

DIRECT MEASUREMENTS OF INSTANTANEOUS LIFT IN DESERT LOCUST; COMPARISON WITH JENSEN'S EXPERIMENTS ON DETACHED WINGS

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SUMMARY

Instantaneous values of lift in the locust *Schistocerca gregaria*, flying in a wind tunnel, were measured by means of a piezo-electric probe. The air-flow velocity was adjusted to be equal to that which would have been experienced by the freely flying insect.

In order to obtain the true aerodynamic forces, the inertial forces must be subtracted from the gross forces measured. These inertial forces were calculated from the movement of the centre of gravity and from the mass of the different wing sections.

The lift curves obtained have a shape similar to the curves deduced by Jensen from measurements on isolated wings in steady flows, but an approximately doubled amplitude. These amplitude differences appear to be caused by the existence of significant unsteady effects.

INTRODUCTION

Among authors who have investigated flapping flight, many have considered the existence of unsteady effects to explain the performance characteristics of certain birds and insects. Among these are the works of Magnan (1934).

At present, it has been proved that unsteady effects are significant in the presence of high rates of wing twist (Nachtigall, 1966; Bennett, 1970), and in certain cases of hovering flight, in which the average lift coefficients are abnormally high (Weis-Fogh, 1973).

However, theories based exclusively on the principles of conventional aerodynamics (Walker, 1925; Holst & Küchemann, 1941, 1942; Osborne, 1951) generally give results which are compatible with the average performance values observed, when correct experimental data are available (Weis-Fogh & Jensen, 1956). Hence it is often felt that flapping flight can be considered, as a first approximation, as a succession of steady states (Pringle, 1957).

This postulate is supported by the remarkable work of Jensen (1956) concerning locust flight. Jensen first measured the average forces produced by insects flying in a wind tunnel and determined the different wing postures by accurate cinematographic analysis. After then measuring the forces applied to detached wings by steady flows,

Jensen succeeded in plotting the variations in these forces occurring during a wing-stroke cycle. He observed that average lift and thrust values calculated by integrating these curves were practically equal to the corresponding values measured in flight. He concluded that 'the good conformity between the measured and the calculated forces makes it probable that the principles of steady-state aerodynamics can be applied to locust flight'.

In this study, we measured (using piezo-electric probe) the instantaneous lift in flying locusts, to confirm whether the values obtained by Jensen on detached wings effectively correspond to the true values. We shall see that this is not the case.

It appears that few direct measurements of instantaneous forces have been taken hitherto. Baird (1964) investigated small insects (*Galleria mellonella*, *Oncopeltus fasciatus*, *Sarcophaga bullata*). Tests were carried out on *Locusta migratoria* by Zarnack (1969) during his investigations of wing movements, but no quantitative results were obtained. Experiments were also conducted on *Anoxia villosa* and *Lucanus cervus* by Termier, Devillers & Diep (1971). More recently, P. Wilkin (Brunel University) obtained lift and thrust curves as a function of time for *Schistocerca gregaria*, using strain gauges cemented to the rod supporting the locusts in the wind tunnel. Except in these latter investigations, however, the contribution of the inertial forces of the wings to the measured forces was not accounted for; furthermore, all measurements were taken either in an air-flow in which the velocity was not equal to that which would have been assumed by the freely flying insect, or even in still air, yielding results of questionable validity, as pointed out by various authors (Wood, 1970).

In our experiments (Cloupeau, Devillers & Devézeaux, 1978), velocity matching was obtained by a method similar to that used by Weis-Fogh (1956) and Jensen (1956). We also determined the inertial forces which must be subtracted from the gross forces measured to obtain the true aerodynamic forces. We nevertheless restricted ourselves to lift measurements for which inertial corrections are one order of magnitude lower than for thrust forces.

METHODS AND MATERIALS

General

In order to take significant measurements, free flight conditions must be reproduced as closely as possible. In our experiments, the values selected for ambient temperature (30 °C), relative humidity (60%) and the angle made by the locust's body with the horizontal (7°) corresponded to the values determined by Weis-Fogh (1956) for normal flight.

In attempting to obtain regular, long duration flights, we found the work of Michel (1972) to be very useful. This author showed that locusts exhibit a cyclic tendency to flight. It is practically nil in females in the breeding period. In both sexes, flight tendency declines with age. These results enabled us to make the optimum age selection of the insects used in our experiments.

The locusts (in general *Schistocerca gregaria*, but *Locusta migratoria* in some tests) were supplied by the Laboratoire d'Entomologie et d'Ecophysiologie Expérimentale at Orsay, and by the Ecole d'Agriculture de Grignon.

The experimental system employed is shown schematically in Fig. 1. It consists of

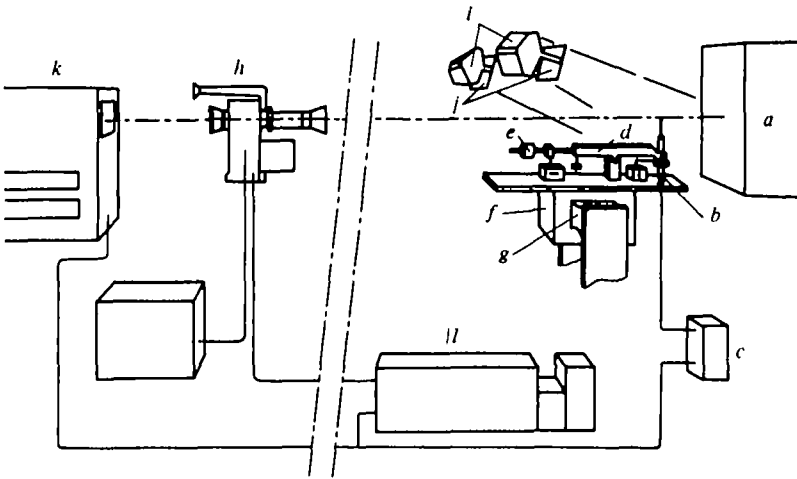


Fig. 1. Schematic diagram of the apparatus used to measure instantaneous lift in locusts. a, Wind tunnel exit; b, force probe; c, charge amplifier; d, arm of balance for measuring average lift; e, balancing counterweight; f, metallic block; g, antivibration support; h, high-speed camera; i, projectors; j, heat-reflecting filters; k, oscilloscope; l, direct writing oscillograph.

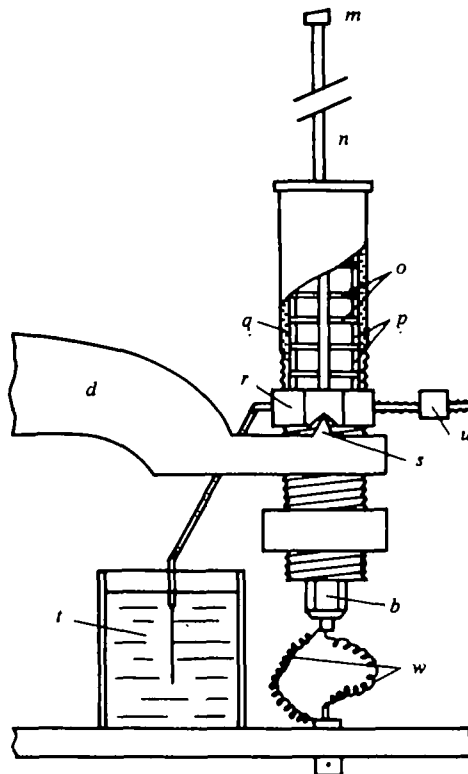


Fig. 2. Detail of mechanical assembly of force probe. b, Probe; m, micromagnet for attaching insect; n, support rod; o, rubber washers; p, washer clamping rings; q, cylinder screwed on probe body; r, support of probe system resting on knife-edges; s, t, dashpot; u, balancing fly-weight; w, probe connection wires.

a variable-speed wind tunnel, a unit designed to measure instantaneous forces, including essentially a piezo-electric probe combined with an amplifier, a balance measuring average lift, a high-speed camera and an oscilloscope.

Wind tunnel

The insect was placed at the outlet of an open throat wind tunnel (*a*) with a working section of 15×33 cm. The uniformity and laminarity of the air-flow in the working zone were checked by means of a hot wire anemometer. The freestream turbulence level is about 0.4%. The wind velocity was adjusted by varying the speed of rotation of the turbine, and by a sliding screen system placed upstream from the turbine and controlled manually.

Force probe

We used a Kistler type 9203 piezo-electric probe (*b*) combined with a Kistler type 5001 charge amplifier (*c*). The maximum sensitivity of the unit was 0.5 V/g wt. The locust was attached to the free end of a 10 cm long rod screwed into the probe body. In the first experiments, the insect was attached by means of a low-melting point wax, but this method has several drawbacks. Finally, a samarium-cobalt micromagnet (*m*, Fig. 2) was cemented to the free end of the rod (*n*), its upper face making an angle of 7° with the horizontal. A 0.5 mm thick soft iron disc was cemented permanently under the pterothoracic plastron of all locusts used in the tests. This circular disc fitted on the magnet, which was surrounded by a thin band to prevent sideslip. This type of attachment allows rapid positioning of the insects.

The piezo-electric probe essentially responds to axial stresses, but also, to a lesser degree, to transverse forces. This system is sensitive to the horizontal forces produced by the insect, for example to thrust. To eliminate these spurious responses, we built the assembly shown in Fig. 2. Rubber washers (*o*) were threaded on the bottom of the rod (*n*) and secured peripherally between rings (*p*) stacked in a cylinder (*q*) screwed on the probe body. This system makes it possible to obtain a ratio lower than 5:1000 between the responses to a given force applied horizontally and then vertically at the free end of the rod.

The probe-rod-cylinder system was able to oscillate about a horizontal axis perpendicular to the flow, by means of the part (*r*) resting on two knives (*s*). The pendular movements of this unit were damped by means of a blade plunged into a dashpot (*t*). In the absence of flow, with the locust at rest, the verticality of the support rod was adjusted by means of a fly-weight (*u*). When the locust was in flight, the flow velocity was adjusted by means of the sliding screen system to maintain the rod vertical. In this way, the absolute value of flow velocity was equal to that which would have been assumed by the freely flying insect.

In order to prevent the probe-amplifier connexion from creating a spurious mechanical resistance, this connexion was made by very fine spiral-wound wires (*w*). These were protected from electrical disturbances by metallic shielding. The signals obtained at the amplifier output were fed to an oscilloscope and a recorder which will be discussed later.

The measurement system including the probe and amplifier responded, in principle, to stresses with frequencies from 0 to 25 kHz. In actual fact, the pass band did not quite reach zero frequency and a small thermal drift generally existed. In these

conditions, the zero ordinate on the recorded curves is not known. It can be determined from the average lift measurement of the insect: the position of the zero ordinate is such that the integral of the gross force curve over a wing-stroke period is equal to the average lift.

Balance measuring average lift

The system employed to measure the average lift is shown schematically in Fig. 1. The knife-edges supporting the probe unit (see Fig. 2) were positioned at one end of the arm of a balance (*d*) pivoting about a horizontal axis perpendicular to the flow. The arm oscillations were damped by means of a blade plunged in a dashpot. The arm equilibrium was adjusted before positioning the locust by means of the fly-weight (*e*). The new equilibrium position assumed during flight directly gave the difference between the average lift and the weight of the insect (plus the weight of the disc cemented to the thorax). This difference was measured by means of a concave mirror (not shown) forming the image of a light source on a graduated rule 3 m from the mirror. The measurement error was less than $2 \cdot 10^{-8}$ g, or, for a lift value approaching the weight of the locust (about 2 g) a relative error of about 1%.

The top of the rod supporting the insect was protected from the air-flow by a thin transparent sleeve of adjustable height. The latter was fastened to a streamlined case surrounding the balance-probe assembly. Since the forces to be measured were small, special care was observed in eliminating spurious vibrations. In order to damp the disturbances from the environment, the measurement assembly was installed on a 70 kg metallic block (*f*) fixed to the wind tunnel frame by means of two Kléber-Colombes antivibration supports (*g*). Furthermore, the natural frequencies of the system were determined by inserting a plate subjected to a strong acoustic field in place of the insect. Measurements of the probe signal amplitude taken as the excitation frequency varied from 4 to 3000 Hz confirmed that the final assembly exhibited no harmful resonance.

High-speed camera and oscilloscope

The same camera (*h*, Fig. 1) was employed to film the insect and to record the force signal. This was a Hycam type K20S1W rotary prism type 16-mm camera, with an Angénieux reflex zoom as the main lens. It was placed 1.5 m downstream from the insect. A mirror located outside the flow made it possible to obtain both the back view and the profile view of the insect.

For a given setting, the magnification ratio varied with camera-object distance and was thus not strictly the same for the different wing elements during their movements. However, the errors made in the measurement of inertial forces when this effect is not accounted for were negligible.

Lighting was first provided by a stroboscope, which has the advantage of supplying very sharp images. This system was subsequently abandoned because the triggering of a stream of flashes creates a stimulus for the animal, which abruptly changes its flight rhythm. Continuous sources were therefore used: two 800 W projectors (*i*, Fig. 1) were placed symmetrically on either side of the flow, and at the rear of the insect. This symmetry was necessary to obtain correct flight. The light beams were focused on the insect by means of lenses coupled with heat-reflecting filters (*j*).

In these conditions, the insect could be filmed at 1000 frames/s, giving about

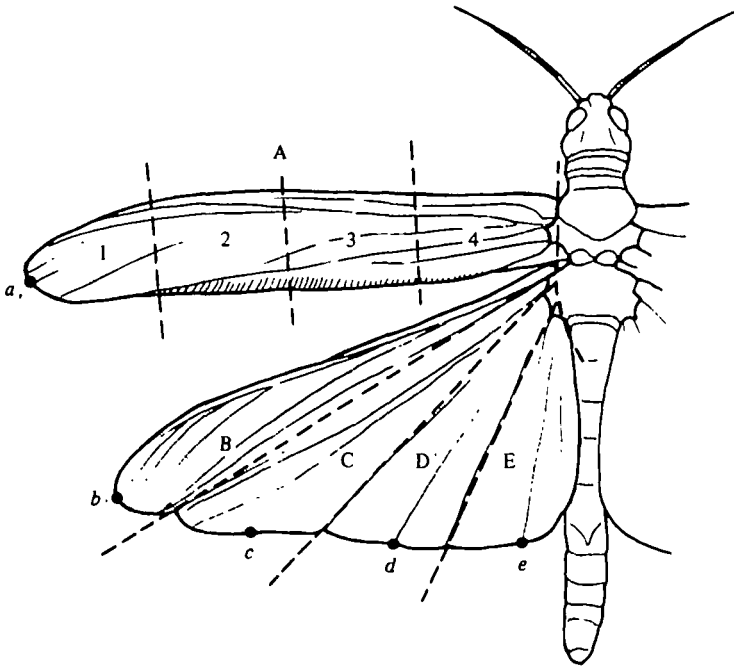


Fig. 3. Unfolded wings of *Schistocerca gregaria*. *a-e*, Reference points for movement analysis. After a flight, the hindwing was cut along the dotted lines into four segments *B-E*. The forewing *A* was only cut into four parts 1-4 for a single test (see Discussion).

50 pictures per wing cycle for the locust. Since the shutter constant was 2.5, the vertical movement of the forewing tip at the moment of maximum speed was about 1 mm during the exposure time. During analysis, the centre of the image of a reference point on the wing was determined with accuracy far better than 1 mm.

A second lens at the rear of the camera allowed formation of the image of an oscilloscope spot on the film emulsion. The signal produced by the charge amplifier (*c*) was fed to the first channel of a Tektronix type 7704 A double-beam oscilloscope (*k*), used without time base. The film movement allowed continuous recording of the shifting of the spot corresponding to the first channel; the second was employed for time marking. In this way, each picture gave the position of the insect's wings and the value of the corresponding vertical force, at a given instant.

The amplifier output signal was also sent to the first channel of a Beaudouin ACBA0300 direct-writing oscillograph (*l*). Two other channels were used to record a 50 Hz signal from the mains, and the pulses emitted by the camera when taking each picture. This allowed monitoring of the time and force scales on the film, as well as the regularity of the insect's flight during the two seconds which preceded and followed the wing-stroke cycle selected on the film for detailed analysis.

Procedure and use of recordings

The raw signal generated by the probe represented the sum (F_z) of the vertical components of the instantaneous aerodynamic forces (L) and the inertial forces (F_i) due to the accelerations of the different moving parts of the insect. To determine the

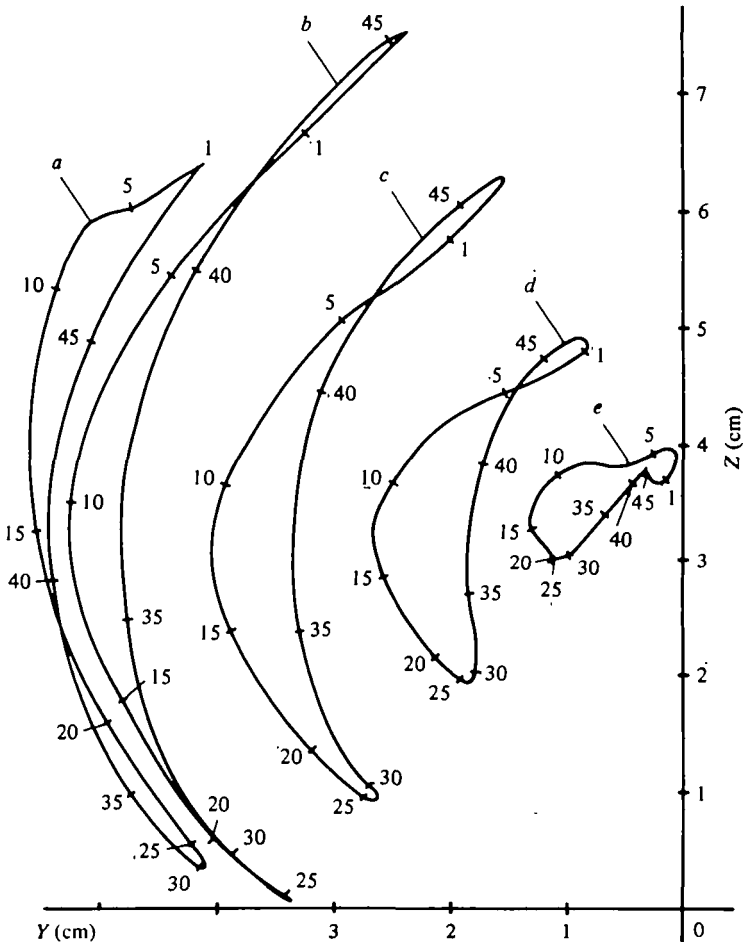


Fig. 4. Projection on a plane perpendicular to the flow of the movement of reference points, *a-e* of the left-hand wings during a typical flight. Each curve is plotted from 50 points. *Z*-axis: vertical; *Y*-axis: horizontal perpendicular to the flow direction.

lift, it was therefore necessary to determine the inertial forces likely to be created by the wing movements, the other visible parts of the body, and also the internal organs of the insect. Since the latter undergo relatively small movements, we assumed that their contribution was negligible. Furthermore, except in the case of one flight which will be discussed later (see Discussion), we selected, among the recorded flights, those for which no movement was detected in the legs and abdomen. In these conditions, only the inertial forces due to the wing movements were taken into consideration. To calculate them, it was necessary to know the movement of the centre of gravity and the mass of the different wing sections. These data were determined as indicated below.

A few hours before the tests, the animal was narcotized with carbon dioxide. The wings were spread out, white paint marks were made at the points indicated in Fig. 3, and the insect was photographed. For each forewing, a single reference point (*a*) was marked near the tip. For each hindwing, whose fan structure permits significant flexing perpendicular to the ribs, four reference points (*b-e*) were marked on the trailing edge.

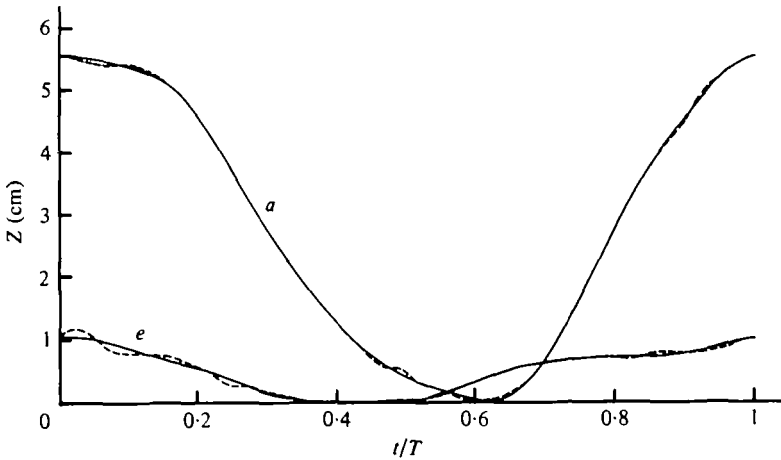


Fig. 5. Vertical movements of reference points *a* and *e* of the right-hand wings during flight I. Abscissa: time normalized by period T ; the origin corresponds to the topmost position of the forewing. Ordinate: height in cm; for each curve, the zero value corresponds to the lowest position of the reference point. Dotted line: experimental curve. Solid line: analytical representation by Fourier series limited to the six first terms.

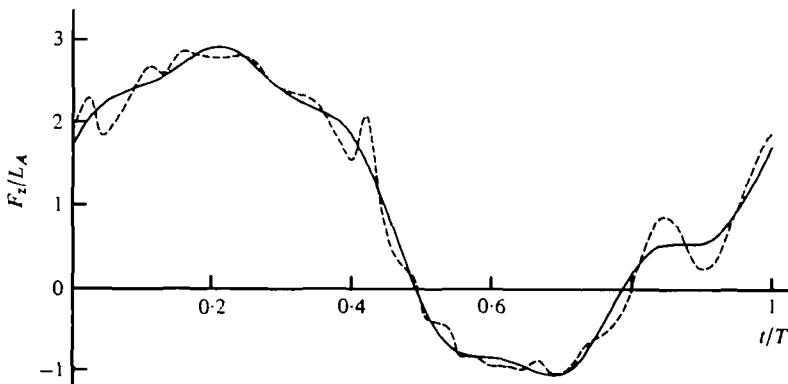


Fig. 6. Gross force signal during flight I. Abscissa as in Fig. 5. Ordinate: vertical force F_z normalized by average lift L_A . Dotted line: experimental curve. Solid line: analytical representation by Fourier series limited to the six first terms.

Immediately after a wind tunnel test, the animal was weighed and killed. The wings were separated from the body and the hindwings were cut into segments B-E (Fig. 3), corresponding to the four above reference points. The position of the centre of gravity of each wing or wing segment was determined as the location indicated by the point of a needle on which horizontal equilibrium was achieved. This element was pierced at the centre of gravity, photographed for subsequent distance measurements, and weighed.

The test film was projected and analysed frame by frame. For each picture of the selected wing cycle, the following were marked on the screen: (1) the position of the oscillograph spot, enabling reconstruction of the curve of variations in the vertical force F_z produced by the insect as a function of time (Fig. 6); (2) the position of the different wing reference points; the curves obtained by connecting these points

represented the projection of the movement of the reference points on a plane perpendicular to the flow (Fig. 4).

The marked points corresponding to a given picture were given the same serial number, starting the numbering at the topmost position of the forewing.

Taking account of object:film and film:screen magnification ratios, the curve giving the ordinate of the point as a function of time was plotted for each reference point. By multiplying the ordinates by the ratio of the attachment-centre of gravity distance to the attachment-reference point distance, the vertical movement $z_i = f_i(t)$ of the centre of gravity of the corresponding wing segment of mass m_i is obtained. If acceleration is taken to be positive when directed upward, the total inertial force is:

$$F_I(t) = - \sum_{i=1}^n m_i \frac{d^2 z_i}{dt^2}, \quad (1)$$

where n is the number of reference points for the two pairs of wings, generally 10.

In order to calculate the acceleration values $d^2 z_i / dt^2$ as a function of time, it was necessary to obtain an analytical expression for the curves of vertical movement. For this purpose we used a computer program giving the Fourier series expansion of a tabulated function. This gives z_i for each of the ten reference points, in the form:

$$f(t) = A_0 + \sum_{p=1}^k \left(A_p \sin 2\pi p \frac{t}{T} + B_p \cos 2\pi p \frac{t}{T} \right), \quad (2)$$

where $k = \frac{1}{2}(N-1)$, N being the number of different values of z used as data in the program; this odd number is always taken as equal, to within one unit, to the number of pictures contained in the wing-stroke period T considered.

The experiment showed that the second derivative of this function exhibited a number of oscillations which failed to correspond to real variations in acceleration, but which were due to measurement uncertainties concerning wing positions. Hence it proved necessary to 'smooth' the stroke curves. This was achieved by limiting the number of terms of the series. In practice, five harmonics are enough in order for the Fourier series to correspond to a good approximation of the experimental curve. In these conditions, the acceleration curve does not exhibit spurious oscillations.

Fig. 5 shows one example of true vertical movements as a function of time and their analytical representation. The curves correspond to reference points (a) and (e) of the right-hand wings of a locust (flight I).

Since the inertia correction curves are thus limited to a pass band of about 120 Hz, it is impossible to state whether the variations in the force signal corresponding to higher frequencies should be attributed to rapid changes in lift or in inertial force. Hence it is logical to limit the gross force curve to about 120 Hz also. This limitation was achieved in the same manner as for the wing-stroke curves, the term A_0 in (2) being equal to the average lift. Fig. 6 shows one example of the force signal and its analytical representation, leading in this case to an appreciable loss of information.

All the operations required for lift calculations were carried out by computer.

The overall measurement system was tested by positioning small weights in place of the insect, and by subjecting the balance support to high-amplitude oscillations by means of an air-actuated device. The inertial forces measured directly coincided with

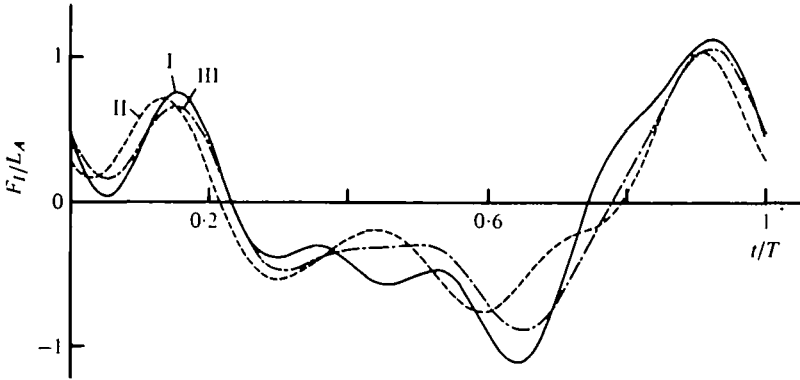


Fig. 7. Total inertial forces for flights I-III (see Table 1). Abscissa as in Fig. 5. Ordinate: inertial force F_i , normalized by average lift L_A .

the values calculated from the movement of the weights and the support rod. This constituted overall substantiation of the force measurement system and the inertial force computation programme.

RESULTS AND DISCUSSIONS

Among all the tests performed, we completely analysed one wing cycle in recordings corresponding to six different flights in which the average lift L_A ranged from 86 to 113% of the insect weight. Qualitative analysis of the force signal and of wing movements relative to other flights showed that the same general characteristics were observed in all cases. In the following discussion we shall restrict ourselves to three flights, the principal parameters of which are given in Table 1.

Inertial forces. Fig. 7 shows the variations in total inertial forces F_i during one wing cycle, for the three flights considered. As in all the curves which we present, these forces are normalized by the average lift L_A of the insect. The comparison of these curves with signals fed by the probe (Fig. 9) shows that the amplitude of the gross vertical forces is only about twice as great as the amplitude of the inertial forces. The corrective terms are therefore high, and it becomes important to examine the different causes of errors occurring in measurement of the inertial forces.

We have already shown the need to apply a frequency limitation to the analytical representation of the wing reference point movements. However, this only leads to elimination of the more rapid variations in inertial forces.

Movements of the abdomen and hindlegs of the insect are liable to produce non-negligible inertial forces. These movements were only observed in the case of a flight with low average lift (not presented here) in which one hindleg of the insect was unfolded; even in this case, the corresponding inertial forces, determined in the same way as for the wings (based on the movement of the centre of gravity and the mass of these organs), were very low.

Segment E of a hindwing (Fig. 3) exhibits complex movements, so that a reference point other than (e) would give a significantly different movement curve for the centre of gravity. However, since the contribution of these wing elements to the total inertial

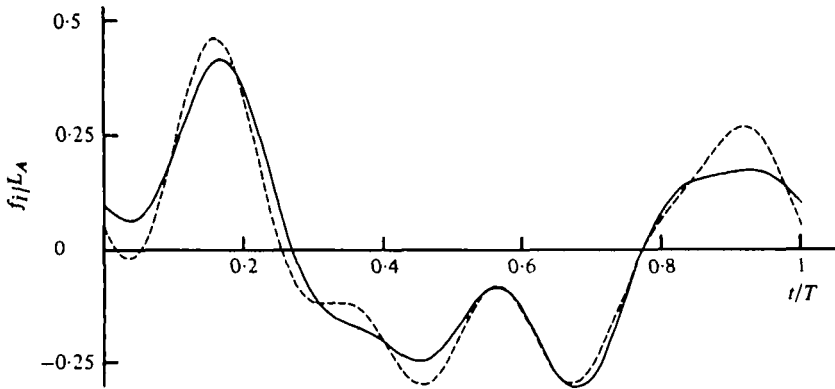


Fig. 8. Inertial force of left-hand forewing in flight I. Solid line: calculated from the movement of reference point *a*, with the wing assumed rigid. Dotted line: calculated from the movement of parts 1-4 shown in Fig. 5. Abscissa as in Fig. 5. Ordinate: inertial force f_i , normalized by average lift L_A .

force is very small, the errors made in these segments have little effect on the accuracy of the values obtained for the total inertial force.

Calculation of the inertial forces from reference point movements implies that each wing segment can be considered as rigid along the lines joining the reference point to the attachment point. In actual fact, the main ribs of the wings exhibit non-negligible flexure at certain instants of the wing cycle. Since this is particularly visible in the forewings, we estimated the errors thus committed by evaluating accurately the inertial force of a wing in the case of flight I. For this purpose, the left-hand forewing was cut as indicated in Fig. 3, into four approximately equal length parts (1-4), whose masses and positions of the centre of gravity were determined. Since the entire wing was clearly visible in each frame of the film, we managed to trace the curves showing the movement of each centre of gravity. Fig. 8 allows comparison of the inertial forces thus obtained ('flexible' wing) with those obtained using the wing tip reference point alone ('rigid' wing). The maximum errors occur before and after the topmost position of the wing. Neglect of the flexibility of the main ribs was certainly the first source of error in our inertial force measurements.

It should be pointed out that in determining instantaneous lift, we assumed that the aerodynamic forces acting on each wing element were transmitted instantaneously to the probe. In actual fact, a time lag occurs, longer for elements further from the insect's body, so that the measured force does not represent exactly the sum of the elementary forces exerted on the wings at a given moment. However, if the speed of propagation of a disturbance along a locust wing is about 5×10^3 cm/s (Weis-Fogh, 1973, p. 211), the propagation time from one tip to the other remains small, about 1 ms. Even if the propagation times are significantly longer, only the very rapid force variations are poorly represented by the probe signal.

Finally, the different effects discussed above are liable to modify certain shape details of the lift curves, but they cannot cause large amplitude errors in the lift curves. Our conclusions are based on the latter characteristic.

Lift forces. Fig. 9 shows the raw signal sent by the force probe for each of the three flights considered, and the lift curve (normalized by average lift) obtained after sub-

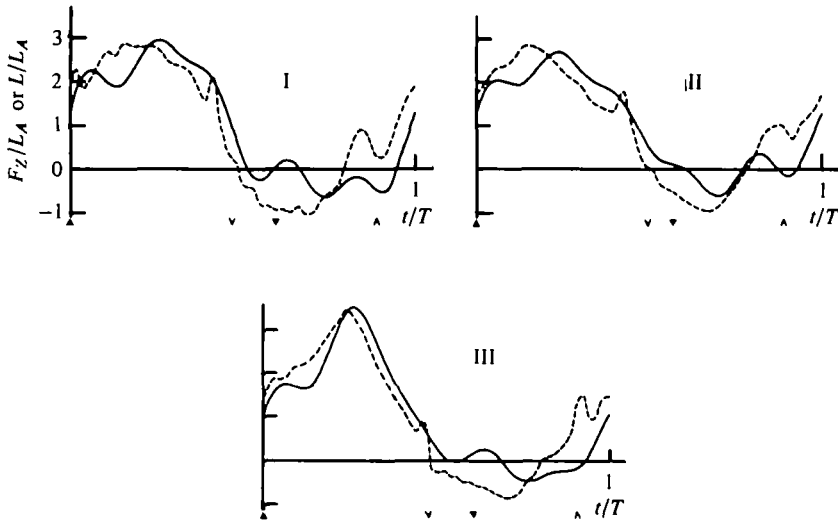


Fig. 9. These curves represent, for flights I-III respectively, the gross vertical force (dotted line) exerted on the probe, and the real lift (solid line) obtained after subtraction of inertial forces and limitation of the pass band to the fifth harmonic. Abscissa: time normalized by period T ; the origin corresponds to the topmost position of the forewings. Ordinate: F_z or L normalized by average lift L_A . The top and bottom wing tip positions are indicated by arrowheads directed upward and downward. Solid signs, forewings; open signs, hindwings.

traction of inertial forces and by restricting the pass band to six times the wingbeat frequency. The curves relative to the raw signal exhibit a number of rapid fluctuations. In particular, a transient force increase occurs just before the lowest position of the hindwing tip. This phenomenon, which must have special significance, occurs to varying degrees in the locusts, but we observed it in all the recordings made, including those made for flights of *Locusta migratoria*. However, as shown above, the frequency limitation of the wing movement curves makes it impossible to determine whether this rapid variation corresponds to an increase in lift or in inertial forces.

The corrected curves show that maximum and minimum lift occur respectively during the downstroke and upstroke. This agrees with the results obtained by Jensen on the lift of detached wings, placed in steady-state flows.

To make a more accurate comparison of our experiments with those of this author, we have assembled in Fig. 10 some results concerning normal performance flights, i.e. in which the average lift L_A differs from the weight of the locust by less than 15%. The dotted curve reproduces the results given in fig. III, 18 in the article by Jensen (1956), relating to flights with relative lift equal to 97 and 111% (see Table 1).

Our results are significantly different from Jensen's, essentially in two aspects: (1) direct measurements on the insect in flight show that lift can be negative at certain moments during the upstroke. The extent of this effect was too large for the appearance of negative lift to be attributed to measurement errors. This occurrence was not observed in any of the results of Jensen, at least with respect to the sum of the forewing and hindwing lifts; (2) the lift variations observed during a wing cycle were far greater than those observed from measurements on detached wings.

The amplitude of these variations may be characterized by the difference between

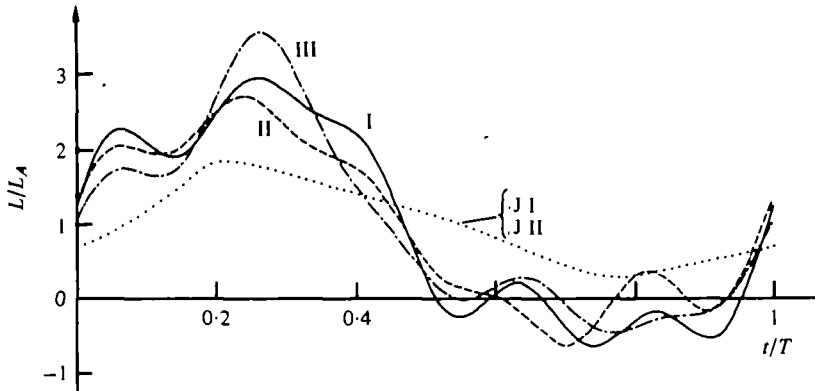


Fig. 10. Variations in lift during a wing-beat cycle, for normal flights. Dotted line: Jensen's results derived from flights J I and II (see Table 1). Other curves: flights I, II and III of the present study. Abscissa as in Fig. 9. Ordinate: lift L normalized by average lift L_A . On the average, the amplitude of the lift variations observed in flight (I-III) is about twice as great as that obtained with detached wings placed in steady-flow conditions (J I and II).

Table 1

Flight no. ...	Present experiments			Jensen's experiments		
	I	II	III	J I	J II	J III
Flight velocity (m/s)	3.4	3.9	3.6	3.5	3.6	3.2
Wingbeat frequency (Hz)	21.9	20.1	19.3	17.5	18.3	21.2
Insect weight (g)	1.75	2.12	1.95	2.3	2.04	1.69
Average lift L_A (g)	1.97	2.28	1.68	2.23	2.26	2.74
Relative lift L_A /wt (%)	113	107	86	97	111	162
Relative amplitude ($L_{\max} - L_{\min}$)/ L_A	3.5	3.3	3.9	1.6 (mean)		$\approx 1.7^*$

* This result is derived from fig. III,17 in Jensen (1956). Note that in this figure the ordinate represents the lift normalized by the weight of the insect and not by the average lift as stated in the text of the article.

maximum and minimum instantaneous lift L , normalized by average lift L_A . The values of the ratio ($L_{\max} - L_{\min}$): L_A , which we call 'relative amplitude', are given in Table 1 for the different flights. It may be observed that the mean value of this ratio is greater than 3.5 in our curves, and less than 1.7 in Jensen's curves, even if the latter include the very high performance flight J III.

Hence the relative amplitude obtained by direct measurements on insects in flight is about twice that obtained by measurements in steady-flow conditions. This large discrepancy between the amplitudes casts serious doubt on Jensen's conclusion that locust flight can be considered as a succession of steady states; our results are only compatible with those of Jensen if the existence of significant unsteady effects is acknowledged.

Since by definition these effects are transient phenomena, it is not surprising that they can be highlighted by investigations of instantaneous forces, whereas the study of average forces failed to reveal their existence. Jensen's observation that the *average* aerodynamic forces measured in flight are practically equal to those derived from tests in steady-flow conditions does not preclude the existence of significant unsteady effects. This equality merely shows that, if they exist, these effects successively produce

increases and decreases in the aerodynamic forces which practically offset each other in the course of a wing cycle. This may be observed to occur, for example, in the case of profiles oscillating in a constant velocity flow, when the average angle of attack approaches the stalling angle; experiments and computations carried out at high Reynolds number, but reduced oscillation frequencies comparable to those of the locust (Philippe & Sagner, 1973), showed that instantaneous lift and drag values are alternately higher and lower than steady values at the corresponding angles of incidence.

The power required to overcome the aerodynamic forces was calculated by Jensen (1956) from his experimental results on wing movements in flight and instantaneous values of lift and thrust obtained by simulation in steady-flow conditions. It would be interesting to make the same calculation from the instantaneous forces measured during a real flight, and to compare the aerodynamic powers calculated in both cases. This comparison would have been possible for an insect possessing a single pair of wings; unfortunately, it is impossible in the present case, because direct measurements on locusts in flight do not provide a knowledge of the respective contributions of the forewings and hindwings to the instantaneous aerodynamic forces.

The work which suggested a new mechanism of lift generation (Weis-Fogh, 1973; Lighthill, 1973) showed again recently the value of continued investigations on the flight of insects. However, these studies encounter several difficulties of a theoretical and experimental nature, due, for example, to the complexity of wing structure and movements, to the lack of flight reproducibility, and to the impossibility of varying the parameters. It is probable that with respect to the role played by unsteady phenomena in flapping flight, conclusive experimental results will be derived from the study of mechanical models rather than from measurements on living animals.

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