{60\times3{\cdot}36\times10^{-6}} = 0{\cdot}9\text{ s.}$$

$$\text{With } 3{\cdot}8\times10^{-4}\text{ J it gives } \frac{3{\cdot}8\times10^{-4}}{60\times3{\cdot}36\times10^{-6}} = 1{\cdot}9\text{ s.}$$

In fact, for the jump considered, *Athous* needed only 0·4 s to build up tension for the jump. However, Weis-Fogh (1952) quoted a power output figure based on total heat production in *Apis mellifera* of 2400 kcal/kgh. Assuming 14 % efficiency (as in locust dorsal longitudinal flight muscle) this is equivalent to about 400 W/kg. If this power output figure is used for *Athous*, the M4 muscle would need either 0·13 s or 0·28 s. Mammal skeletal muscle may produce even higher power outputs in single contractions—as for instance human leg muscles in standing jumps (Davies & Rennie, 1968).

These figures suggest that the M4 muscle of *Athous* is an efficient skeletal muscle giving a high power output (of at least 130 W/kg at 25 +°C) from a single, tetanic contraction. Nevertheless, because of the short period of time the beetle remained in the 'set' position during this particular jump, it is likely that the M4 muscle must have produced and stored energy for the whole of this pre-jump period.

2. Forces and tensile stresses produced

2a. Forces produced

The force produced by the M4 muscle during the jump—or just prior to it—can be calculated from the work done, i.e. the energy output. Two figures have been estimated from this.

(i) To do $1{\cdot}8\times10^{-4}$ J work in rotation of the two parts of the beetle about H (Fig. 4) through 62° (1·08 rad), the muscle must exert an average moment about the joint of

$$\frac{1{\cdot}8\times10^{-4}}{1{\cdot}08} = 1{\cdot}67\times10^{-4}\ \text{Nm}.$$

Since the perpendicular distance of MD (the M4 muscle) from H (the hinge) is 0·35 mm, the average force produced by the muscle is

$$\frac{1{\cdot}67\times10^{-4}}{0{\cdot}35\times10^{-3}} = 0{\cdot}48\text{N}.$$

If the muscle operates as a catapult, and the force falls to zero as it shortens, the initial (maximum) force will be double the average force, i.e. 0·96 N.

(ii) To do $3{\cdot}8\times10^{-4}$ J work in rotation through 1·08 rad, the average moment about the joint would be

$$\frac{3{\cdot}8\times10^{-4}}{1{\cdot}08} = 3{\cdot}5\times10^{-4}\ \text{Nm}.$$

The average force produced would be $\dfrac{3{\cdot}5\times10^{-4}}{0{\cdot}35\times10^{-3}} = 1{\cdot}0$ N,

and the initial (maximum) force would be 2·0 N.

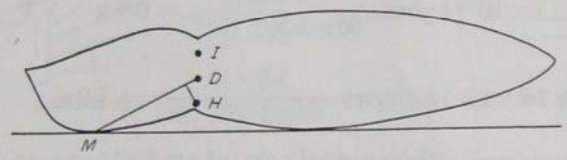

FIG. 4. Profile of *Athous* in set position with ventral surface uppermost (For explanation see text.)

2b. Tensile stress developed by the M4 muscle

Each M4 muscle is pinnate, with about 150 bundles of fibres in each muscle. Thus, the cross-sectional area of 1 mm² half way along the pair of muscles gives too high a figure for the maximum tensile stress produced. Conversely, since the muscle originates obliquely on the pronotum, the sum of the areas of origin of all the fibres—5 mm²—gives too low a figure. Alexander (1968) has given a simple method for estimating the increase in force produced by a pinnate muscle as compared with the parallel fibred muscle of the same length. Given certain assumptions, such a muscle—of length ℓ and width y—will produce $\dfrac{0{\cdot}9\ell}{y}$ times the force of a similar sized non-pinnate muscle. The factor for the *Athous* M4 muscle is about 2·7. Alexander (1969) has also given another method for calculating the force exerted by a pinnate muscle, but this depends on measuring the area of insertion of the muscle on its tendon. The apodeme of M4 is a composite of many individual apodemes, which gives the main apodeme the appearance of having long, "frilly" edges when the muscle is dissolved away. Thus the simplest way of measuring the tensile stress developed by the M4 muscles seems to be to use the area of muscle origin, and correct this

figure to give the equivalent area of cross-section at right angles to the fibre bundles (Fig.5).

To obtain this figure, the muscle was divided up as in Fig. 5, and the area of muscle origin represented by $AB+BC+CD+DE$ was corrected to $AW+BX+CY+DZ$.

This gave the corrected figure for cross-sectional area of the pair of M4 muscles as 2·8 mm². (This figure is in close agreement with the force factor of 2·7 quoted above.)

Since the total force developed by the M4 muscle (at well above 25°C) ranges from (i) 0·96 N to (ii) 2·0 N, the maximum tensile stress developed is:

$$\text{(i)}\quad \frac{0{\cdot}96}{2{\cdot}8\times10^{-6}} = 3{\cdot}4\times10^{5}\ \text{N/m}^2 \text{ or } 3{\cdot}4\ \text{kg/cm}^2,$$

$$\text{(ii)}\quad \frac{2{\cdot}0}{2{\cdot}8\times10^{-6}} = 7{\cdot}0\times10^{5}\ \text{N/m}^2 \text{ or } 7{\cdot}0\ \text{kg/cm}^2.$$

These figures are rather more than the maximum tensile stress developed by the dorsal longitudinal flight muscles of the locust. Weis-Fogh (1956) estimated this as 3·0 kg/cm² at 25°C, and 4·0 kg/cm² at 35°C.

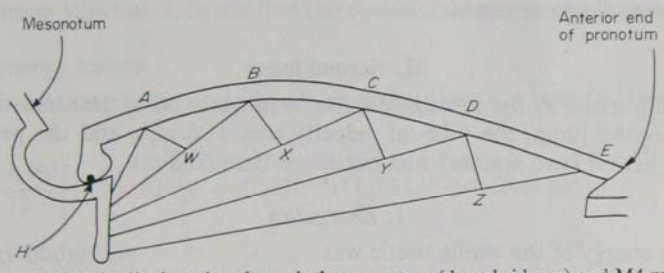

FIG. 5. Diagrammatic longitudinal section through the pronotum (dorsal side up) and M4 muscle. (For further explanation see text.)

2c. *Tensile stress on the M4 apodemes*

The posterior end of the M4 apodeme is a wide, but very flattened strap attached to the anterior, lateral margin of the mesonotum. It is about 0·35 mm wide but only about 0·01 mm deep, on average. This gives a cross-sectional area of $3{\cdot}5\times10^{-3}$ mm². Since the force produced by one muscle is between

(i) 0·48 N (0·048 kg wt) and (ii) 1·0 N (0·1 kg wt),

the tensile stress in the apodeme is between

$$\text{(i)}\quad \frac{0{\cdot}048}{3{\cdot}5\times10^{-3}} = 13{\cdot}7\ \text{kg/mm}^2,$$

$$\text{and (ii)}\quad \frac{0{\cdot}1}{3{\cdot}5\times10^{-3}} = 28{\cdot}6\ \text{kg/mm}^2.$$

Jensen & Weis-Fogh (1962) have estimated the tensile strength of locust tibial cuticle at 9·6 kg/mm², and Brown (1963) estimated the strength of the locust tibial extensor tendon at 18 kg/mm², so the first figure for the M4 apodeme seems reasonable, although the second figure may be rather high.

2d. Decelerating force in the M4 muscle

The jack-knifing movement of the beetle is finally halted by the collision of the prothoracic "bumpers" with the mesothoracic "buffers". The smallest angle between the prothorax and hindbody is reached at this point, and this position is not regained by succeeding vibrations (Fig. 2(a)). Successive vibrations occur about an equilibrium angle (119° in this jump). Thus it seems likely that the prothorax is decelerated in relation to the hindbody once this equilibrium position is first passed, and that the oscillations are due to "bouncing" on the M4 muscle.

The decelerating force in the M4 muscle can be calculated from the muscle's stiffness, S, which is $1{\cdot}35\times10^{-3}$ Nm/rad, and the initial amplitude of vibration, which is 19° (0·33 rad). Then the moment at 19° is $1{\cdot}35\times10^{-3}\times0{\cdot}33 = 4{\cdot}5\times10^{-4}$Nm. The distance at which the muscle is acting is $3{\cdot}5\times10^{-4}$m. Therefore, the force in the muscle is

$$\frac{4{\cdot}5\times10^{-4}}{3{\cdot}5\times10^{-4}} = 1{\cdot}3 \text{ N}.$$

Since the accelerating force in the muscle was probably between 0·96 N and 2·0 N, this decelerating force seems reasonable.

II. Second jump

A second jump made by the same beetle has been analysed in the same way as the first jump. In the second jump, the take-off velocity was 2·26 m/s, and the period from the set position to lift-off (two frames) was not more than 0·53 ms.

1. Energetics

The translation energy of the whole beetle was

$$\tfrac{1}{2}\times40\times10^{-6}\times2{\cdot}26^2 = 1{\cdot}02\times10^{-4}\text{ J}.$$

a. Angular velocity of prothorax—42° in 0·53 ms—$\omega_p = 2770$ rad/s.

Angular velocity of hindbody— 7° in 0·53 ms—$\omega_h = 460$ rad/s.

b. Moments of inertia about the respective centres of gravity, P and A, were as in jump I, i.e. $I_p = 0{\cdot}17\times10^{-10}$ kg m² and $I_h = 1{\cdot}7\times10^{-10}$ kg m².

c. Kinetic energy of rotation

$$\tfrac{1}{2}\,I_p.\omega_p{}^2 = \tfrac{1}{2}\times0{\cdot}17\times10^{-10}\times2770^2 = 0{\cdot}65\times10^{-4}\text{ J}.$$
$$\tfrac{1}{2}I_h.\omega_h{}^2 = \tfrac{1}{2}\times1{\cdot}7\times10^{-10}\times460^2 = 0{\cdot}18\times10^{-4}\text{ J}.$$

d. Kinetic energy of translation for prothorax and hindbody.

Terminal velocity P is $\dfrac{11\times10^{-4}\times2}{5{\cdot}3\times10^{-4}} = 4{\cdot}15$ m/s.

Terminal velocity A is $\dfrac{4{\cdot}0\times10^{-4}\times2}{5{\cdot}3\times10^{-4}} = 1{\cdot}5$ m/s.

K.E.$_p$ is $\tfrac{1}{2}\times10^{-5}\times4{\cdot}15^2 = 0{\cdot}86\times10^{-4}$ J.

and K.E.$_h$ is $\tfrac{1}{2}\times3\times10^{-5}\times1{\cdot}5^2 = 0{\cdot}34\times10^{-4}$ J.

e. Thus, *total energy* needed for the jump is $2{\cdot}03\times10^{-4}$ J. This is the same as for the first jump, and again implies that about 50–60 % of the energy is expended in actually raising the beetle.

f. *Energy of vibration* (Fig. 2(b)).

As with the first jump,

J_p (with respect to the pivot) is $0{\cdot}65\times10^{-10}$ kg m^2.
and J_h (with respect to the pivot) is $5{\cdot}38\times10^{-10}$ kg m^2.

The initial period of vibration (Fig. 2(b)) is 1·8 ms, thus $S = 7{\cdot}2\times10^{-4}$ Nm/rad.

Since the amplitude of the first period is 21°—0·37 rad—the energy of vibration is $\frac{1}{2}\times7{\cdot}2\times10^{-4}\times0{\cdot}37^2 = 0{\cdot}5\times10^{-4}$J. The body is initially bent through 44°—0·77 rad—so the energy for this is $\frac{1}{2}\times7{\cdot}2\times10^{-4}\times0{\cdot}77^2 = 2{\cdot}1\times10^{-4}$ J.

The difference in energies of $1{\cdot}6\times10^{-4}$ J is thus more than sufficient to provide the translational energy (either $1{\cdot}02\times10^{-4}$ J or $1{\cdot}2\times10^{-4}$ J) of the jump.

(N.B. The data are not sufficient to plot the change of S with time and so extrapolate back to a maximum value of S. In the first jump, this only gave a small correction.)

g. *Alternative energy budget*

The speed of rotation of the whole beetle after the jump is 123 rad/s, thus its energy of rotation is:

$$\tfrac{1}{2}\times\frac{40\times10^6}{12}\left[(12\times10^{-3})^2+(2\times10^{-3})^2\right]\times123^2 \simeq 0{\cdot}04\times10^{-4}\text{ J}.$$

Then the energy budget is

Energy of translation of whole body	$1{\cdot}02\times10^{-4}$ J
Energy of rotation of whole body	$0{\cdot}04\times10^{-4}$ J
Energy of vibration (first period)	$0{\cdot}5\ \times10^{-4}$ J
Total	$1{\cdot}56\times10^{-4}$ J

This figure is fairly close to the initial energy of $2{\cdot}1\times10^{-4}$ J.

h. *Power produced*

In this jump, the figures calculated for the total energy budgets are fairly close, i.e. $2{\cdot}03\times10^{-4}$ J, $1{\cdot}56\times10^{-4}$ J and $2{\cdot}1\times10^{-4}$ J. The highest of these figures will be used to calculate power output. As in the first jump, the M4 muscle weighed 3·36 mg, but the jumping action (to lift/off) lasted not more than 0·53 ms. This gives a power output of 118×10^3 W/kg (118 W/g) for the jump.

The time needed to build up the energy produced was

(i) Using Machin & Pringle's (1959) figure of 60 W/kg—1·0 s.

(ii) Using Weis-Fogh's (1952) figure of 400 W/kg—0·16 s.

In fact, the set position was maintained for 0·43 s. This suggests that the power output of the M4 muscle just before the jump was 145 W/kg.

2. *Forces and tensile stresses produced*

2a. *Forces produced by the M4 muscle*

To do $2{\cdot}1\times10^{-4}$ J work in rotation of the two parts of the beetle about H (the pivot) through 65°—1·13 rad—the muscle must exert an average moment about the joint of

$$\frac{2{\cdot}1\times10^{-4}}{1{\cdot}13} = 1{\cdot}86\times10^{-4}\ \text{Nm}.$$

Thus, the initial (maximum) force produced by the muscle will be

$$\frac{1{\cdot}86\times10^{-4}\times2}{0{\cdot}35\times10^{-3}} = 1{\cdot}06\ \text{N}.$$

2b. *Tensile stress developed by the M4 muscle*

The tensile stress developed will be

$$3{\cdot}8\times10^{5}\ \text{N/m}^2,\ \text{or}\ 3{\cdot}8\ \text{kg/cm}^2.$$

2c. *Tensile stress on the M4 apodeme*

This will be 15·1 kg/mm².

2d. *Decelerating force in the M4 muscle*

Calculated stiffness, S, of muscle—$7{\cdot}2\times10^{-4}$ Nm/rad.
The moment at 21°—0·37 rad—(see Fig. 2(b)) = $2{\cdot}7\times10^{-4}$ Nm.
Since the muscle acts at a distance of $3{\cdot}5\times10^{-4}$ m, the force in the muscle is

$$\frac{2{\cdot}7\times10^{-4}}{3{\cdot}5\times10^{-4}} = 0{\cdot}77\ \text{N}.$$

This is about three-quarters of the accelerating force of 1·06 N, and thus seems reasonable.

III. Discussion

The calculations presented in this paper are all based on data from two fairly high jumps made by a single specimen of *Athous haemorrhoidalis*. They suggest that the jump is produced by a muscle (M4) which is highly efficient in its production of energy and force, but not unusually so. Similarly, the apodemes of the M4 muscles are subjected to stresses which must lie near their limits of strength, i.e. they are no thicker than is necessary to transmit their appropriate forces. However, the evidence suggests that the actual method of jumping is rather inefficient. Only about 50–60 % of the energy expended in the jack-knifing movement is energy of translation, which actually raises the beetle. The rest is energy of rotation which must be expended to accomplish this. In contrast, jumping with legs is far more efficient. Energy of rotation is only expended in turning the parts of the legs involved, and most of the energy output is as energy of translation.

One slight advantage gained by click beetles from their method of jumping is the fact that skeletal parts have not had to be greatly modified to accommodate enlarged jumping muscles, as with the greatly expanded hind femora of a grasshopper. The prothorax has room to accommodate the enlarged dorsal lateral (M4) muscles without being markedly distorted. However, the elongate shape of the prothorax and the hindbody may well be adaptations for jumping. The elongate pronotum provides origin for larger M4 muscles

than in most beetles, and the long prothorax and hindbody enable jack-knifing to raise their respective centres of gravity as much as possible.

The sclerites of the mesoternum and mesopleuron and the anterior ends of the elytra are all massively constructed, and well fitted to absorb the impact shock without being damaged. Thus, it is of great interest that a recent study (Sannasi, 1969) has shown the presence of resilin in the mesosternal endocuticle of an Elaterid. Sannasi demonstrated that the colourless, lamellated endocuticle of the "entire mesosternal plate" of *Melanotus communis* (Gryll.) contained resilin, and was covered by an amber exocuticle. Such a composite structure could not be compressed or stretched to any marked extent, but it could be bent, and might resemble a stiff spring in this sense. I have previously suggested (Evans, 1972) that the energy store for the jump consists of the series elastic component of the M4 muscle together with a temporary distortion of the prothoracic cuticle. It now seems possible that the mesosternum may also help muscle tension to be built up by bending very slightly. The presence of resilin in the mesosternum may also help it absorb the impact of the prothoracic bumpers, and then rapidly regain its original shape.

It is likely that the type of jump performed by Elateridae is only possible in a small animal with low mass and inertia, because the accelerations inflicted upon the brain (as an example of a delicate organ) are surprisingly large. For instance, the deceleration of the brain after the jack-knifing movement can be estimated from Fig. 2. In sinusoidal motion of amplitude a and period T, peak deceleration, $A = 4\pi^2 . \frac{a}{T^2}$ (following Prentis, 1970). For the first jump, the period is 1·4 ms and the amplitude 19°—0·33 rad. Thus

$$A = \frac{4\pi^2 \times 0{\cdot}33}{(1{\cdot}4 \times 10^{-3})^2} = 6{\cdot}6 \times 10^6 \text{ rad/s}^2.$$

For the brain 3·5 mm from the pivot, this is equivalent to $6{\cdot}6 \times 10^6 \times 3{\cdot}5 \times 10^{-3} = 2{\cdot}3 \times 10^4$ m/s², or about 2300 **g**. For the second jump, with a period of 1·8 ms and an amplitude of 21°—0·37 rad—the equivalent acceleration imposed on the brain is about 1600 **g**.

From an evolutionary point of view, the first adaptation required for jumping must have been a prothorax which could move freely upon the mesothorax. A small back-projecting prosternal process is present in many beetles, and the elongation of this peg would be an easy means of providing a stay for the displaced prothorax so that the M4 muscles could build up tension. The mesosternal pit is a more specialized feature, however, and in its present form it is apparently restricted to Elateridae (and the closely related Trixagidae). It must have deepened as the prosternal peg elongated, since the two structures are co-adapted. However, in the ancestral Elaterid, a short peg together with a small mesosternal depression could probably have allowed a short jack-knifing movement to occur. Even a small movement of the prothorax upon the mesothorax could have produced a small jump if it were rapid enough. As in many beetles found on vegetation, the click beetle's usual first line of escape from predators is to drop from its perch; improvement of the jumping mechanism would then provide a second method of escape.

IV. Summary

Some aspects of the energetics and mechanics of two jumps made by a single specimen of the click beetle *Athous haemorrhoidalis* (Fab.) have been considered.

For each jump, an energy budget was constructed by adding the kinetic energies of

translation and rotation of the head plus prothorax and the hindbody. It was possible to construct an alternative energy budget for each jump which was based upon the "bouncing" of the prothorax upon the hindbody following the jack-knifing action which initiated the jump.

In the first jump, the 40 mg beetle had a take-off velocity of 2·4 m/s, and the jack-knifing action (to take-off) took place in not more than 0·64 ms. In the second jump, the take-off velocity was 2·26 m/s and the jack-knifing action took place in less than 0·53 ms. The energy budget figures calculated for both jumps lay between $1{\cdot}6\times10^{-4}$ J and $3{\cdot}8\times10^{-4}$ J. Estimates of power outputs during the jumping actions lay between 80×10^{3} W/kg muscle and 180×10^{3} W/kg muscle. The energy for the jump is stored during the pre-jump "set" period which lasts for about 0·4 s. The power output during this period must be at least 130 W/kg muscle (at over 25°C).

The force produced by the muscle just prior to jumping was estimated to be about 1·0 N (although it may have been as much as 2·0 N). This implied tensile stresses in the jumping (M4) muscle of between 3 and 4 kg/cm^2 (or as much as 7 kg/cm^2), and tensile stresses in the muscle apodemes of 14 or 15 kg/mm^2 (or as much as 29 kg/mm^2).

These calculations suggest that the jump of the click beetle is produced by a muscle which is highly efficient in its production of energy, but not unusually so, and that the muscle apodemes are subjected to stresses which approach their limits of strength. The actual method of jumping seems to be fairly inefficient in that only about 50–60 % of the energy expended in the jack-knifing movement is energy of translation which actually raises the beetle.

One remarkable feature noted was the high acceleration inflicted upon the brain during the first part of the jump when the head and prothorax were "bouncing" on the hindbody. Peak deceleration during the first jump was estimated at about 2300 **g**.

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