THE EFFECT OF AIR RESISTANCE ON THE JUMPING PERFORMANCE OF INSECTS

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SUMMARY

A spring gun was constructed to propel objects at known velocities of between 1 and 4·5 m.s^{-1}. This was used to project insects and various models in a vertical trajectory. By comparing the height attained in air by the insects or models with the height theoretically possible *in vacuo*, the energy lost against air resistance was observed. Small insects have a higher frontal area to mass ratio than larger ones so have relatively more aerodynamic drag and attain lower heights.

The observed effect may be expressed in terms of the drag coefficient, C_D. Fleas and locusts have C_D of about 1. Winged flies have C_D of about 1·5 which falls to about 1 when the wings are amputated and to about 0·8 when the legs are amputated. Aptery is advantageous in jumping insects.

From experiments with models, it appears that the optimal condition for small jumping insects is that the body should be as compact as possible to reduce the frontal area to mass ratio. Thus dense spherical bodies are favoured. Some species of jumping insect have densities of about 1 mg.mm^{-3} while some flying beetles and flies have densities between 0·3 and 0·8 mg.mm^{-3}.

The Reynolds number at which the experiments were performed was from 65–205 for fleas up to 740–2340 for locusts. The models operated in similar ranges.

At a velocity which would propel a larger animal to a height of 1 m, fleas weighing 0·4 mg only reach about 0·4 m. At lower initial velocities, proportionately less energy is wasted against air resistance so the jump efficiency is higher. Most fleas jump to a height of about 0·1 m with an efficiency of 0·8 while locusts jump to a height of 0·35 m with an efficiency of over 0·9. Air resistance is thus an important scale effect in jumping insects and provides its own design constraints.

INTRODUCTION

Jumping insects store the energy required for their jump (see Bennet-Clark, 1976). The stores of energy act as power amplifiers and so, according to the simplest theory, the range of the jump is proportional to the work done in a single contraction of the

jumping muscles (Bennet-Clark, 1977). Since insects have similar proportions of muscle to other animals, they should, in principle, be able to jump similar distances. Small insects, however, jump less far than larger ones (Bennet-Clark, 1977).

One explanation for this that has been offered is that with decreasing size the frontal area to mass ratio increases and so the effect of aerodynamic drag forces increases. This has been examined theoretically elsewhere (Bennet-Clark, 1977) stimulated by a calculation by Alexander (1971) but has not been examined experimentally.

Two main approaches are possible. Firstly, the insect in question can be suspended in a fluid stream on a force transducer and the drag due to the body can be measured over a range of velocities. From these measurements, the drag over a jump trajectory could be computed. This method would be costly in time and equipment. Alternatively, by projecting insects at a known velocity and measuring the trajectory, the energy lost against air resistance can be found directly and a representative drag coefficient for the body can be calculated. This simpler and more direct approach is adopted here.

MATERIALS AND METHODS

A variety of species of insects were used for experiments. In particular, larval and adult *Schistocerca gregaria* Forskål, adult *Drosophila melanogaster* Meigen, adult *Calliphora erythrocephala* Meigen and the fleas *Ctenophthalmus nobilis* Roths. and *Hystricopsylla talpae* Curtis were used for experiments to measure the effects of air resistance. Before experiments, insects were killed with ether, were weighed with either a precision single-pan balance to the nearest 0·1 mg if over 5 mg in weight or on a torsion balance to the nearest 0·01 mg if under 5 mg weight. After weighing, the insects were measured under a calibrated microscope; from these measurements, the maximum frontal area of the body was calculated. The values for weight and area were used subsequently to calculate the drag coefficient (see Results 1). Where parts of insects were amputated, the insects were weighed and measured again after the operation.

As some of the insects were not plentiful, they were stored from day to day in a deep-freeze at −18 °C. Before further experiments were carried out, they were re-weighed and re-measured.

Model insect bodies were made in two ways: pieces of both balsa wood and pine wood were carved with a scalpel into the closest possible approximations of spheres and cylindrical rods. Pine wood is about 5 times as dense as balsa wood. Alternatively, gelatine medicine capsules of 6·22 mm diameter were modified to make hemispherical-ended cylinders 9, 18 and 30 mm long. These capsules were then loaded internally with wooden or plasticine blocks.

Insects and models alike were projected vertically using a spring gun. This gun (Fig. 1) was powered by a pair of springs, the effective length of which could be adjusted to alter the force required to cock the gun and so alter the height to which objects were propelled. As the mass of the moving block of the gun was around 100 g, the velocity with which objects were propelled was not significantly affected by objects which weighed less than *ca.* 100 mg. When heavier objects were fired, the gun was calibrated by using a ball bearing of similar weight to the test object.

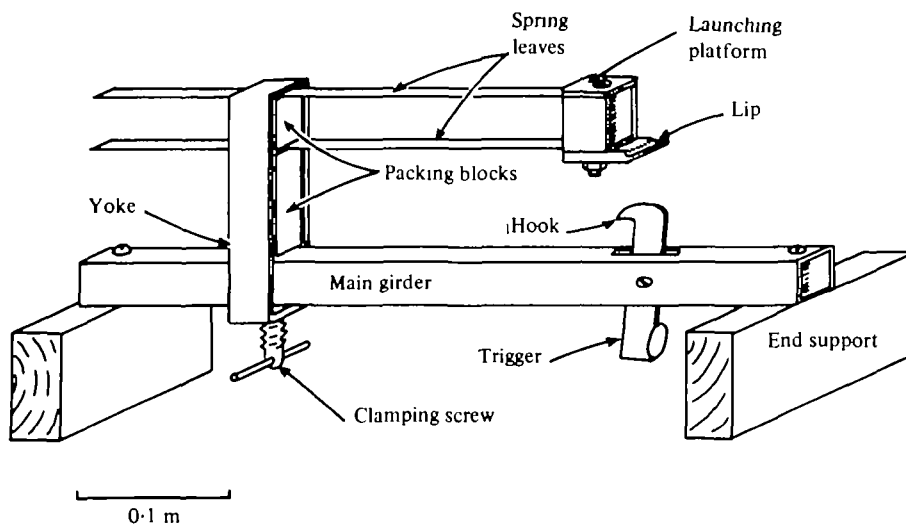The height to which objects were fired was measured visually against a scre

Fig. 1. Diagram of a spring gun used to propel small objects at a known velocity. The gun is cocked by pushing the launching platform down until the lip engages with the hook of the trigger and can be fired by pressing the trigger. The force required to cock the gun is adjusted by lengthening or shortening the springs by sliding the yoke along both the springs and the main girder. This adjusts the height to which objects are fired.

ruled horizontally at 10 mm intervals. With practice, the maximum height of the trajectory could be estimated to the nearest 1 mm when the height was below 0·5 m and to the nearest 2 or 3 mm at heights up to 1 m. Throughout the experiments, great care was taken to ensure that the eye was level with the expected height of the trajectory, as previously found by ranging shots. For any given object and setting of the gun, at least eight measurements of height were made; the standard deviation of the mean of measured height rarely exceeded 1·5 % and was usually far less.

After adjusting the springs of the gun, the setting was calibrated by firing $\frac{1}{8}$ in, $\frac{3}{16}$ in or $\frac{1}{4}$ in ball bearings. These, being spherical and of high density, had a small and, below trajectory heights of 0·25 m, negligible air resistance. Above these heights, a small correction based on the mass and diameter of the ball and an estimated drag coefficient of 0·5 was made.

Before each experiment, the calibration was checked, the barometric pressure and air temperature were recorded, to allow calculation of air density (using the tables in Weast, 1974), and then test objects were fired. At the end of the experiment, the calibration was re-checked but normally did not alter significantly.

Density measurements were made with either newly killed or anaesthetized specimens by either of two methods. In the first, the insect was weighed and its volume was calculated by Pappus' theorem. For the calculation of volume, a plan outline was drawn by camera lucida, the outline was cut along the sagittal axis and weighed against a piece of paper of known scale area. The centre of gravity of the outline was found and the volume of the body was found by treating the insect's body as a surface of rotation of the outline.

Alternatively, the body was dropped into water, fully submersed, and allowed to ɩt to the surface. The volume projecting was estimated by eye.

It appeared that the first method under-estimated density of dorso-ventrally flattened insects and over-estimated density of laterally flattened insects. The second method under-estimated density, particularly of smaller insects and those with dense bristles which tended to trap an air layer.

While more precise methods could be devised, the present methods were quick and gave a useful indication of density.

THEORETICAL EFFECTS OF AIR RESISTANCE

A body projected vertically in the atmosphere is brought momentarily to rest at the top of its trajectory by the forces of gravity and of aerodynamic drag. The aerodynamic drag force can itself be divided into two components. These are the viscous force, due to fluid friction at the body surface, and the inertia force, due to the lateral displacement of air ahead of the body. The relative magnitudes of the two drag force components are given by the Reynolds number (Re) defined as follows:

$$Re = \rho v \, L/\mu, \tag{1}$$

where ρ is the density of air, v is the body velocity, L is the width of its frontal cross-section, and μ is the viscosity of air. The viscous force dominates when Re is less than about 10. The inertia force dominates when Re exceeds about 1000.

The total drag force, F, is conveniently expressed in terms of the body drag coefficient, C_D, as follows:

$$F = C_D \rho A v^2/2, \tag{2}$$

where A is the frontal cross-section area of the body. The value of C_D is primarily a property of the body shape. A flat disc has a C_D of about 1·1 whereas a sphere, being more streamlined, has a C_D of about 0·4 (Massey, 1975). However, the drag coefficient is also dependent on the Reynolds number when Re is less than 1000. When Re is 100, the values of C_D for the disc and sphere are 1·5 and 1·0 respectively. Nevertheless, it will be assumed in the present work that C_D remains constant at a value representative of the body shape. The assumption can be justified on the grounds that the values of C_D are used only in a qualitative discussion of body shapes.

For the upward-moving phase the equation of motion of the vertically projected body may be written as follows:

$$m\frac{d^2x}{dt^2} + \frac{C_D \rho A}{2}\left(\frac{dx^2}{dt}\right) + mg_n = 0, \tag{3}$$

where m is the mass of the body, x is the distance above the ground, t is the time since leaving the ground, and g_n is the acceleration due to gravity. The first term in equation 3 is the acceleration force experienced by the body, the second term is the drag force (equation (2) with $v = dx/dt$), and the third term is the gravitational force. By setting the drag force term to zero, we may solve equation (3) to obtain the height, h_v, theoretically achieved by the body *in vacuo*:

$$h_v = \frac{v_p^2}{2g_n} = \frac{E}{m \cdot g_n}, \tag{4}$$

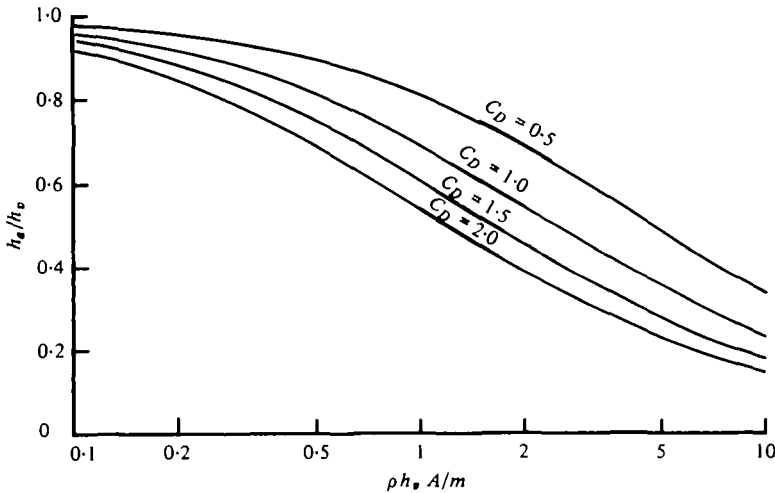where v_p is the initial projected velocity and E is the initial body energy. The solution

Fig. 2. Graph of equation 6 showing the effect on jump efficiency (h_a/h_v) of drag coefficient (C_D), frontal area to mass ratio (A/m) and the initial energy per unit mass (represented by h_v).

of equation 3 for the case of constant C_D gives the height, h_a, attained by the body in air:

$$h_a = \frac{m}{C_D \rho A} \ln \left[\frac{C_D \rho A v_p^2}{2 m g_n} + 1 \right]. \tag{5}$$

We may combine equations 4 and 5 to give:

$$h_a/h_v = \frac{1}{C_D} \left(\frac{m}{\rho h_v A} \right) \ln \left[C_D \frac{\rho h_v A}{m} + 1 \right]. \tag{6}$$

Equation 6 is plotted in Fig. 2 for several values of C_D and shows that the problem can be expressed in terms of three dimensionless parameters, h_a/h_v (by which we define the jump efficiency), the group $\rho h_v A/m$, and C_D (which is a function of the body shape). The values of the first two parameters can be obtained experimentally and, by reference to Fig. 2, the value of C_D may be determined.

The results expressed by equation (6) and Fig. 2 allow some tentative conclusions to be drawn regarding the characteristics of jumping insects. Firstly, these are likely to have body shapes with low drag coefficients; an effective lower limit on C_D at the Reynolds number of interest here is probably around 0·7. Secondly, jumping insects might be expected to operate with low values of $h_v A/m$ so as to achieve high jump efficiencies. The most significant factor here is A/m, the frontal area to mass ratio, suggesting that the best jumping performance would be achieved by animals with dense, compact bodies. However, very small animals such as fleas will inevitably have large values of A/m and will manage high efficiencies only at low values of h_v in order to limit the value of the product $h_v A/m$. We would therefore expect to find that small animals attempt only small jumps so as to achieve good efficiencies.
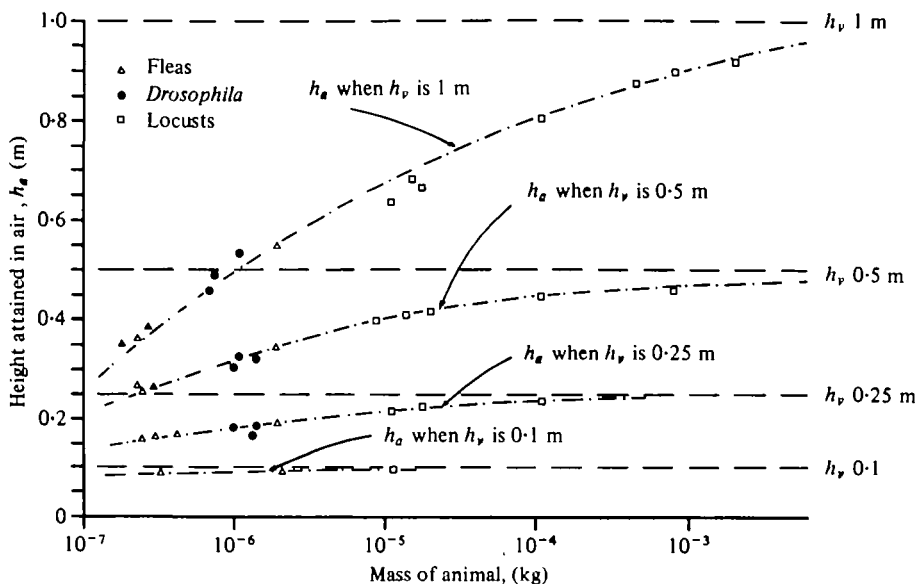
Fig. 3. Graph of height attained in air (h_a) against body mass for various insects. Insects were fired at initial velocities which would have projected them to height *in vacuo* (h_v) of approximately 1·0, 0·5, 0·25 and 0·1 m. The horizontal lines (– – –) show the various heights that would have been attained if there was no air resistance. The curved lines (–·–) have no theoretical basis but serve to unite observed points for different species of insects fired at the same initial velocity or to the same h_v.

<div align="center">RESULTS</div>

<div align="center">1. *The effect of air resistance on the trajectory of insects*</div>

Dead specimens of two flea species, of *Drosophila* from which the wings had been amputated and of various larval instars of *Schistocerca* were projected upwards and the maximum height attained was recorded. The insects were placed on the spring gun with their dorsal sides upwards and were arranged in as lifelike posture as possible, to imitate the jumping posture. When propelled thus, the insects' bodies appeared to maintain the same attitude throughout the trajectory; this could be seen clearly with the larger locusts. With smaller insects, this was harder to see, but the bodies did not normally appear to be rotating at the top of the trajectory.

In successive experiments, the spring gun was set to project at velocities giving a value of h_v of 0·1, 0·25, 0·5 and 1 m. The heights attained by the different sizes of insect are shown on Fig. 3. On this figure, the standard deviation of the observed height is not shown because, in the main, this was less than 10 mm even at the greatest heights.

The original data have been replotted to show the ratio between height in air and height *in vacuo* (h_a/h_v) against the frontal area to mass ratio (A/m) for the various insects (Fig. 4).

It will be seen that the effect of air resistance is greatest at the highest initial velocities with the lighter and smaller insects.

From the data the drag coefficient, C_D, can also be obtained. This is shown in Table 1, with typical dimensions of the various insects examined. In calculating
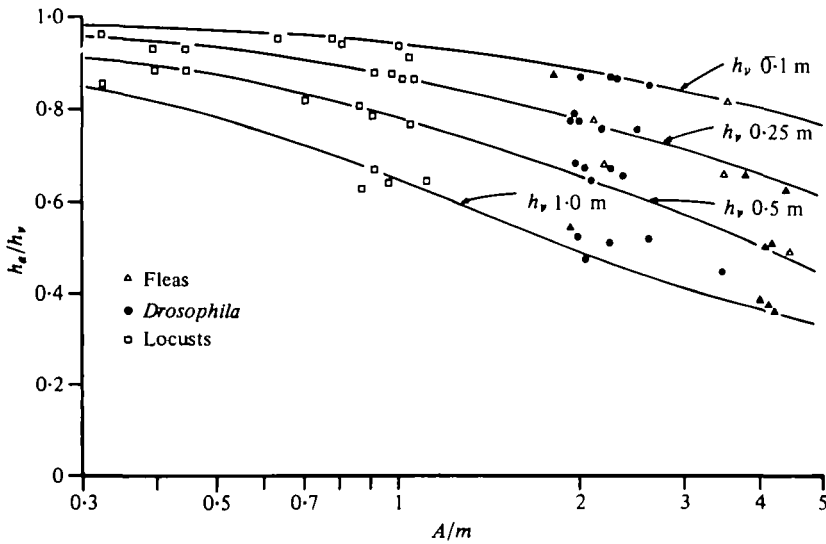
Fig. 4. Graph of ratio between height attained in air and height *in vacuo*, h_a/h_v, against frontal area to mass ratio, A/m, for various insects propelled upwards at velocities which would have projected them to heights *in vacuo* of 0·1, 0·25, 0·5 and 1 m. The symbols show observed points for various species of insects and the continuous lines show theoretical values for bodies with C_D of 1.

Table 1. *Dimensions and aerodynamic drag of the bodies of various insects*

		Dimensions of typical individual			
Insect	Mass (mg)	Length and max. width (mm)	Frontal area (mm²)	Frontal area per unit mass (mm². mg⁻¹)	Drag coefficient (mean of all determinations)
Fleas					
Ctenophthalmus	0·32	2·05 × 0·7	1·125	3·25	0·96, S.D. 0·14, $n = 96$
Hystricopsylla	1·90	3·7 × 1·7	3·49	1·84	1·02, S.D. 0·29, $n = 48$
Flies (wings amputated)					
Drosophila adult	1·00	2·5 × 0·9	2·25	2·25	1·18, S.D. 0·24, $n = 152$
Calliphora adult	55	12 × 5·2	49·7	0·9	0·95, S.D. 0·10, $n = 16$
Locust *Schistocerca*					
1st instar	14·8	7·3 × 3	15·3	1·03	1·08, S.D. 0·21, $n = 128$
2nd instar	105	15 × 3·5	41·2	0·39	0·97, S.D. 0·12, $n = 40$
4th instar	440	27 × 7·5	198	0·45	0·88, S.D. 0·09, $n = 16$

the frontal area of fleas and *Calliphora*, it has been assumed that the body is ellipsoidal; in *Drosophila*, that the body is rectangular and, in larval locusts, that the body is a truncated cone. The error resulting from these assumptions is probably not more than ± 10 % and leads to a similar error in the calculation of the drag coefficient.

The specimens of the various insect species had drag coefficients of about 1. As there is some uncertainty about the true value of the frontal area of the body, both from measurements and from the unknown effect of bristles, it is pointless to attach any significance to differences between species.
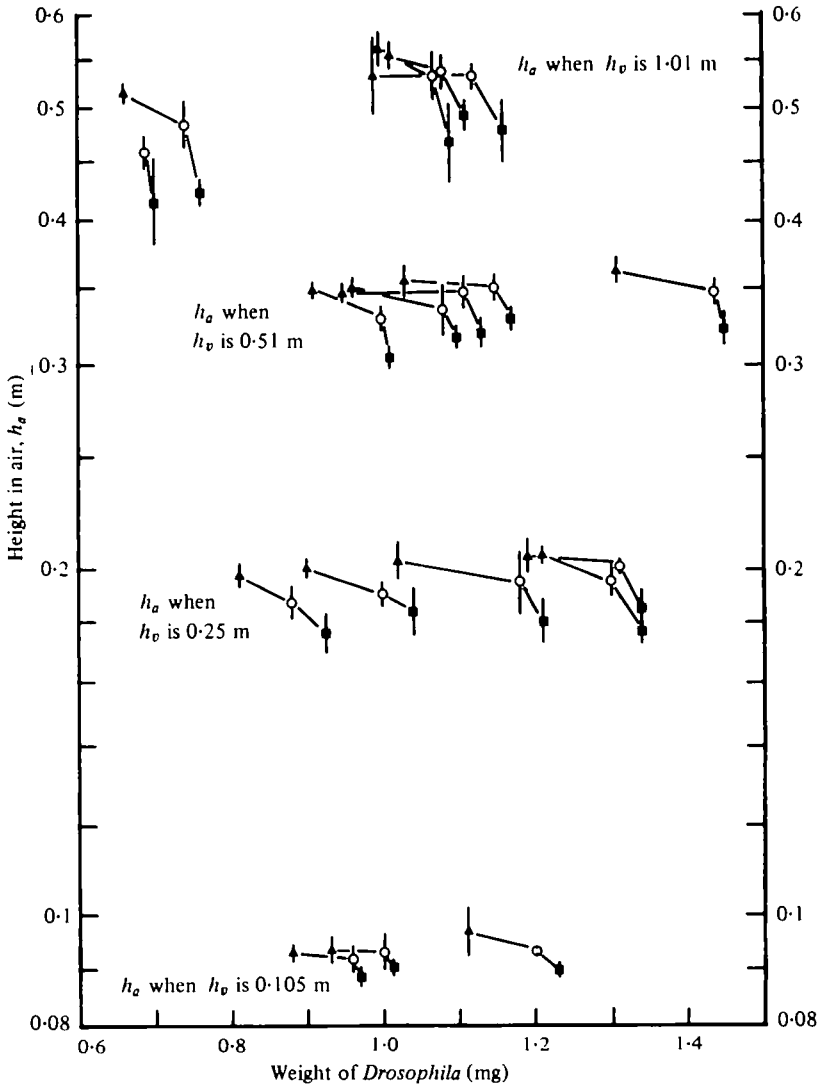
Fig. 5. Height attained in air against body weight for adult *Drosophila* projected vertically at velocities equivalent to various values of h_v. Each set of points represents means from one insect, first projected intact, then after amputation of the wings and finally after further amputation of the legs. The bar lines show two standard deviations of means calculated from eight measurements. ■, Intact; ○, without wings; ▲, without wings and legs.

As part of the same series of experiments, the effect of wing and limb amputation was examined. The same specimens of adult *Drosophila* and 1st-instar larval *Schistocerca* were projected upwards intact, then after amputation of first the wings of the flies and finally after amputation of the flies' legs and the locusts' legs and antennae. After each successive amputation, the bodies were re-weighed and re-measured.

The effect of the amputation on the height attained is shown for each individual in Figs. 5 and 6. The change in drag coefficient is shown in Table 2. Amputation of the wings resulted in a small decrease in the mass of *Drosophila* but a highly significan
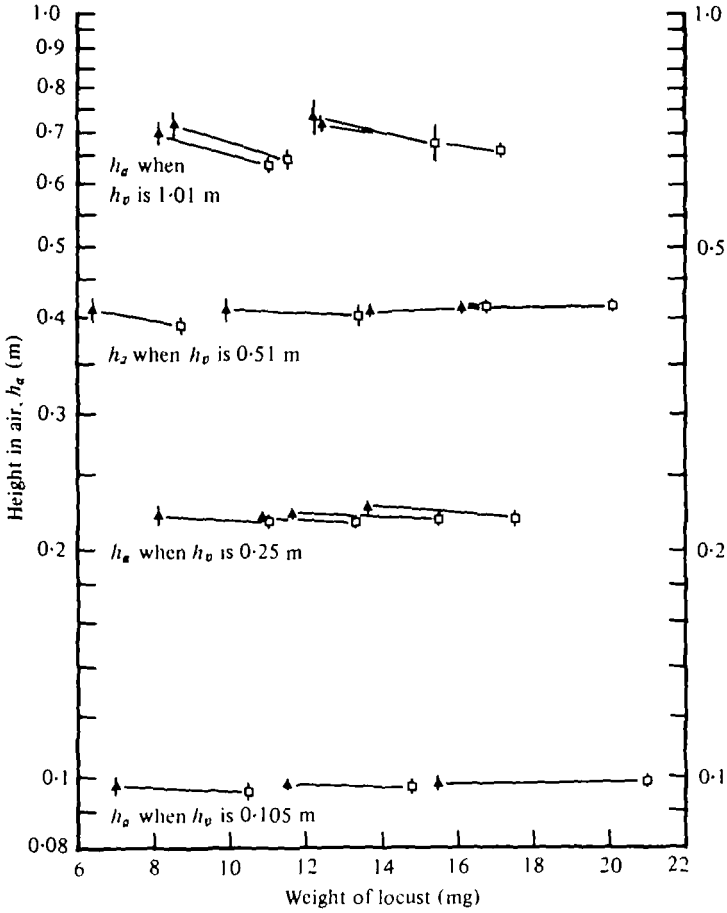
Fig. 6. As Fig. 5. but for 1st-instar *Schistocerca*. The insects were projected intact and then after amputation of all legs and the antennae. The bar lines show 2 standard deviations of eight measurements. Points joined by a line are from the same insect. □, Intact; ▲, without legs.

Table 2. *Effect of wing and leg amputation on drag coefficient,* C_D

Species	C_D (intact)	C_D (without wings with legs)	C_D (without wings without legs)
Drosophila adults	1·58, s.d. 0·35 $n = 152$	1·18, s.d. 0·24 $n = 152$	0·89, s.d. 0·12 $n = 144$
Schistocerca, 1st instar	1·08, s.d. 0·21 $n = 128$	—	0·73, s.d. 0·19 $n = 128$
Calliphora adult	1·34, s.d. 0·52 $n = 16$	0·95, s.d. 0·10 $n = 16$	0·84, s.d. 0·08 $n = 16$

Table 3. *Heights attained by wooden models*

Type of model	Mass (mg)	Length and diameter (mm)	Frontal area (mm²)	Frontal area per unit mass (mm².mg⁻¹)	Mean height attained, m ($h_v = 0.51$ m)	Mean height attained, m ($h_v = 0.98$ m)	Mean C_D ($n = 16$)
Balsa ball	4·11	4·15 × 4·00	15·7	3·16	0·35	0·49	0·62, S.D. 0·08
Balsa ball	0·55	1·8 × 1·8	2·83	5·15	0·29	0·37	0·66, S.D. 0·08
Balsa rod	4·17	13·2 × 1·9	22·1	5·30	0·26	0·34	0·80, S.D. 0·05
Balsa rod	0·46	5·4 × 1·0	5·4	11·74	0·185	0·225	0·71, S.D. 0·06
Pine ball	4·17	2·8 × 2·2	4·45	1·07	0·43	0·71	0·67, S.D. 0·04
Pine ball	0·69	1·2 × 1·6	1·51	2·19	0·37	0·55	0·70, S.D. 0·03
Pine rod	4·26	6·85 × 1·12	7·67	1·80	0·36	0·56	0·87, S.D. 0·03
Pine rod	0·57	3·0 × 0·68	2·04	3·58	0·29	0·42	0·85, S.D. 0·03

reduction in the drag coefficient and increase in the height attained. Leg amputation in both locusts and *Drosophila* caused a very significant reduction both of body weight and drag coefficient but had a relatively small effect on the maximum height attained.

A similar experiment was performed with adult *Calliphora*. The value of h_v was 1·04 m. The drag coefficient fell from 1·33 with wings to 0·95 without wings and 0·84 without wings or legs; these differences were highly significant. The frontal area to mass ratio of adult *Calliphora* is similar to that of the far lighter 1st-instar locusts (Table 1) and they attain similar heights of around 0·7 m.

2. *Experiments with various models*

Wooden models were projected upwards using the same methods as with the insect bodies but, because the effects of air resistance are greater when the velocity of the projectile is high, experiments were only carried out for calibrated heights of about 0·5 and 1 m. The test objects were either rod shaped or spherical but were of two approximate weights, around 4 mg and around 0·5 mg. The results of the experiment are shown in Table 3.

The rod-shaped models have a significantly higher drag coefficient and larger frontal area than the spherical models and so, for both these reasons, attain lower maximum heights. Although the balsa wood models have similar drag coefficients to the similarly shaped pine wood models, they attain a lower height because the frontal area to mass ratio is larger since balsa wood is less dense than pine wood.

It was difficult to make accurate spherical or cylindrical models of either small size or high frontal area to mass ratios. In another series of experiments, gelatine drug capsules were used. These have excellently formed hemispherical ends and cylindrical sides. When the two halves of the capsule are fitted together, there is a lip about 0·15 mm high, which is probably too small to have any major aerodynamic effect (Alexander, 1971).

The three different capsules were loaded so that they presented constant frontal area to mass ratios regardless of shape. Three different frontal area: mass ratios were used and all capsules were fired upwards with the same initial velocity, equivalent to a value of h_v of 1·04 m. The capsules were placed with their long axes horizontal and did not appear to rotate during the trajectory. The results are shown in Table 4.

The longest capsule had significantly the highest drag coefficient and the short

Table 4. *Heights attained by gelatine capsules*

Type of capsule	Frontal area (mm²)	Mass* (mg)	Area per unit mass (mm².mg⁻¹)	Mass per unit volume (mg.mm⁻³)	Height attained ($h_v = 1.04$ m)	C_D	Mean C_D (all masses)
Short	52·03	34·6	1·50	0·15	0·70	0·59	
9·70 mm long		52·0	1·0	0·22	0·76	0·58	0·60, S.D. 0·05
6·22 mm diam.		104	0·5	0·45	0·88	0·61	$n = 32$
		260	0·2	1·12	0·97	0·60	
Medium	104·7	58·5	1·79	0·12	0·63	0·71	
18·16 mm long		104·7	1·0	0·21	0·74	0·72	0·73, S.D. 0·07
6·22 mm diam.		209·4	0·5	0·43	0·87	0·70	$n = 32$
		523·5	0·2	1·07	0·95	0·75	
Long	181·6	97·9	1·86	0·11	0·60	0·78	
30·53 mm long		181·6	1·0	0·21	0·73	0·77	0·79, S.D. 0·05
6·22 mm diam.		363·2	0·5	0·42	0·84	0·80	$n = 32$
		908	0·2	1·05	0·95	0·82	

* Mass was altered by adding internal loads to the capsules.

Table 5. *Reynolds number (Re) of objects used in experiments*

Insects	Characteristic dimension (mm)	Minimum initial velocity (m.s⁻¹)	Re	Maximum initial velocity (m.s⁻¹)	Re
Ctenophthalmus	0·7	1·40	65	4·43	205
Hystricopsylla	1·2	1·40	110	4·43	350
Drosophila	1	1·40	92	4·43	290
Schistocerca					
1st instar	2·5	1·40	230	4·43	730
4th instar	8	1·40	740	4·43	2340
Models					
Pine ball	1·12	3·13	230	4·43	330
Pine rod	0·68	3·13	140	4·43	200
Gelatine capsule	0·22	—	—	4·43	1820

capsule had significantly the lowest drag coefficient. The drag coefficients found here were also significantly lower than those found for insects and rather lower than those found for the hand-carved small wooden models (Table 2).

3. *Reynolds number*

A typical value for the density of air is 1·2 kg.m⁻³ and for the viscosity of air is $18·2 \times 10^{-6}$ kg.m⁻¹.s⁻¹ at 18 °C (Weast, 1974). From these, Reynolds number has been calculated using equation 6. Typical values for some of the objects fired from the spring gun have been calculated and are shown in Table 5. The characteristic dimension used in all cases was the width of the body or its equivalent, the diameter of a cylindrical model. The characteristic velocity used was the initial velocity at the bottom of the trajectory; as the object rises, both velocity and Reynolds number will fall to reach zero at the top of the trajectory.

4. *Insect body density*

Although the two methods of estimating body density gave similar results, neither peared very precise and the results presented here only provide a rough indication

Table 6. *Density of insects' bodies*

Species, Order and stage	Density by flotation (mg.mm^{-3})	Density by Pappus' theorem (mg.mm^{-3})
Schistocerca gregaria Forskål, Orthoptera		
1st instar larvae	0·9–1·05 (sank)	0·83–1·15
4th instar larvae	0·95–1·05 (sank)	1·05–1·20
Adults	0·7–0·8	—
Acheta domesticus L., Orthoptera		
5th instar larvae	0·95–1·0	—
Adults	0·8–0·9	—
Forcipula auricularia L., Dermaptera		
Adults	0·9–0·95	
Tenebrio molitor L., Coleoptera		
Late larvae	1·05 (sank)	—
Adults	0·8	
Coccinella septempunctata L., Coleoptera		
Adults	0·45–0·5	—
Pachnoda ephippiata Gerst., Coleoptera	0·5	—
Drosophila melanogaster Meigen, Diptera		
3rd instar larvae	1·05 (sank)	
Adults	0·6–0·8	0·75–0·9
Calliphora erythrocephala Meigen, Diptera		
3rd instar larvae	1·05 (sank)	
Adults	0·3–0·4	0·32–0·38

of body density. It is known that the relative volume of air sacs, viscera and gonads change markedly during the course of an instar (Clarke, 1957).

The estimated densities for a variety of species of insect are shown on Table 6. Where an insect sank when placed in water, it is assumed that its density just exceeded that of water. Two main points emerge: that the larvae of a species are denser than the adults and that insects that are highly specialized for flight are less dense than even closely related terrestrial cursorial or jumping insects. This can be seen when the densities of orthopteroid insects which do not fly well (*Acheta, Periplaneta, Forcipula*) are compared with those of flying beetles or flies (*Pachnoda, Calliphora*), when *Tenebrio*, which is flightless, is compared with the flying beetles and when adult *Schistocerca* and *Acheta* are compared. Live but unanaesthetized larval locusts may sink but swim well enough to propel themselves to the surface of water.

DISCUSSION

1. *Drag coefficients of insect bodies*

Although it is apparent (Fig. 2) that a low drag coefficient would be beneficial to jumping performance, none of the insect species used in the present experiments show low values of C_D when compared with either those of fish (Webb, 1977) or even small water beetles (Nachtigall, 1977). Indeed, when compared with the drag coefficients calculated for wooden models of similar dimensions (Tables 1 and 2) the insect bodies appear to be very rough. This can partly be attributed to the insects' legs, which clearly provide considerable drag (Figs. 5 and 6) but also to the bristles and other protuberances of the body which operate at a very low Reynolds numb

and so extend the boundary layer and increase the effective frontal area of the body. Thus, the bristle-covered bodies of *Drosophila* appear to have higher drag coefficients than the relatively smooth bodies of larval locusts.

It is clear that the wings of flies greatly increase the drag (Fig. 5, Table 2). While the amputation of the legs of both locusts and flies decreases the drag of the body, it also decreases the mass of the animal so that although drag coefficient falls, the mass to frontal area ratio also falls. The increase of range that might result from the possession of fewer or smaller protuberances is partly offset by the loss of the mass of the protuberances.

These insects operate at Reynolds numbers where it is difficult in any case to obtain very low drag coefficients (Vogel, 1967; Alexander, 1971; Rees, 1975). This is because viscous effects provide a high proportion of the total drag force and modifications to the body shape, such as streamlining, do not help very much. Spherical bodies have lower drag coefficients than long cylinders moving normal to the long axis (Table 3). Similarly, an ellipsoid has the highest C_D when moving normal to its major axis, so it is perhaps surprising that this is an attitude commonly adopted by fleas (Bennet-Clark & Lucey, 1967; Rothschild *et al.* 1972) by click beetles (Evans, 1972) and by locusts (Bennet-Clark, unpublished observations and films). In fact, these animals may have no choice in the matter for, in the approximate Reynolds number range 50 < Re < 200, a body moving through a fluid will automatically orientate itself in the position of *maximum* drag (Becker, 1959).

2. *Effect of body-shape and density*

The theoretical analysis leading to equation 6 and whose predictions are plotted in Fig. 2, shows that the body frontal area to mass ratio (A/m) is an important factor determining jumping performance. This is supported by the model experiments. For a similar mass, the value of A/m for the cylindrical wooden models was around twice that of the wooden balls and the height attained by the cylindrical models was correspondingly lower (Table 3). The results suggest that the effects of aerodynamic drag may be reduced in two complementary ways, both of which decrease the value of A/m. These are firstly, that the density of the body should be maximized and secondly, that elongated body shapes should be avoided.

The exploitation of a high body density is seen in fleas, which have few or no air sacs, and in larval locusts which have a density of about 1 mg.mm^{-3} (Table 6). The effect of density has been examined theoretically by evaluating equation 6 for a series of spherical objects of diameters 1, 3, 10, 30 and 100 mm and of densities 1, 0·5 and 0·25 mg.mm^{-3}. The value of the drag coefficient was assumed to be 1. The results of the calculations are shown in Fig. 7, where height attained (h_a) has been plotted against mass. It is clear that for a given mass, a greater height is attained by objects of greater density and hence smaller A/m values.

Elongated bodies, especially in the smaller insects, would appear to have a double penalty. Not only is the drag coefficient of such bodies higher but the frontal area to mass ratio will tend to be higher than with shorter bodies. This has been examined theoretically for a series of regular ellipsoids of density 1 mg.mm^{-3}. The value of A/m increases as the square root of the major axis to minor axis length ratio (Table 7).
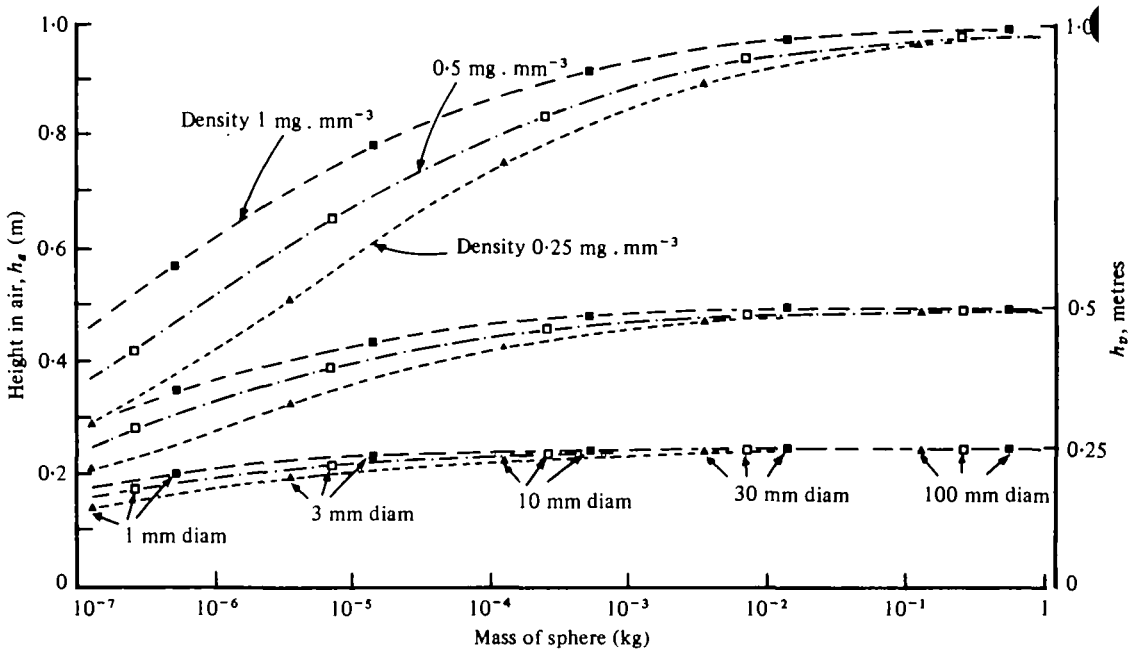
Fig. 7. Graph of height attained in air (h_a) against mass, calculated for spheres of a range of diameters and three different densities projected upwards at a series of velocities equivalent to values of h_v of 0·25, 0·5 and 1·0 m. The lines joining points for spheres of the same density have been fitted by eye. It is assumed that the C_D of the spheres is 1 and that air density is 1·2 kg.m⁻².

Table 7. *Frontal area and mass of ellipsoidal bodies*

Lengths of axes (mm)	Frontal area (mm²)	Mass (mg)*	Frontal area per unit mass (mm².mg⁻¹)	Area/mass with respect to sphere of same mass
Sphere, diam. 2	3·142	4·19	0·75	1
Ellipsoid, 1·41 × 2·82	3·142	2·96	1·06	1·41
Ellipsoid, 1·15 × 3·46	3·142	2·42	1·30	1·73
Ellipsoid, 1 × 4	3·142	2·09	1·5	2
Ellipsoid, 0·5 × 8	3·142	1·05	3·0	4

* It is assumed that all bodies are made of material of density 1 mg.mm⁻³.

The aerodynamic effect of the elongated body will be similar to that of a low body density and will tend to impair jumping performance.

Body density can be increased by reducing the relative volume of air sacs and making the overall design more compact. Insects that are adapted for cursorial loco-motion do not have as extensive air sacs as those adapted for flight (e.g. Chapman, 1969). In a jumping animal, it will thus be advantageous to reduce wings and flight muscles. Aptery, which occurs in many jumping Orthoptera, jumping Hemiptera and in all Siphonaptera, also reduces the aerodynamic drag of the body. This will be particularly important in a small animal such as a flea.

In a flying animal, the design constraints are complex but, because body attitude is controlled in flight, body form may be optimized to reduce drag in a certain

Table 8. *Maximum possible height for jumping insects*

(It is assumed that available energy per unit mass sets an upper limit to the height *in vacuo* of 2 m.)

Species	Frontal area per unit mass (mm². mg⁻¹)	Height attained in air (m)	Jump efficiency (h_a/h_v)
Fleas			
Ctenophthalmus	3·5	0·53	0·27
Hystricopsylla	1·8	0·77	0·39
Locusts			
Schistocerca			
1st instar	1·0	1·02	0·51
4th instar	0·45	1·36	0·68

attitude. The presence of air sacs liberates the exterior contours of the body from the control of form by viscera that tends to occur in animals that lack air sacs. Air sacs thus appear particularly advantageous in flying animals and are possibly disadvantageous in small jumping animals.

3. *The limits on the performance of jumping insects*

It has been suggested elsewhere that the maximum specific energy available to a jumping animal will not exceed 20 J.kg⁻¹ (Bennet-Clark, 1977). This will propel a body to a height of 2·04 m *in vacuo* or accelerate it to an initial velocity of 6·32 m.s⁻¹. Using these figures and the frontal area to mass ratios and drag coefficients found for various sizes of jumping insects (Table 1) the maximum height they can attain may be calculated from equation 6. This is shown in Table 8. For simplicity it has been assumed that height *in vacuo* is 2 m, that the drag coefficient is 1 and the air density is 1·2 kg.m⁻³. Values of A/m have been rounded to two significant figures.

The jump of a small insect is less economic than that of a larger animal. At the limit set by the maximum possible specific energy, a flea is only able to use about a quarter of the energy in moving its body. For a late larval locust the situation becomes less wasteful. It is clearly better, in terms of efficiency, for both animals to make a series of smaller jumps.

For fleas, the practical limit seems to be a high jump of about 0·2 m (Mitzmain, 1910) which requires a height *in vacuo* of 0·32 m and efficiency of 0·63. For a 5th-instar larval locust, the maximum recorded long jump is 0·6 m (Hoyle, 1955) which converts, from his data, to a high jump of about 0·35 m. To achieve such a jump, the locust must produce the energy for a jump *in vacuo* of 0·38 m with an efficiency of 0·92. Most species of fleas do not jump much higher than 0·1 m and thereby attain efficiencies of around 0·8. There seems to be little reason from the design of the body why fleas should not achieve higher jumps – it merely becomes grossly uneconomic.

In this work only vertical jumps have been examined. This is because calculations of the trajectory of a long jump must be made as a series of approximations which renders them lengthy and imprecise. It is clear, though, that the majority of animal jumps are long jumps – but that the effects described here with high jumps will also affect performance in long jumps. Many jumping insects such as Cercopid bugs, grasshoppers and Halticine beetles appear well shaped as projectiles and possibly

have lower than normal drag coefficients; this would be advantageous but has not as yet been examined.

We thank D. McDiarmid for painstakingly collecting fleas from small rodents captured during the course of his own research. The earlier part of this work was carried out while H. C. Bennet-Clark was a member of the Zoology Department of Edinburgh University.

APPENDIX

Derivation of equation (5)

We are concerned with the solution of equation (3):

$$m\frac{d^2x}{dt^2}+\frac{|C_D\rho A}{2}\left(\frac{dx}{dt}\right)^2+mg_n = 0 \qquad (3)$$

for the case where C_D is constant. The boundary conditions are $x = 0$ and $dx/dt = v_p$ at $t = 0$.

We may rearrange equation 3 and set $dx/dt = v$ to obtain:

$$\frac{\alpha^2}{g_n}\frac{dv}{dt}+v^2+\alpha^2 = 0,$$

where $\alpha^2 = 2mg_n/C_D A$. Further rearrangement gives:

$$\frac{dt}{dv} = \frac{-\alpha^2}{g_n(v^2+\alpha^2)}. \qquad (A\ 1)$$

Solving equation A 1 for t and substituting the condition $v = v_p$ at $t = 0$ leads to:

$$t = \frac{\alpha}{g_n}\left[\tan^{-1}\frac{v_p}{\alpha} - \tan^{-1}\frac{v}{\alpha}\right]. \qquad (A\ 2)$$

Equation A 2 may be rearranged to give an expression for v as follows:

$$v = \frac{dx}{dt} = \alpha \tan\left[\tan^{-1}\frac{v_p}{\alpha}-\frac{g_n t}{\alpha}\right]. \qquad (A\ 3)$$

Solving equation A 3 for x and substituting the condition $x = 0$ at $t = 0$ gives:

$$x = \frac{\alpha^2}{g_n}\ln\left[\cos\left(\tan^{-1}\left(\frac{v_p}{\alpha}\right)-\frac{g_n t}{\alpha}\right)\bigg/\cos\left(\tan^{-1}\frac{v_p}{\alpha}\right)\right]. \qquad (A\ 4)$$

Our interest lies in the top of the trajectory where $v = 0$ and $x = h_a$. Setting $v = 0$ in equation A 2 gives t_a, the time to the top of the trajectory, as follows:

$$t_a = \frac{\alpha}{g_n}\tan^{-1}\frac{v_p}{\alpha}.$$

When this expression for t_a is substituted into equation A 4 we obtain:

$$h_a = \frac{\alpha^2}{g_n}\ln\frac{1}{\cos\left(\tan^{-1}\left(v_p/\alpha\right)\right)}. \qquad (A\ 5)$$

Noting that $\cos(\tan^{-1} v_p/\alpha) = (1 + v_p{}^2/\alpha)^{\frac{1}{2}}$ and setting $\alpha^2 = 2\ mg_n/C_D\rho A$, we obtain:

$$h_a = \frac{m}{C_D\rho A} \ln \left[\frac{C_D\rho A v_p^2}{2mg_n} + 1 \right], \tag{A6}$$

which is the equation numbered (5) in the main text.

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