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Biology and Physics of Locust Flight. II. Flight Performance of the Desert Locust (Schistocerca gregaria)

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BIOLOGY AND PHYSICS OF LOCUST FLIGHT

II. FLIGHT PERFORMANCE OF THE DESERT LOCUST *(SCHISTOCERCA GREGARIA)*

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[Plate 9]

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The main purpose is to analyze how a number of wing-stroke parameters are related to the *lift* (average vertical force) and *thrust* (average horizontal force) produced by the insect under well-defined aerodynamic conditions.

The locust was suspended from a complicated balance and flew against a uniform horizontal wind from an open-jet wind tunnel. The wind speed was automatically adjusted to the preferred *flying speed* (air speed), i.e. the speed at which the thrust equals the *extra-to-wing drag*. The lift was measured as the apparent reduction in weight; it is given as a percentage of the weight which the individual would have if it had flown for about one hour, was full-grown and well fed but, if a female, with undeveloped eggs (=basic weight). This figure is the *relative lift*, and it is used because the actual weight changes much with age, feeding, sexual development, etc., while the dimensions of the flight motor remain constant. The angle between the wind and the long body axis is the *body angle* and was chosen by the observer or by the insect itself. Most experiments took place at 30° C (constant temperature room), but series were run at the upper and lower limits for flight, including experiments with small flocks of locusts suspended from a roundabout. The rate of evaporation of water from the thorax was kept constant.

In a large number of individuals *sustained steady-state flight* was studied; at regular intervals a set of *simultaneous* readings were taken consisting of the lift, the speed, the body angle, the stroke frequency, the extreme angular positions of the wings, and of the inclination to the vertical of the stroke planes. In addition, the angular movements of the entire wings relative to the body were estimated from slow-motion films. The results are seen in §§4 to 7.

The frequency distribution of the *relative lift* has its maximum about 100 %, showing that, in this respect, the flight comes near to free flight. It varied from 35 to 175 %, i.e. about five times. During continuous horizontal flight the *flying speed* was $3{\cdot}5 \pm 0{\cdot}1$ m/s and may increase to 4·2 m/s in free flight. At larger lifts (climbing) the steady-state speed could reach 4·5 m/s. During the first minutes the speed was often 4·5 to 5·0 m/s, the maximum observed being 5·5 m/s. No locust lifted its own weight at speeds less than 2·5 m/s. The power necessary to overcome the extra-to-wing drag only corresponds to 1 to 3 % of the total metabolic rate. The effect of altering the *body angle* is fundamentally different from that of altering the pitch of an aircraft; the lift is controlled and kept constant by the locust and proved to be independent of alterations in the body angle amounting to as much as 20°. This is the basis for the technique and for the treatment of the results.

In spite of the large variations in lift, the following stroke parameters varied little or not at all: the *stroke angles*, the *stroke-plane angles*, the *middle position of the wings*, and the *time course* of the angular movement of the entire wing, $\gamma = \gamma(t)$. The latter function deviates considerably from a simple harmonic oscillation. According to figure II, 20, the average points are determined with an accuracy of better than ±1 %, permitting graphical differentiation. The *stroke frequency* was rather constant but increased with the reflexly controlled lift, contrary to Chadwick's experiments on *Drosophila*, and decreased with increasing size, according to Sotavalta's findings in other insects. The maximal changes were small, however, amounting to 8 % (lift) and 15 % (size) respectively.

The flight performance and the stroke parameters were independent of changes in *air temperature* (no radiant heat) within 25 to 35° C, although the pterothorax is subjected to similar changes. *Sustained* flight does not take place below 25° C and above 35° C, but *short* performances were observed between 22 and 24° C as well as above 37° C.

The great variation in lift could not be explained by changes in the measured stroke parameters, and by analogy with a variable-pitch propeller, it must be caused by differences in *wing twisting* $\theta(r, t)$. It was also found that lift and thrust varied in a more intricate way than in a simple actuator disk.

The regularity of the stroke and its independence of temperature makes it possible to define a *standard stroke*, making it easy to compare a given performance with the normal.

1. Introduction

In a general review of flapping flight (part I of this series) it was concluded that our present knowledge of the kinematics is too incomplete to permit a quantitative analysis of the dynamics and energetics of the flight of any flapping animal. It was stressed that such estimates must be based upon simultaneous observations of a large number of flight parameters made under conditions which come as close as possible to the natural ones.

The most satisfactory technique for studying insect flight was described by Hollick (1940). The dipteran fly, *Muscina stabulans*, was suspended from a delicate balance and made to fly. The magnitude and the direction of the resulting average force acting on the body was measured both in still air and in a wind of known and varied velocity. No attempt was made to adjust the wind speed to the preferred flying speed, the main purpose being to study the sensory adjustments of the wing-tip curve to the wind stimuli. Although this procedure is unsuited for a mechanical analysis, further technical refinements make it possible to investigate the flight phenomenon quantitatively, as has been attempted in this paper. Recently Wootten & Sawyer (1954) have studied the pick-up of spray droplets by locusts flying at their preferred speed in a wind tunnel; their technique resembled that described here (see discussion on pp. 500 and 502).

The attempt has been made to design a wind-tunnel technique by means of which sustained flight of a desert locust can be studied under well-defined aerodynamic conditions and which gives the best possibility of measuring *several* flight parameters at the same time. The main purpose is to obtain information on how the stroke parameters are correlated with the lift and thrust produced during steady-state flight and how they are influenced by temperature. Problems of stability and control will not be dealt with here apart from the features which are related to the technique used.

The general procedure is discussed in §3, but technical details are described in the appendices. The results are given in figures and tables in §§4 to 7 and are discussed in relation to natural flight in §8. They serve as a basis for more detailed studies of the flight in the succeeding papers of this series.

2. Material

The desert locust (*Schistocerca gregaria* Forskål) was found especially suited for these experiments. It is large and proved to be an extremely steady and persevering flyer in the laboratory. Although a two-winged insect might be easier to analyze theoretically, the four-winged locust has the advantage of representing a more primitive evolutionary type which is of great economic importance. It will furthermore be shown that the two pairs of wings only exert an insignificant aerodynamic effect upon each other (part III). They represent extreme cases of rigidity and flexibility; the forewings are only twisted by active movements, whereas the shape of the hindwings is also modified by the wind forces.

The insects were bred in crowded cages at the Anti-Locust Research Centre, London, and belonged to the gregarious or transient phase. They were sent to Copenhagen by plane 5 to 7 days after the final moult but were not used for experiments until they had reached the weight and development of immature, full-grown locusts, resembling the 'full migrants' described by Weis-Fogh (1952). In that paper it is shown that the exoskeleton (for instance the wings) and the flight muscles of full-grown male and female individuals of different sizes are geometrically similar. The proportions of the locomotor system of an individual can therefore be expressed in terms of simple indices calculated from the length of the forewing E (elytron) and from that of the hind femur F, the standard deviations (s.d.) all being small. In a full-grown, immature desert locust of average size, a so-called *standard Schistocerca*, these indices amount to: *length index* $l=(EF)^{\frac{1}{2}}=3{\cdot}78$ cm, s.d. $=2\,\%$; *surface index* $s=EF=14{\cdot}3$ cm^2, s.d. $=4\,\%$; and *volume index* $v=(EF)^{\frac{3}{2}}=54{\cdot}1$ cm^3, s.d. $=6\,\%$. It weighs 2·08 g before flight. After $\frac{1}{2}$ to 1 h of flight its weight is reduced to 1·98 g because of the faeces given off.

Whereas the geometric proportions of the flight system, including the dimensions of the body, remain constant, the weight of an individual varies with age, nutritional state, amount of egg material, etc. When comparing the lift produced by various individuals, i.e. the apparent reduction in weight due to flight, it is therefore necessary to refer the lift of an individual to a figure which is more representative for the flight system than would be the actual, instantaneous weight. The lift of an individual is therefore always given as a percentage of its *basic weight* w_b, where $w_b=v1{\cdot}98/54{\cdot}1$. v is the volume index of the individual (cm^3), and $1{\cdot}98/54{\cdot}1$ is the weight per unit volume index (g/cm^3) of a flying *standard Schistocerca*.

Each locust was numbered and the distal parts of the mesotarsi and metatibiae were cut off so that the insect could not cling to the suspending bar or free itself. This procedure influenced neither the weight nor the flight (complete flight posture) significantly (Weis-Fogh 1952). Only healthy and undamaged specimens were used and their ability to fly was tested in a roundabout (Krogh & Weis-Fogh 1952). If an individual repeatedly behaved irregularly during two or three roundabout flyings, of about 2 h duration each, it was discarded. This procedure was justified for several reasons. The parental stock of locusts had been bred in the laboratory for many years at about four generations per year. From time to time new blood has been introduced but without any selection according to their ability to fly. In nature a selection of able flyers takes place in every migrating generation, bad flyers being left behind. Finally, unidentified chronic diseases could hamper the flight performance in the laboratory. Details of the treatment immediately before the experiment are given on p. 468.

Apart from bacterial infections which generally killed quickly, a slowly developing malign fungus disease (species unknown) caused much trouble. The infection did not become observable macroscopically until a localized growth had caused black necrosis (anthraconecrosis), mainly in the coxal musculature including some of the flight muscles. Both bacterial and fungal infections were practically eliminated, however, after thorough cleaning and weekly sterilization of the cages with ultra-violet light. In some batches heavy attack by parasitic Mermitidae reduced or impeded flying, but, by avoiding the use of grass or fodder from damp fields, this trouble was overcome. Even massive infection by gregarines did not seem to influence flying significantly.

3. METHODS

(*a*) *Co-ordinate system of observation* (figure II, 1)

The locust was suspended with its head facing a horizontal uniform stream of air from the outlet of a free-jet wind tunnel. The midpoint between the mesonotum and the metanotum was placed 10 cm from the outlet and in the centre line of the stream. This point was taken as the origin of the rectangular co-ordinate system x, y, z in figure II, 1. The locust is represented by a hatched arrow in the direction of flight. All geometric measurements refer to this system. Angles in the co-ordinate planes were called δ, γ and β as indicated in the figure.

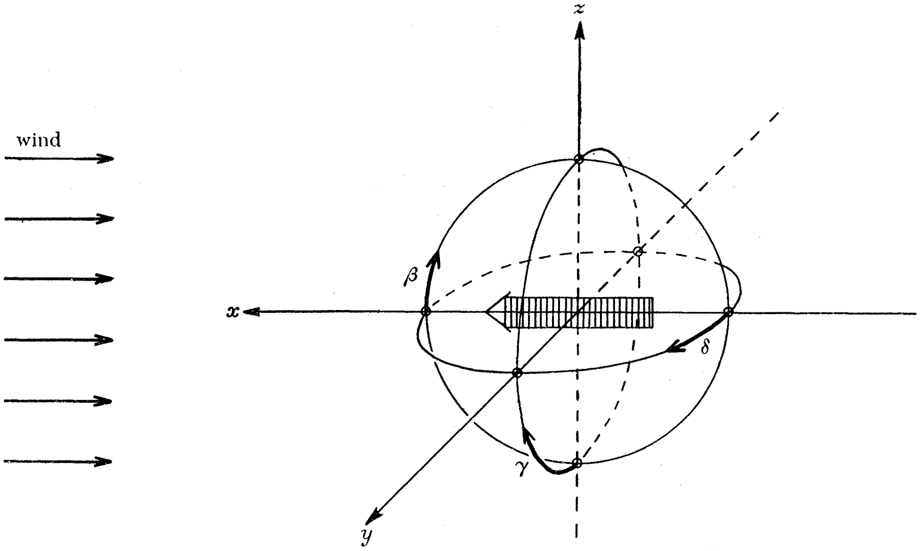

FIGURE II, 1. Co-ordinate system of observation. The x-axis coincides with the horizontal centre line of the wind tunnel. The hatched arrow represents the locust flying against the wind.

(*b*) *Definitions* (figure II, 2; table II, 1)

Posture

Like other insects (cf. Hocking 1953), locusts have a characteristic flight posture (Krogh & Weis-Fogh 1952); the antennae are stretched obliquely forwards, the forelegs are drawn up, the middle legs and the hind femora are stretched backwards along the abdomen, the hind tibiae are drawn up against the shallow groove on the underside of the femora, and the abdomen points straight backwards in continuation of the pterothorax as seen in figure II, 2. Apart from the first minutes of flight, the bending up of the hind tibiae was mainly observed during continuous flight against a properly adjusted wind and after adjustment of the body angle. When only one of the hind tibiae was drawn up the posture was also designated as *complete*, the animal sometimes omitting to bend the other hindleg; a light push might then stimulate the locust to draw it up. If the hindlegs remained stretched but the other attitudes were taken up, the posture was *incomplete*. All measurements refer to either of these two postures.

Body angle

By analogy to aircraft the angle of pitch, or the *body angle B* (figure II, 2), was the acute angle between the incoming horizontal wind and the plastron of the pterothorax, i.e. the fused, nearly flat, sternal sclerites. When the animal was viewed from the side and with its wings folded, the dorsal margin of the forewings was practically parallel to the plastron. Being well defined, it was used as a reference.

Stroke parameters

The wing movements will be described in detail elsewhere (parts III and VII) and only the basic parameters are mentioned here. Suffixes 1 and 2 indicate fore- and hindwings respectively. A *wing stroke* is the complete cycle of an *oscillating* wing, the *upstroke* being the ascending and the *downstroke* the descending phase. The number of complete wing strokes per minute is the *frequency* N. In the forewings the long axis moves approximately in a plane including its upper and lower positions. The hindwings were partially unfolded during some parts of the beat so that the *angle of plication* δ* ranged from 60 to 90°. The wing tip moves approximately in a plane including its extreme positions. This plane was called the *stroke plane* and its inclinations to the z-axis are the *stroke-plane angles*, measured as b_1 and b_2 in figure II, 2; the intersections of the stroke planes with the zx-plane are indicated by the lines (1) and (2). In this simplified system the instantaneous position of a wing could be described by the angle between the intersection of the stroke plane with the zx-plane and the projection upon the stroke plane of the long axis of the wing. It is called the positional angle γ'. The positional angle was calculated from its projection upon the yz-plane, γ. When γ and b were measured, γ' was

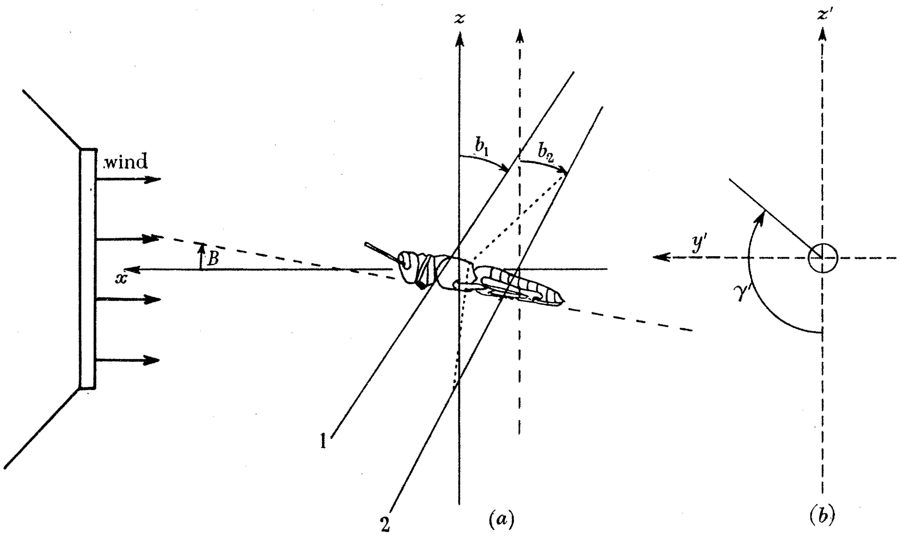

FIGURE II, 2. (*a*) The body angle B and the stroke-plane angles b_1 and b_2. (*b*) The stroke plane viewed from behind the locust; the projections of the z-axis (z'), and of the line through the wing base parallel to the y-axis (y') are hatched; the positional angle γ' is indicated. The locust is shown in complete flight posture but without wings.

$$\gamma' = 90 - \zeta, \quad \text{where} \quad \tan\zeta = \cot\gamma/\cos b.$$

During standard experiments b and the upper and lower value of γ were measured at regular intervals giving $\gamma'_{\text{max.}}$, $\gamma'_{\text{min.}}$, and the medium position $\gamma'_{\text{av.}}$. The stroke angle ϕ is given by

$$\phi = \gamma'_{\text{max.}} - \gamma'_{\text{min.}}.$$

The twisting of the wings about the long axis is a function both of the distance from the fulcrum and of time (cf. part I, $\theta = \theta(r, t)$); it was *not* measured in this investigation and need not be defined any further.

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* i.e. the angle between the long wing axis and the centre line of the abdomen.

Average forces

The wing movements result in a cyclic system of aerodynamic forces which act upon the locust. The average resultant could be resolved into a positive component parallel to the z-axis and a positive component parallel to the x-axis. The former is called the *lift* and the latter the *thrust*; they differ from the ordinary definitions of lift and thrust in being *average* values as well as being force components in a *fixed* co-ordinate system. The directions are therefore fixed and independent of the relative wind over the wings.

The lift L was measured directly as the apparent reduction in weight of the flying locust. It is given as the *relative lift* L_r, i.e. the lift as a percentage of the basic weight of the individual (p. 462). The relative lift thus expresses how much lift is produced in relation to the lift which would be necessary for free horizontal flight if the actual weight of the individual corresponded to its basic weight.

The *thrust* T was estimated indirectly by determining the wind speed at which the extra-to-wing drag D (i.e. the drag from the body and the legs) equalled the thrust. This was the *flying speed* v. As in all wind-tunnel experiments, flight was thus parallel to the fixed wind direction and need not, of course, occur in the same direction if the locust were suddenly released. The extra-to-wing drag was measured at varying wind speeds and body angles so that determinations of B and of the flying speed of a locust would give the thrust.

(*c*) *General flight procedure* (figure II, 3; appendices A to C)

In principle the locust was suspended from the lower end of a sensitive, vertical pendulum (see appendix A). When it started to beat its wings the pendulum moved forwards towards the wind tunnel, but the wind speed was then increased so that the flying animal on the pendulum was brought back to the equilibrium position and kept there by continuous regulation of the speed of the wind-tunnel propeller. When this was the case thrust and extra-to-wing drag neutralized each other and the wind speed equalled the flying speed. The technique adopted has been illustrated in a film (Martin Jensen & Weis-Fogh 1953).

Wind tunnel

The diagram in figure II, 3 represents a horizontal section of the wind tunnel. The working section is a free jet of air with circular cross-section. At the outlet the diameter is 16·5 cm, but the *smooth* part of the jet has a decreasing diameter because of the mixing up with the surrounding 'still' air; the zone of mixing is dotted on the figure. The origin of the co-ordinate system is 10 cm from the outlet where the diameter is 14 cm, i.e. 1 to 3 cm larger than the wing span of the biggest locusts used. The inlet is at the left-hand side, where AC is an axial compressor consisting of rotor and stator. The air speed is reduced in the ratio of about 1:5 in the diffusor D and the honeycomb HC serves to diminish the turbulence. Beyond the honeycomb the cross-section decreases so that the air speed in the nozzle N is six times that in the honeycomb, considerably reducing the turbulence.

The induction motor M_1 works the axial compressor via a continuously variable transmission G. The regulation of the number of revolutions takes place by moving the rubber belt connecting the gear cones. The handlebar H serves for manual adjustments, but the wind speed can also be regulated within 2·3 and 7·0 m/s by means of a servo-motor which is operated by means of relays at the suspension pendulum. The accuracy is better than 0·1 m/s. The speed was calibrated by means of a small pitot static tube and was equal at all points within the hatched space.

We are indebted to Professor C. Refslund for the design of the axial compressor.

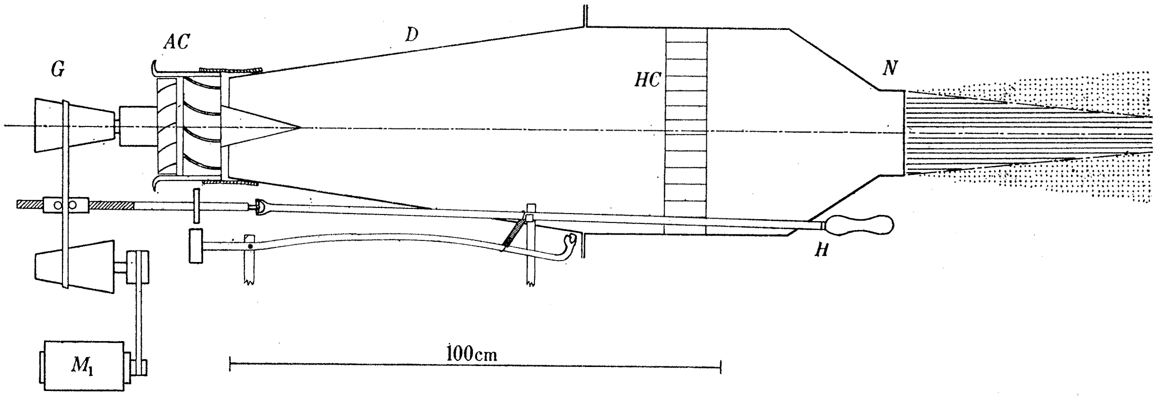

FIGURE II, 3. The wind tunnel. The hatched area is the undisturbed free jet surrounded by the turbulent (dotted) zone.

Suspension and flight balance

The suspension of the locusts depended on the type of experiment. Three types are described in appendix A. In the first (1) a small saddle was moulded over the first abdominal tergum of each individual. The saddle was glued to the integument by means of wax and served as an intermediate piece between the animal and the suspending bar. It was found that this part of the tergum moves only insignificantly during flight so that the locust could beat its wings unhampered, but it was necessary to narcotize the insect in order to fix the saddle and the suspending bar; repeated treatments with melted wax also tended to damage the aorta lying just beneath the cuticle. This suspension was especially used for measuring alterations in flying speed in relation to the extra-to-wing drag and to the body angle.

In the second type of suspension (2) a small suction cup was attached to the plastron of the locust. The leading edge of the streamlined bar was a thin cannula, the lower end of which was bent round the abdomen and turned forwards at the underside where it ended in a small horizontal suction cup covered by a streamlined shield. The locust merely had the plastron covered with a *thin* layer of wax to give a smooth surface; no other treatment was necessary. An animal could therefore be used repeatedly without the slightest damage. All standard experiments with the compound flight balance (see below) were performed with this type of suspension. The suction cup with the shield did not increase the drag to any measurable degree.

A third type (3), which was a modification of the second, was used for studies on the temperature balance. The suction cup was then replaced by three small vertical pegs to which the plastron was glued by applying a minimum of wax so that the working pterothorax was exposed to streaming air at all external surfaces and the heat exchange little altered. This suspension will be further discussed in part VIII.

The drag of the first type of suspension was compensated by electromagnets, but the second and third offered so little resistance against the wind that the complication of compensating could be avoided.

The *body angle* could either be adjusted by means of a small hinge on the lower end of the suspension bar (1) or the bar (2 and 3) was itself fixed to a semicircular bow which was turned round a horizontal axis placed perpendicular to the wind direction. A pointer on the axis indicated the body angle directly with an accuracy of about 1° (appendices B and C). The bow was clear of the air stream, and the extension of the axis passed through the common centre of gravity for the locust and for the empty, combined device for suspension and turning. The other end of the axis carried electromagnets. The body angle could be adjusted, without direct interference with the locust, either by the animal itself or by sending current through the coils. The turning device was part of the compound flight balance.

The suspended locust was placed at the lower end of a *pendulum* (appendices A and B), the sensitivity and equilibrium position of which could be regulated by jockey weights placed above the axis of pivoting. The equilibrium point was so adjusted that the origin of the co-ordinate system fell between the wing bases of the two pairs of wings. Since the centre of gravity of both animal and turning device fell on the axis of turning, the equilibrium of those parts was neutral. By adjusting the wind speed so that the pendulum occupied the same position as it did before flight, the *flying speed* could be estimated for any value of the body angle. The wind speed must be adjusted to the flying speed during the entire experiment if steady and continuous flight is to be obtained, allowing measurements of one simultaneous set of parameters. In the compound balance, therefore, the flying locust adjusted the tunnel itself within 2 to 3 s by means of contact points on the pendulum connected with a servo-mechanism. The accuracy of a single reading of the flying speed was ±0·1 m/s. The turning moments caused by migrations of the action line of the lift were too small to play a quantitative role, except during the very first minutes of vigorous flight.

The *lift* was measured gravimetrically by means of the balance described in appendix B. The total system consisting of locust, suspension, turning device and pendulum was simply placed at one end of the horizontal beam while the apparent weight of the flying locust was indicated by the deflexion at the other end. The values were only correct when the wind speed equalled the flying speed. Equilibrium of the damped balance was obtained in 1 to 2 s and the lift was estimated with an accuracy of about ±30 mg (or ±1·5 % of the weight of a locust). This means that a single reading of the *relative lift* was estimated with an accuracy of about ±6 %, the standard deviation in estimating the *volume index* being about 6 %.

Simultaneously with measurements of lift, flying speed and body angle, the following wing-stroke parameters were measured in quick succession, the technique being described in appendix C. The wing-stroke frequency was read on an electronic stroboscope (General Radio Co. 'Strobotac') with an accuracy of about 0·5 %. The upper and lower angular positions of the four wings were estimated by measuring $\gamma_{\text{max.}}$ and $\gamma_{\text{min.}}$ (accuracy of ±1°), which together with the *stroke-plane angles* (accuracy ±2°) gave an estimation of the true positional angles, $\gamma'_{\text{max.}}$ and $\gamma'_{\text{min.}}$.

A *set of observations* consisted of simultaneous readings of speed, lift, body angle, frequency, stroke-plane angles and of the extreme angular positions of all four wings, i.e. of fourteen figures.

(*d*) *Slow-motion films* (appendix D)

For detailed kinematic studies of the movements and deformations of the wings a series of slow-motion films were taken. However, the locusts were strongly influenced by white light when flying in the laboratory (discussion, p. 499), but in subdued, or better in red, light they flew steadily with symmetrical wing movements for extended periods of time, darkness being no hindrance to vigorous flight activity in front of the tunnel. Strong light therefore had to be abandoned. High-speed cinematography is expensive. For these reasons the stroboscopic film technique described in appendix D was decided upon. Besides its applicability for the present task, it combined a low cost and good working conditions with a reasonably good quality. Each film strip of 1 m comprised four or five apparent wing beats of about 20 flash exposures each. It must be kept in mind that two successive exposures belong to two successive wing strokes, so that a film strip derives from about one hundred wing beats and not only from the apparent five or four. A stroboscopic slow-motion film therefore represents a better average of the movements than would a high-speed film with the same number of exposures when, as in locusts, the flight is comparatively steady.

About seventy slow-motion films were taken of typical flight performances, the flying speed, the lift and the body angle being measured both before, during and after the filming.

It was important to avoid sudden changes in the level of high-pitched noise because it influenced the flight. However, the noise and light from the two stroboscopic flash lamps (General Radio Co. 'Strobolux'), which were triggered by the stroboscope, made it difficult entirely to prevent the wing movements from deviating somewhat from the movements observed during ordinary continuous performances in red light. These small deviations are discussed on p. 488.

(*e*) *Treatment before flight*

In a special roundabout (Krogh & Weis-Fogh 1952) it was observed that the initial high flying speed decreased during the first half-hour and that a steady level was seldom reached until 1 h after the start (Weis-Fogh 1952). The same tendency was found in wind-tunnel experiments where speed and lift were often subnormal until a steady state was reached. The main purpose being to study the performance during sustained flight, the locusts were made to fly for about 1 h in a motor-driven roundabout at 3·5 m/s immediately before the experiment and at the same temperature, humidity and illumination. Only specimens which had reached or slightly exceeded the basic weight were used, animals of subnormal nutritional state being inclined to refuse to fly.

(*f*) *Flight*

The roundabout and the wind tunnel were placed in a small, dark, constant-temperature room where the humidity was also regulated. The illumination was subdued red light (see p. 499). In some cases this was supplemented by a short flash of white light (0·5 s) each half-minute, which produced no observable effect.

Immediately after the preparative roundabout flying the locust was fixed to the suspending bar, the balance was adjusted and the flight induced by the jet from the wind tunnel (Weis-Fogh 1949). In addition to the continuous adjustment of the wind speed, the body angle B was adjusted, generally to between 5 and 10°; sometimes it could be decreased to 0°, while the flight of other specimens did not become steady if B was less than 10°. According to photographs, these values seem to be of the same magnitude as in a flying swarm (Gunn, Perry, Seymour, Telford, Wright & Yeo 1948, figs. 22 and 23).

It must be stressed that it was impossible to influence the lift significantly by changing the body angle between 0° and 15 to 20°. This peculiar phenomenon is further analyzed in a following paper (part IV). The original idea was to adjust the body angle to the value at which the lift corresponded to the body weight and then to read the speed. However, the *body angle and the lift turned out to be independent parameters in locusts.* In a conventional aircraft a given propeller thrust and 'body angle' give only one combination of lift and speed.

After about half an hour the locust usually took up the complete flight posture and the measurements could begin. As a rule it then flew steadily for a number of hours. The flying speed increased when the body angle was decreased (p. 474). Therefore, B was adjusted to or varied in the neighbourhood of the lower limit which was consistent with steady flight at unreduced lift. In some cases the locust itself chose the inclination, but since the same range of values was observed and since the turning device had a considerable mass, the flying became more steady when B was regulated and adjusted by the observer.

In a series of experiments on the influence of air temperature upon the flight performance a special roundabout was used in which a flock of locusts chose their preferred average flying speed (Krogh & Weis-Fogh 1952).

(*g*) *Discussion of the flight technique* (figure II, 4)

There are so many physical and biological parameters of importance in free flight that some had to be disregarded or restricted. The purpose being to study the *basic* flight process, such factors which mainly concern stability and control have been considered only to the extent necessary to make the locusts fly at an apparently normal speed and with a lift approximately corresponding to the body weight. The relatively small ability to manoeuvre and the small power possibly used for such purposes by locusts make them suited for a study of the fundamental processes in insect flight.

The fact that a locust never lifted its own weight during sustained flight if the wind speed (flying speed) was less than 2·5 m/s stresses the importance of the aerodynamic conditions. Flying in still air, i.e. tethered flapping, has therefore no aerodynamic relation to free flight, although the metabolic rate sometimes is as big as in the roundabout or in the wind tunnel (cf. Krogh & Weis-Fogh 1951; Weis-Fogh 1952; part VIII). For these reasons it would not be justified to regard a formal relationship between, for instance, power output and wing-beat frequency as having any direct significance for flight of locusts.

The body movements of a flying locust in relation to the air can be described by translatory movements along the three axes in figure II, 4 as well as by the rotations about the same three axes, i.e. rolling, pitching and yawing. During free horizontal flight, the translation along the x-axis is the most important. During the experiment it was chosen by the animal and represented by the flying speed. Translation along the z-axis reflects alterations in the lift. This movement was locked *inter alia* because of the small size of the tunnel, but the lift was measured. In the flight balance, therefore, the locust moved relative to the air as it would do under free conditions if its weight was adjusted to correspond numerically to the lift. Since the lift was given in percentage of the basic weight of the individual, all measurements became comparable.

The lift and the thrust are the two main force resultants. The control movements consist of sidewards drift and rotatory movements, but they hardly require any significant share of the available power. Up and down movements as well as the drift along the y-axis had to be prevented, and rolling and yawing were also locked. Rolling is inconsistent with a gravimetric measurement of the lift, and freedom to yaw would imply that the wind direction must be adjusted at any instant parallel to the tangent of the track followed during free flight (see appendix A). Neither sidewards drift, nor rolling or yawing, were considered of such importance during steady migratory flight as to justify a severe complication of the technique. Concerning pitching, however, alterations of the body angle might alter the angles of attack of all wing profiles and thereby influence the main quantities. The experiments given in part IV show that this was not the case.

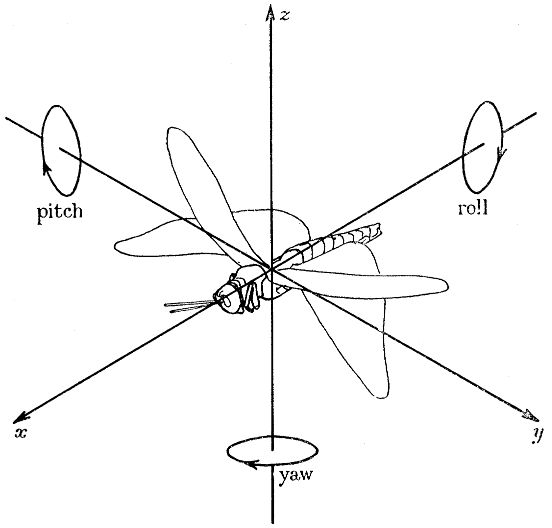

FIGURE II, 4. The possible translations and rotations of a locust flying freely in space. Note the stretched antennae and the folded forelegs.

Apart from the restriction of freedom of the *average* movements, the rigid suspension prevented all *rapid rhythmical* movements. Locking of the translatory movements will be shown to be without aerodynamic significance (part III). Rolling and yawing occur if the wing strokes differ on the right and the left side of the animal, but in steady flight with symmetrical movements they can be disregarded as severe sources of error. In free flight, however, the body angle is likely to vary *during* the stroke because of variations of the lift. Since the lift is controlled by some sensory mechanism which must be stimulated once during each stroke (part IV), a restriction of these pitching movements can hardly affect it. On the other hand, the restriction may very well influence the drag and thus the flying speed, but it is difficult to see in what direction. In some experiments the locust was suspended so that it could pitch freely (appendix A), but this did not result in flying speeds different from those observed in suspension types (1) to (3); the rigid type was therefore decided upon.

The restriction of freedom for rhythmic movements of course tends to deform the skeleton in other ways than during free flight. The prolonged steady-state performances in complete flight posture indicate that such factors are of little biological importance. The forces involved are also much smaller than, for instance, the pull of the flight muscles.

(*h*) *Conclusions and review* (table II, 1)

The degree of freedom of the flying locust could not be restricted any further without impeding the basic movements and their resulting forces. Only such alterations in the flight could be measured which influenced speed and lift, i.e. only manoeuvres involving big changes in power output.

Table II, 1 summarizes the simultaneously observed quantities together with the technique, the symbols and the definitions used.

4. Flight performance under standard conditions

The regularity of the flight performance makes it possible to estimate the normal correlation between the various flight parameters. The angular movements of the wings *during* the stroke will be treated separately (§5), and in this paragraph we shall consider the resulting lift and speed only in relation to the remaining stroke variables.

Most figures derive from flights at $30 \pm 1^\circ$ C and $65 \pm 5\%$ relative humidity (water-vapour deficit between thoracic air and outside air about 26 mm Hg, see p. 492). The locusts had flown for 1 or 2 h in a roundabout immediately before the experiment. In 5 % of the experiments they had only flown for half an hour and in another 5 % they came directly from the cage. When the initial unsteady performance in the balance had been replaced by steady flight in complete posture, the reading began, i.e. not less than 30 min after the start. These conditions are referred to as standard conditions.

(*a*) *Data and lift groups*

A standard *set of observations* consisted of simultaneous measurements of quantities 5 to 12 in table II, 1. For two observers it took about $1\frac{1}{2}$ min. The angular position (nos. 9 to 11) were measured for both pairs of wings and the results are given as the average of the two sides. The material consists of 690 sets from 62 experiments. Of these, 620 (52 experiments) were performed at 30° C, but since temperatures between 25 and 35° C did not influence the performance (p. 493), 70 sets of observations taken at 25 or 35° C were added. Fifteen females and 13 males from two batches were used. Except for the analysis of the wing-beat frequency, the results from 27 slow-motion films of 9 females and 10 males from a third batch were also included, giving 717 sets of observations from 89 experiments of long duration with 47 individuals.

The volume indices were nearly three times less in the smallest than in the largest individuals used, and the material covers the entire range of sizes of cage-bred locusts ($v_{\text{min.}} = 32$ cm^3; $v_{\text{max.}} = 86$ cm^3).

The data showed that the relative lift and the flying speed do not vary with size or sex. In fact, only the wing-stroke frequency was found to be a size-dependent parameter, and the remaining variables could be expressed as simple means of the observed values.

TABLE II, 1. MEASURED QUANTITIES, METHODS, SYMBOLS, DEFINITIONS AND UNITS

The power expenditures (nos. 1 to 4) are dealt with in part VIII, the wing twistings θ (no. 15) and angles of attack α (no. 16) in parts III and IV.

		quantity	method	symbols	definition and units
power	(1)	net rate of heat production	indirect calorimetry	P_n	power necessary for keeping the pterothoracic temperature above air temperature (kcal kg^{-1} h^{-1})
	(2)	power for evaporation	rate of evaporation of water	P_w	power for evaporating water from the pterothorax (kcal kg^{-1} h^{-1})
	(3)	power for positive aerodynamic work	aerodynamic wing torque	P_a	power transferred to the air by the wings (kcal kg^{-1} h^{-1})
	(4)	metabolic rate	summation	P	gross power output, $P = P_n + P_w + P_a$ (kcal kg^{-1} h^{-1})
aerodynamic effects	(5)	lift	weighing (directly)	L_r	average vertical force on the body; percentage of the basic weight
	(6)	thrust	weighing (indirectly)	T	average horizontal force balancing drag (g)
	(7)	flying speed (velocity)	wind speed; pitot static tube	v	average horizontal air speed (velocity) (m/s)
wing-stroke parameters	(8)	stroke frequency	stroboscope	N	number of complete stroke cycles per minute (min^{-1})
	(9)	stroke-plane angle	protractor	b	acute angle between stroke plane and z-axis (degrees)
	(10)	stroke angle	protractor; measurements of γ	ϕ	difference between maximum and minimum positional angles (degrees or radians)
	(11)	positional angle	extremes: protractors; variation with time: slow-motion film	γ'	the angle between the lower intersection of the stroke plane with the zx-plane and the projection of the long wing axis upon the stroke plane (degrees or radians)
	(12)	body angle	protractor	B	the acute angle between x-axis and pterothoracic plastron (degrees)
	(13)	angular velocity	slow-motion films	ω	$\mathrm{d}\gamma'/\mathrm{d}t$, where t is time (rad s^{-1})
	(14)	angular acceleration	slow-motion films	$\mathrm{d}\omega/\mathrm{d}t$	$\mathrm{d}^2\gamma'/\mathrm{d}t^2$ (rad s^{-2})
	(15)	wing twisting	direct: slow-motion films (part III) indirect: wind forces (part IV)	θ	see parts III and IV
	(16)	angle of attack	direct: slow-motion films (part III) indirect: wind forces (part IV)	α	see parts III and IV

The data were grouped according to the relative lift. In locust flight the lift is about twenty times larger than the thrust, and the calculations in part I as well as actual measurements of the metabolic rate (to be given in part VIII) prove that much more power is necessary to produce lift than thrust; the lift is approximately proportional to the total rate of energy consumption. Because of this and since the lift is kept constant and independent of the body angle, the data could conveniently be grouped according to the relative lift L_r. In each individual L_r was estimated with a standard deviation (s.d.) of about 6 % (p. 467) and calculated to the nearest 5 % group. The body of data was divided into double groups each covering 10 % as seen in figure II, 5.

In most cases, an individual gave several observations per lift group (10 % group), often made on different days, so that an average could be taken. If not otherwise stated, the figures in the tables are the means of such averages. The inclusion of results from individuals on which less than four observations were made did not significantly alter either the mean or the standard deviation. The entire body of data was therefore used. When the correlations between the parameters are analyzed on the basis of such mean values, important relations may be hidden. However, the control experiments on p. 485 show that this was not the case.

(*b*) *Lift* (figure II, 5; table II, 2)

During steady-state performances in the laboratory, the relative lift varied as much as five times in different individuals, 35 % being the smallest and 175 % the largest observed value. In free continuous flight of a swarm the average lift must be near to the average weight of the locusts. If the experimental data are to be representative of natural performances, the observed relative lifts should be distributed around 100 %. Figure II, 5 shows the frequency distribution in the 690 sets of direct observations. In fact, two-thirds of all lift readings fall between 75 and 125 %, the peak is about 100 % and the distribution is approximately normal. In other words, the experimental technique worked sufficiently well to permit deductions about normal flight.

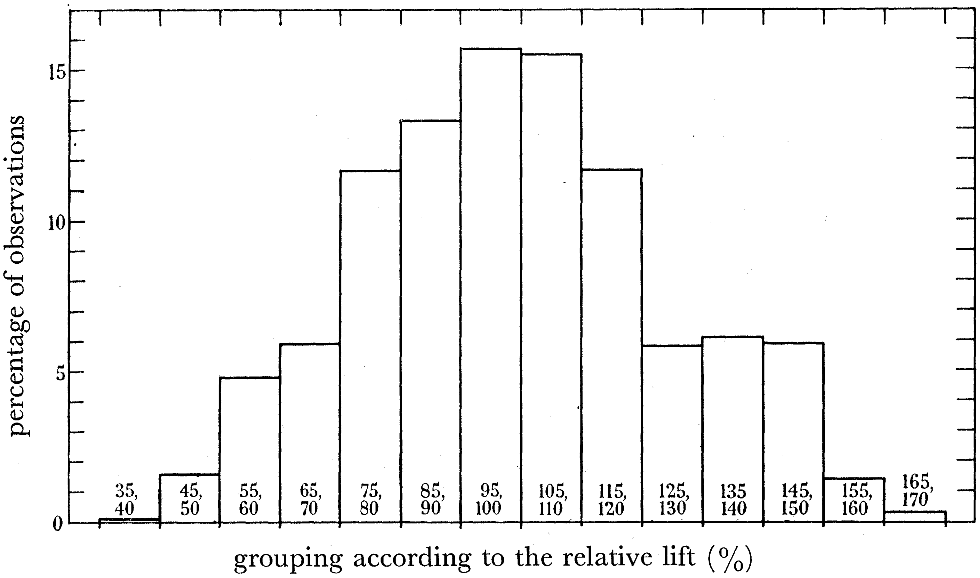

FIGURE II, 5. The frequency distribution of the 10% groups of relative lift found in sixty-two experiments of long duration. Based upon 690 sets of observations from twenty-eight individuals.

In 619 sets of observations there were sufficiently many individuals per lift group to permit an estimate of the scatter. The body angle B varied much from one individual to the next, but the third column in table II, 2 shows that it averaged 6 to 7° in all the eight lift groups (mean 6·9°); no correlation existed between lift and body angle. The standard deviation was of course large (4°) because B ranged from 0° to as much as 20° in the single experiments.

Table II, 2. Body angle and flying speed in relation to lift

The figures are the means of the average values of the individual locusts. The extra-to-wing drag D and the thrust T produced in the flight balance are also given for the standard locust.

					standard	
no. of individuals used*	relative lift (%) lift group	mean body angle B; s.d. = 4° (degrees)	flying speed (m/s) mean ± s.e.	flying speed (m/s) s.d.	extra-to-wing drag, D(mg)	thrust, T (mg)
18 (10)	65, 70	6·3	3·0 ± 0·1	0·4	60	89
27 (20)	75, 80	7·0	3·1 ± 0·1	0·4	65	96
26 (20)	85, 90	6·0	3·3 ± 0·1	0·4	74	109
25 (18)	95, 100	7·1	3·4 ± 0·1	0·4	80	118
26 (19)	105, 110	7·1	3·6 ± 0·1	0·5	90	132
16 (10)	115, 120	7·0	3·6 ± 0·1	0·3	90	132
11 (8)	125, 130	7·1	3·6 ± 0·1	0·4	90	132
9 (7)	135, 140	7·2	3·7 ± 0·1	0·3	95	139
		6·9				

* The number of individuals from which more than three sets of observations were available is given in brackets.

(*c*) *Flying speed* (figure II, 6; table II, 2)

The insect in the flight balance flew with the speed at which the average propulsive force from the wings, the thrust, at any instant neutralized the sum of the air resistances due to the body, the legs and to the suspending bar. In free flight the last term is zero. The resistance of the body + legs is the extra-to-wing drag.

Speed and lift

In table II, 2 the body angle is about 7° in all lift groups, and the variation of speed with lift at this angle is given in figure II, 6*b*. The standard error of the mean is shown by the vertical bars; it amounted to ±0·1 m/s, the standard deviation being 0·3 to 0·5 m/s. At small values of lift, speed and lift increased together. At 100 % of lift v averaged 3·5 ± 0·1 m/s, but at higher lifts it remained nearly constant. When females produce egg material their weight increases to about 135 % of the basic weight (Weis-Fogh 1952). It was observed that this did not change the position of the centre of gravity and it would therefore hardly have any influence on the body angle. According to figure II, 6 one should therefore expect little or no increase in the cruising speed of heavy pregnant locusts compared with full migrants.

Speed and body angle

In a number of locusts the body angle was changed systematically from 0 to 15° without any significant alteration of the relative lift; at all values of B, L_r averaged about 100 %. The details will be described in part IV. The data showed that the flying speed decreased linearly when B was increased, namely, by 0·4 ± 0·1 m/s for each 5° increase in B.

Speed in free flight

In order to estimate how the suspension influenced the speed, a series of flight experiments was made in which the locust was suspended to the pendulum described in appendix A. The drag of the suspension bar was of the same order of magnitude as the extra-to-wing drag of the insect (see following section) and could be compensated by means of an electromagnet. The total drag of locust + suspension was therefore twice as large as that of the locust alone, when no compensation was used. In steady flight at high speed and with compensation the speed, for instance, amounted to 4·0 m/s, the extra-to-wing drag to 114 mg and the resistance of the bar (compensated) to 94 mg. By switching off the electric current the total drag was suddenly increased by 94 mg; the speed thereby decreased by about 0·4 m/s. At the new equilibrium speed (3·6 m/s) the drag was 92 (locust) + 76 (bar) = 168 mg, i.e. one and a half times more than before. The sequence could be reversed. The decrease in speed was therefore *less* than should be expected if speed and drag were related in a simple way. Similar results were obtained at other speeds where the effect of doubling the drag was even less pronounced; at 2·5 m/s the decrease was only 0·1 m/s. They are also consistent with previously published conclusions from roundabout experiments (Krogh & Weis-Fogh 1952). In the compound flight balance which had no drag compensation (suspension types (2) and (3)), the drag of the bar + suction cup was only half as large as that of the above-mentioned, and it can therefore not reduce the

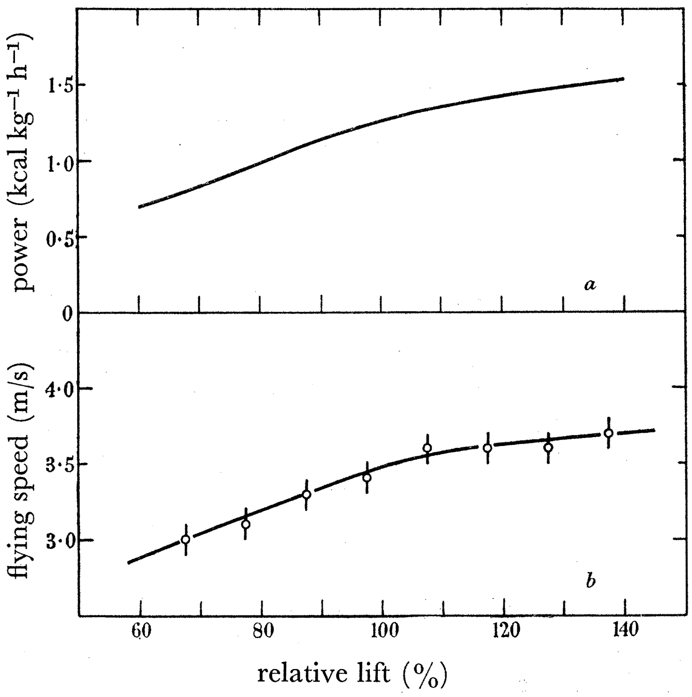

FIGURE II, 6. (*a*) The calculated relationship between relative lift and aerodynamic power necessary to overcome the extra-to-wing drag of a *standard Schistocerca* at the speeds shown in the lower curve. (*b*) The observed relationship between relative lift and flying speed under standard conditions. The body angle averaged 7°. The vertical bars are the standard errors of the means. 619 sets of observations.

flying speed by more than 0·2 m/s at 4 m/s and by 0·1 m/s at 3 m/s, i.e. by an insignificant amount.

A more important source of error in estimating the flying speed of freely flying locusts concerned the variation of the speed with the body angle B, described above. In the laboratory no locust could fly steadily when B was negative, and it is unlikely that freely flying animals would do so. However, they might adopt values lower than the average of 7° in the present material. It therefore appears that the flying speed of freely flying locusts (horizontal flying) is likely to vary between 3·5 and 4·2 m/s (7·8 to 9·4 m.p.h.), the standard deviation being about 0·4 m/s (1 m.p.h.). Average values below 3·5 m/s are less likely to occur, although they cannot be excluded; in the laboratory the lift then tended to become less than the body weight (figure II, 6).

From these experiments it is impossible to decide whether the lower average speed of 3·5 m/s (7·8 m.p.h.) or the higher value of 4·2 m/s (9·4 m.p.h.) is the most probable during natural continuous flight.

Maximum speed

During intensive periods of *continuous* flight in the laboratory 4·5 m/s (10·1 m.p.h.) was sometimes reached or exceeded, but usually such high speeds were only seen just after the start or just after some kind of stimulation. The maximum speed was 5·5 m/s (12·3 m.p.h.). In twenty-two experiments the average maximum, *initial* speed was 4·7 m/s (10·5 m.p.h.), at an average body angle of 3° and a relative lift corresponding to 136 % of the basic weight.

(*d*) *Drag and thrust* (figures II, 7 to II, 10; table II, 2)

The thrust was estimated as the sum of the extra-to-wing drag and the drag of the suspension bar of type (2). The latter amounted to $p_v \times 0{\cdot}052$ g, where p_v is the dynamic wind pressure in mm of a water column.

Extra-to-wing drag

The wings were removed and the locusts were dried at 80° C *in vacuo* with their legs arranged in flight posture. This treatment did not change their external shape. The dried body was attached to the pendulum described in appendix A by means of the suspending bar. In some experiments the suction cup with its streamlined shield was removed in order to estimate the drag of these parts. At all body angles this did not alter the equilibrium speed by more than 0·05 m/s, and the comparatively large suction cup therefore adds no significant amount to the drag. The extra-to-wing drag D was found by subtracting $p_v \times 0{\cdot}052$ g. It depends on the size of the locust, the position of the legs, the body angle and, of course, on the flying speed. In order to compensate for the differences in size, all values were recalculated to that of a *standard Schistocerca*, by means of the surface index s.

The influence of the hindlegs is seen in figure II, 7, where $B = 7°$. When the locust was arranged in complete flight posture (△), D was slightly higher than if the hindlegs were removed (○). When the hind femora were elevated 15° above the horizontal and the tibiae were set perpendicular to them, the drag increased by 48 % (●). Removal of the tibiae without changing the position of the femora, brought D back to the normal (+). The hind tibiae therefore influence the extra-to-wing drag to the same extent as does the suspending bar and can exert little *direct* influence on the speed. However, the posture is an important indicator of whether the locust is in steady-state flight or not. When the femora are not parallel to the abdomen or when the latter is bent, D, of course, increases considerably, but this bears no relation to normal flight.

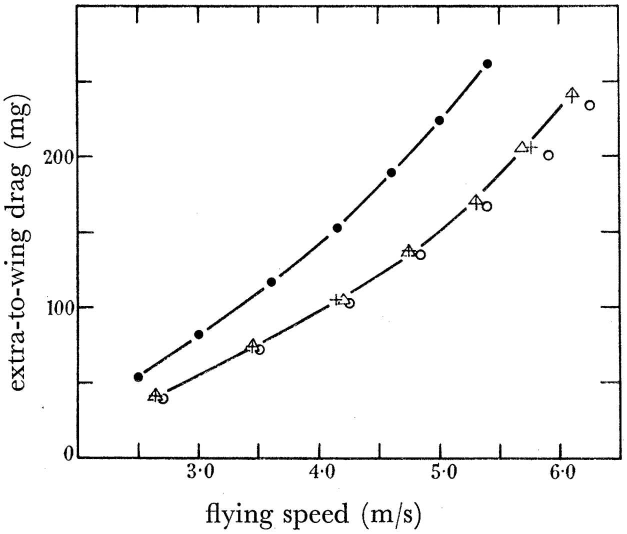

FIGURE II, 7. The extra-to-wing drag of a *Schistocerca gregaria* when $B = 7°$; the legs are arranged in different postures, as explained in the text.

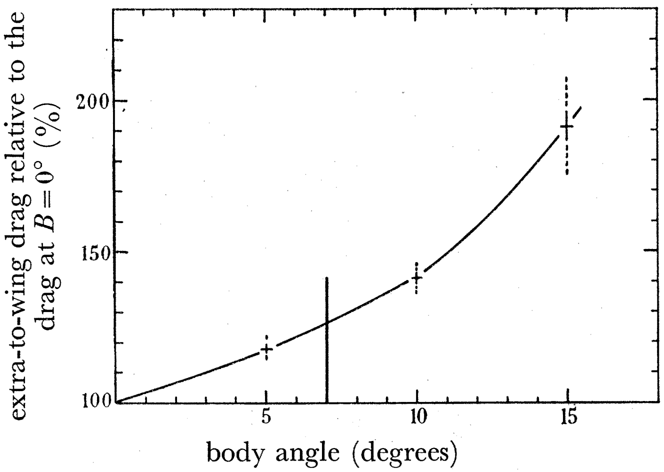

FIGURE II, 8. The extra-to-wing drag as a function of the body angle B. Average angle (7°) indicated by vertical line.

Four animals were arranged in complete flight posture and the body angle was adjusted to 0, 5, 10 and 15°. Figure II, 8 shows the relationship found between B and the extra-to-wing drag, D being calculated as a percentage of its value at $B = 0°$. The data show that D was nearly doubled when B increased from lowest to the highest value seen in flight. When $B = 7°$, D is 25% higher than at zero body angle.

The relationship between the extra-to-wing drag of a *standard Schistocerca* (in mg) and the flying speed (m/s) is plotted in figure II, 9. The flight posture was complete; the heavy line is the average of the four thin curves which were calculated from experiments with small and large locusts. The deviations from the average curve were 7, 11, 11 and 13 % respectively. The values of D in table II, 2 are taken from the average curve.

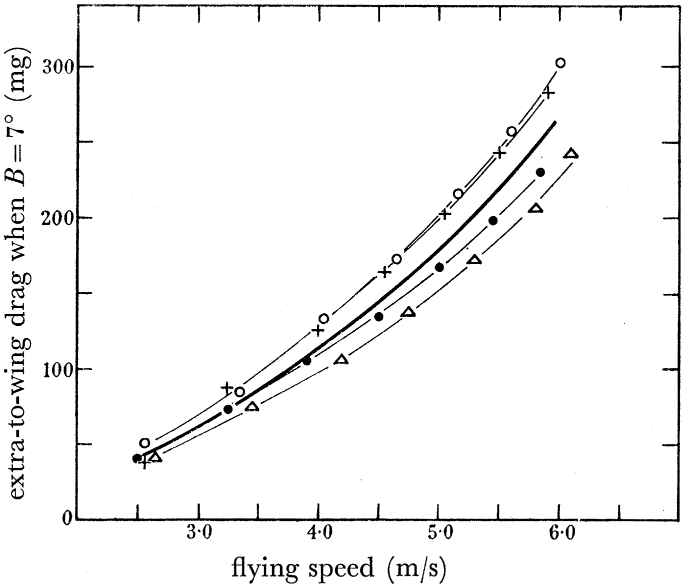

FIGURE II, 9. Extra-to-wing drag of two small and two large desert locusts when recalculated to a *standard Schistocerca* (thin lines) compared with the average curve (heavy line). The extra drag due to the suction cup was less than the accuracy of measurement.

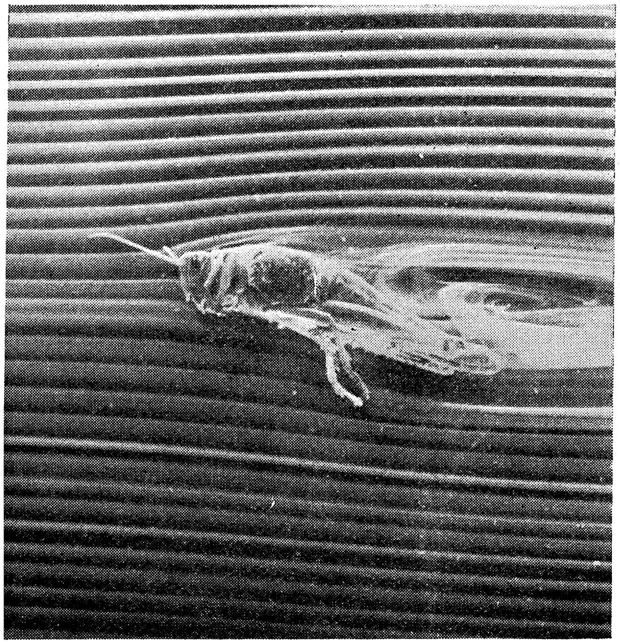

FIGURE II, 10. Photograph from a wind tunnel with body and legs of a *Schistocerca gregaria* arranged in complete flight posture (apart from the middle legs which ought to be stretched more backwards). The flow is indicated by two-dimensional smoke patterns; in the undisturbed stream they run parallel and horizontal. The streaming behind the thorax is always turbulent when $B > -10°$; in this photo $B = 14°$.

The width and height of the pterothorax are both about 1 cm and D was near to the drag of a flat, square plate of 1 cm^2 which is placed perpendicular to the stream (0·128 g/mm H_2O of dynamic pressure). In none of the curves, however, was the drag exactly proportional to the second power of the speed. At 2·5 m/s it is 0·102 g/mm, at 4·0 m/s it has increased to 0·114 g/mm, and at 5·5 m/s to 0·116 g/mm. At these speeds Reynolds's number ($Re = ul/\nu$, u = velocity, l = length, ν = kinematic viscosity) is small and ranges from 1800 to 3900; it is possible that the above deviations are related to this fact. Experiments in a wind tunnel with smoke patterns proved that the flow is highly turbulent behind and above a locust body at *all* positive body angles. This is illustrated in figure II, 10, where $B = 14°$. The body is therefore far from being streamlined.

Thrust and lift

The thrust T of a *standard Schistocerca* flying at $B = 7°$ is given in the right column of table II, 2; the estimates are based upon figure II, 9. While the lift increased about two times, the corresponding thrust only increased 1·6 times. From these data alone it might be suggested that, with greater accuracy of measurement, lift and thrust will turn out to be proportional, as they would be if the resultant force had a constant, forward inclination β to the vertical and only changed its magnitude. But the lack of proportionality is only one of several indications of a more complicated relationship. At 100 % of relative lift and $B = 7°$, a *standard Schistocerca* lifts 1980 mg and has a horizontal thrust of only 122 mg. This means that $\tan\beta = 122/1980$ and $\beta = 3·5°$. When B is decreased to 0°, the lift remains the same while the speed (see p. 474) and thrust (now 134 mg) increase so that the new β becomes 3·9°. Similarly, when $B = 15°$, $\tan\beta = 70/1980$ and $\beta = 2·0°$. These figures show partly how small the thrust is compared with the lift and partly that the inclination of the resultant force changes by only 2° when the body angle is altered by 15^0. The system can *not* be treated simply as an actuator disk which is inclined more or less to the horizontal.

Drag and power

The power expended against the extra-to-wing drag was calculated as Dv (D = drag, v = speed) by combining figure II, 9 with the lift-speed relationship. The result is seen in figure II, 6*a*, expressed in kcal expended per kg of locust per hour. At the average body angle it ranged from 0·7 to 1·5 kcal $\mathrm{kg}^{-1}\,\mathrm{h}^{-1}$, according to the produced lift. In the flight balance the resistance of the suspension can increase the expense by maximally 0·5 kcal $\mathrm{kg}^{-1}\,\mathrm{h}^{-1}$, and in free flight the tibiae can add a similar amount. In any case, the aerodynamic power used to overcome the extra-to-wing drag is small compared with the metabolic rate of the flying desert locust (70 to 80 kcal $\mathrm{kg}^{-1}\,\mathrm{h}^{-1}$; cf. Weis-Fogh 1952) and is about one-fifth or less of the aerodynamic work of the wings (parts III and IX). Little energy can therefore be saved by improving the shape of the body. In absolute units, on the other hand, Dv is considerable and requires an oxygen uptake at least four times as large as that of resting man, calculated per unit weight.

The small correlation between lift and speed when $v \geqslant 3·5$ m/s and the fact that the maximum power expended against drag is 2 kcal $\mathrm{kg}^{-1}\,\mathrm{h}^{-1}$ (maximum continuous metabolic rate is 140 kcal $kg^{-1}\ h^{-1}$), both tend to make the slight uncertainty concerning the free flying speed of little importance for studies on the energetics. These conclusions are in sharp contrast to those of Hocking (1953) who based the power account mainly on *Dv*.

(*e*) *Stroke angles* (table II, 3)

The stroke angles ϕ and the middle positions of the wings $\gamma'_{\text{av.}}$ are seen in table II, 3. In both pairs of wings the mean stroke angles were independent of the lift and varied so little that they can be considered as constant during continuous flight under standard conditions. The average of the mean is seen below the columns:

$$\phi_1 = 67{\cdot}3 \pm 0{\cdot}7^\circ,$$

$$\phi_2 = 109{\cdot}5 \pm 0{\cdot}7^\circ.$$

In the single experiments the movements of the forewings varied more than those of the hindwings. This is shown by the larger standard deviations in the second column compared with the fourth, and indicates that the forewings are concerned with the regulation of the flight. Also, the stroke angles ϕ_2 seldom differed on the two sides, but they often did so in the forewings, especially when flying took place in white light. These regulatory movements were small in subdued red light, and since the average values were constant they could only affect the energy output to a minor degree.

Table II, 3. Stroke angle ϕ and middle position $\gamma'_{\text{av.}}$ of wings in relation to lift

Same experiments as in table II, 2

	forewings				hindwings			
	stroke angle, ϕ_1 (degrees)		middle position, $\gamma'_{\text{av.1}}$ (degrees)		stroke angle, ϕ_2 (degrees)		middle position, $\gamma'_{\text{av.2}}$ (degrees)	
relative lift (%) lift group	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
65, 70	70 ± 3	11	83 ± 1	3	109 ± 2	10	86 ± 1	4
75, 80	69 ± 3	12	87 ± 2	7	107 ± 1	7	86 ± 1	4
85, 90	68 ± 3	13	91 ± 2	7	108 ± 2	8	89 ± 2	6
95, 100	68 ± 3	12	90 ± 2	9	109 ± 2	7	88 ± 1	3
105, 110	68 ± 2	8	91 ± 2	7	111 ± 1	6	90 ± 1	3
115, 120	67 ± 2	8	95 ± 2	6	112 ± 2	6	89 ± 1	4
125, 130	64 ± 3	11	93 ± 2	7	108 ± 2	6	88 ± 1	5
135, 140	65 ± 3	10	94 ± 2	7	112 ± 2	6	89 ± 1	3
	67·3 ± 0·7				109·5 ± 0·7		88·0 ± 0·5	
	s.d. = 2·0				s.d. = 1·9		s.d. = 1·5	

The middle position of the hindwings was constant and nearly horizontal (88·0 ± 0·5°). In the forewing $\gamma'_{\text{av.}}$ increased somewhat with increasing lift and was 90° at 100 % of lift. A similar increase of the middle position was observed in both pairs of wings when the illumination or the level of noise was *suddenly* changed. In the slow-motion films, for example, $\gamma'_{\text{av.1}} = 97 \pm 2^\circ$ and $\gamma'_{\text{av.2}} = 98 \pm 1^\circ$ at about 90 % of lift. This increase in $\gamma'_{\text{av.}}$ was accompanied by an increased wing-stroke frequency and supports the hypothesis that the elastic deformations of the pterothorax during flight assist in determining the frequency; the average forces increase when $\gamma'_{\text{av.}}$ increases as will be shown in part VI.

(*f*) *Stroke-plane angles*

When the body angle was varied the stroke-plane angles b_1 and b_2 referred to the fixed co-ordinate system, also varied in the same direction but to a somewhat lesser degree. This feature is described in part IV as part of the compensatory mechanism which keeps the lift constant. The angles b_1 and b_2 did not vary directly with lift or speed, however. In thirty experiments with sixteen individuals flying steadily 45 min or longer after the start they averaged

$$b_1 = 33 \pm 1^\circ, \quad \text{s.d.} = 4^\circ;$$

$$b_2 = 29 \pm 1^\circ, \quad \text{s.d.} = 3^\circ.$$

(*g*) *Wing-stroke frequency* (figure II, 11; tables II, 4 and II, 5)

The stroke frequency N was always found to be identical in forewings and hindwings. In part VI it will be shown that the mesonotum and the metanotum are firmly attached to each other, so that a difference in frequency of the two pairs of wings is prevented by the mechanical design of the pterothorax.

In the same individual N increased when L_r increased. In different individuals which produced the same relative lift, N was lowest in the largest locusts and highest in the smallest. N therefore depends both on lift and on size. It is convenient first to analyze the size dependence.

Frequency and size

The data obtained from each lift group were inserted into a theoretically derived *interpolation formula* relating N with l, i.e. with the length index (see p. 462). Within a lift group the aerodynamic forces are of the same relative magnitude in all individuals, so that the relationship between frequency and size must be due to other factors. Sotavalta (1952) has shown that in many insects the power P_i necessary for accelerating the oscillating wing mass in an undamped, non-elastic system is large compared with the metabolic rate. In the following papers it will be shown that the construction and function of the pterothorax of locusts are such that the actual expense due to the accelerations is much reduced and only amounts to one-third of the total mechanical power. However, the accelerations of the wing mass give rise to torques about the fulcrum which are two or three times larger than those due to aerodynamic and elastic forces and must strongly influence the dimensions of skeleton and muscles. Since the locusts are similarly shaped with respect to skeleton (e.g. wing mass) and flight muscles (Weis-Fogh 1952), it is therefore reasonable to assume that P_i calculated per unit basic weight is the same in individuals of different sizes when they produce the same relative lift.

In a sinusoidal oscillation we have (cf. part I, equation (I, 9))

$$P_i \propto I N^3 \phi^2. \qquad \text{(II, 1)}$$

According to part VI, the moment of inertia of the wing mass is

$$I = \tfrac{1}{6} M l_w^2 \sin^2 \delta. \qquad \text{(II, 2)}$$

M is the wing mass and is proportional to the basic weight; l_w is the wing length and is proportional to l; and δ is the angle of plication which does not vary with size and therefore could be considered as a constant. Since the stroke angles ϕ were also constant, the power P_i per unit basic weight becomes

$$P_i \propto l^2 N^3. \qquad \text{(II, 3)}$$

The assumption that P_i is constant and independent of size at a given relative lift implies that

$$N = C\, l^{-\frac{2}{3}}. \qquad \text{(II, 4)}$$

C is called the *frequency constant* and has the dimension cm$^{\frac{2}{3}}$ min^{-1}.

The frequency constant was calculated for each individual in each of the eight lift groups. Since N increased a little during the exposure of the slow-motion films (p. 488), this part of the material has been excluded. The result is seen in table II, 4. The standard deviation of the mean frequency constant varied from 3·5 to 5·8 % and averaged 4·3 %. If we assume that equation (II, 4) expresses the exact relationship between l and N at a given relative lift, the standard deviation of C would be determined only by the following deviations: s.d. of $l^{-\frac{2}{3}}$ (=1·6 %); s.d. of the relation between C and L_r (=0·8 %); the accuracy of measuring N (=0·5 %); and, finally, the probable deviation resulting from the grouping into lift groups (=3 %). This determines C with a theoretical s.d. of 3·5 %.

Table II, 4. The frequency constant C in the different lift groups

relative lift (%) lift group	no. of individuals (females in brackets)	C, frequency constant (cm$^{\frac{2}{3}}$ min^{-1})			
		$C\pm$s.e.	;	s.d.	
				(numerical)	(%)
65, 70	14 (8)	2440 ± 40	;	140	5·7
75, 80	20 (11)	2410 ± 30	;	140	5·8
85, 90	22 (13)	2480 ± 20	;	100	4·0
95, 100	21 (10)	2560 ± 20	;	90	3·5
105, 110	21 (8)	2540 ± 20	;	110	4·3
115, 120	13 (3)	2580 ± 20	;	90	3·5
125, 130	11 (2)	2620 ± 30	;	100	3·8
135, 140	10 (1)	2610 ± 30	;	110	4·2
				mean	4·3

The additional scatter caused by deviations from the proposed formula therefore averaged about 2·5 % but ranged from zero at medium lifts to 4·6 % at the lowest lifts. Within this relatively small scatter the dependence of the frequency upon the size of the locust is faithfully described by (II, 4).

Frequency and lift

The frequency constant has been plotted against the relative lift L_r in figure II, 11, the *standard errors* being indicated by vertical bars. Within the range of lifts encountered a fairly good rectilinear relationship between the mean value of C and L_r could be expressed as

$$C = 3{\cdot}30 \times L_r + 2190, \quad \text{s.d.} = 1{\cdot}2\,\%.$$

When the accuracy of the estimate of C in table II, 4 was taken into account, equation (II, 4) could then be written

$$N = l^{-\frac{2}{3}}(3{\cdot}30 L_r + 2190)\ \text{c/min}, \quad \text{s.d.} = 4{\cdot}5\,\%. \qquad \text{(II, 5)}$$

Equation (II, 5) permits the frequency of any individual, whose lift is known, to be compared with the frequency it would probably adopt when flying steadily under standard conditions at the same relative lift. This was a great help in selecting typical slow-motion films for detailed analyses of the flight.

Some calculated extreme values of N are shown in table II, 5. Since P_i is proportional to N^3, the latter quantity is also given. When the lift increased 2·3 times, N^3 only increases by 37 %; the corresponding alteration of P_i cannot explain the change in metabolic rate with increasing lift, as will be demonstrated in another paper (part VIII).

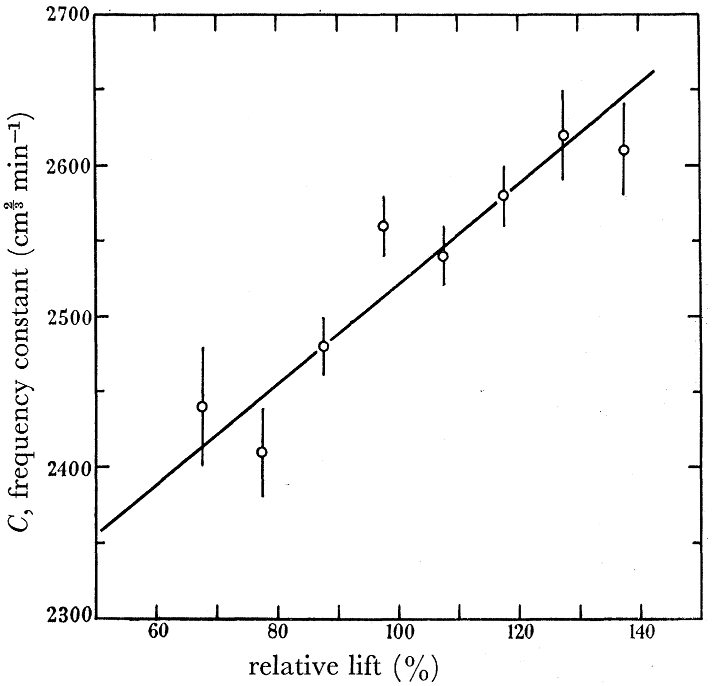

FIGURE II, 11. The relationship between the relative lift and the frequency constant C.

TABLE II, 5. WING-STROKE FREQUENCY N IN RELATION TO SIZE AND LIFT OF AVERAGE INDIVIDUALS

N is calculated from equation (II, 5); l is the length index. N^3 is proportional to P_i and is increased by 37 % when the lift increases from 60 to 140 % of the basic weight.

relative lift (%)	average male, $l=3{\cdot}59$		average female, $l=3{\cdot}97$		*standard Schistocerca*, $l=3{\cdot}78$	
	N (min^{-1})	$N^3\times 10^{-9}$ (min^{-3})	N (min^{-1})	$N^3\times 10^{-9}$ (min^{-3})	N (min^{-1})	$N^3\times 10^{-9}$ (min^{-3})
60	1020	1·06	955	0·86	985	0·95
100	1075	1·24	1005	1·02	1040	1·12
140	1130	1·44	1060	1·18	1090	1·30

(*h*) *Control* (figures II, 12 to II, 14)

The conclusions in the preceding sections were based upon group treatment of data obtained from forty-seven different individuals which flew more or less intensely. Only in some of them could observations be made at many different lifts and speeds. It might therefore be the case that the results reflect the variation as between bad and excellent flyers and do not show the true relationship between the flight performance (lift and speed) and the stroke parameters. This could be tested by using the *same individuals* over the entire range of relative lifts.

Figure II, 12 shows the relationship between lift, speed, frequency and stroke angles in the same eight locusts (all males). The circles indicate the means of the measured quantities. The triangles are the means found in all forty-seven individuals used; since the frequency depends on the size, N was estimated from equation (II, 5) by using the average index of the eight males instead of that of the entire material. The vertical lines are the standard errors, estimated from the standard deviations and the number of individuals in a lift group (given below the speed curve). None of the four curves deviate from what would be expected from the previous sections.

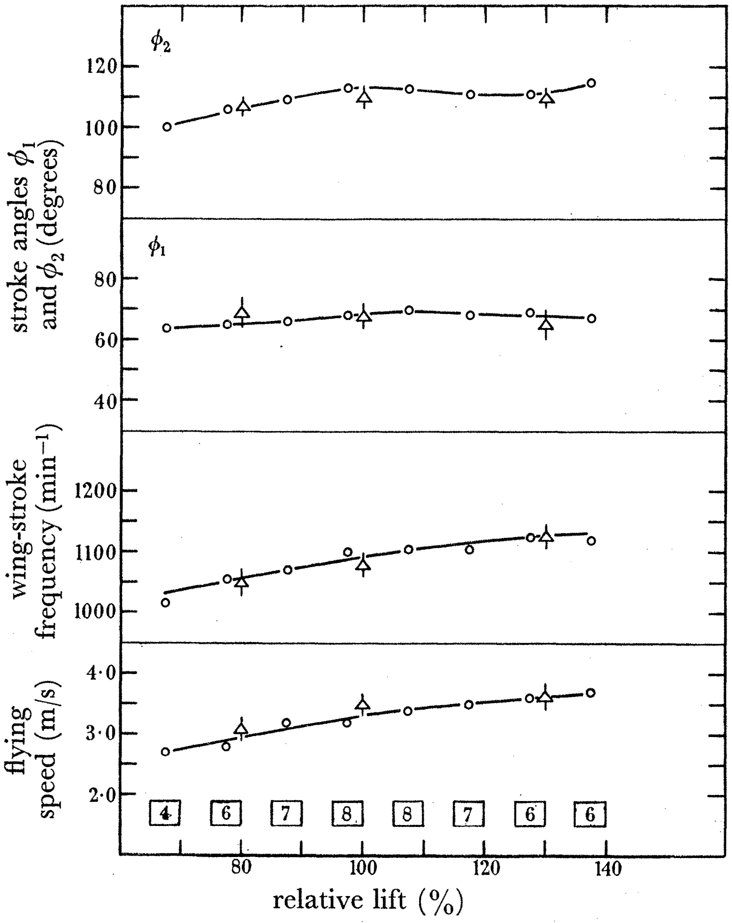

FIGURE II, 12. Relationships between flying speed, wing-stroke frequency, stroke angles and relative lift in the *same eight* individuals flown at different days. The number of individuals in each lift group is given below the speed curve. The triangles are the means from the entire body of data derived from forty-seven individuals; the vertical bars indicate the standard errors estimated according to the number of insects in each lift group.

A *single* male *Schistocerca* was flown four times in the course of 3 weeks. The results of seventy-seven sets of observations are seen in figure II, 13. The standard deviation from the mean result is shown by the height of the columns. Where less than seven sets were available it was estimated from the maximum deviation and indicated by the broken lines. The triangles show the mean from the total material (N was again calculated according to equation (II, 5)), and the corresponding standard deviations are given as vertical lines. The flying speed and the stroke angles of the forewings of this specimen were subnormal at the low lift groups. But the same general features of regularity and constancy and the same type of variation were found in the single specimen as in the mean material from many individuals. In this animal, the standard deviations were as big as the standard deviation of the means in the entire material. As regards ϕ_1, it was even larger in some lift groups. There might therefore be a correlation between a high-stroke frequency and a low value of ϕ_1, but figure II, 14 shows no such correlation in those lift groups which gave the largest scatter. This means that, at a given lift, the parameters vary at random.

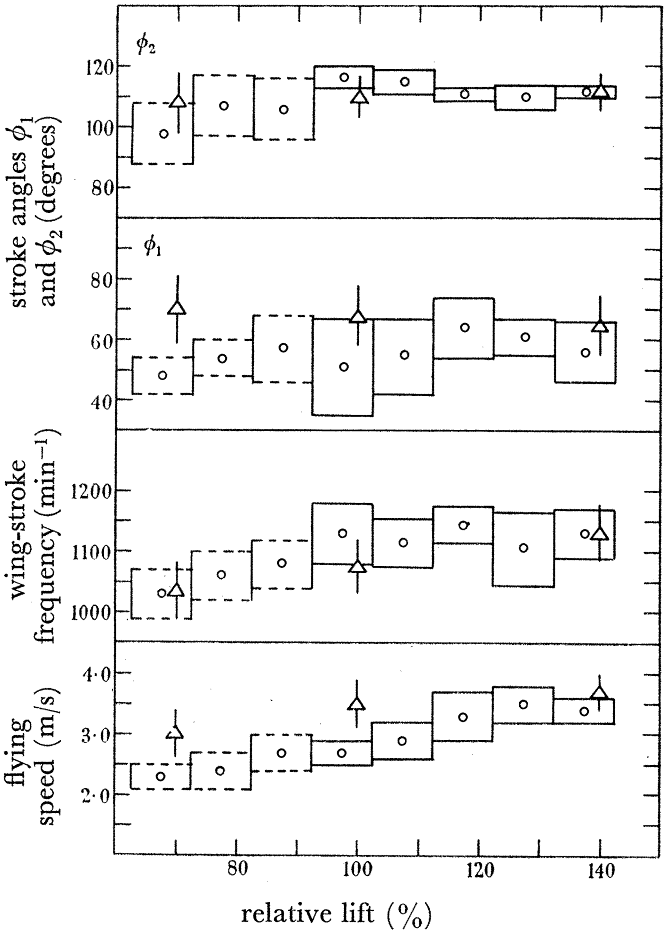

Figure II, 13. Flying speed, wing-stroke frequency and stroke angles against relative lift in a single male *Schistocerca gregaria* which was flown four times in the course of three weeks. The height of the rectangles and the length of the vertical bars indicate the standard deviations of the readings from this individual and from the total material respectively. Seventy-seven sets of observations.

We may then conclude that the results seen in the tables and figures also hold for small groups and even for single individuals; they show the normal correlation between the flight performance and the stroke parameters in the desert locust.

(*i*) *Conclusions*

At 30° C, the lift of locusts flying in the compound balance on average equalled the body weight but varied considerably from individual to individual. These facts made it possible to analyze how a number of parameters are normally correlated with the resultant aerodynamic force. The vertical component of this force (= the lift) is about twenty times larger than its horizontal component (= the thrust).

The lift is independent of the body angle provided the latter does not go beyond 0 and 20°. In the laboratory the average speed was 3·5 m/s at 100 % of relative lift and may be 3·5 to 4·2 m/s in free flight. The thrust is positively correlated with the lift, but the relationship is neither very pronounced nor simple. Although the stroke-plane angles are nearly fixed relative to the body, the flight system cannot, even as a first approximation, be compared with an actuator disk whose plane is fixed in the animal.

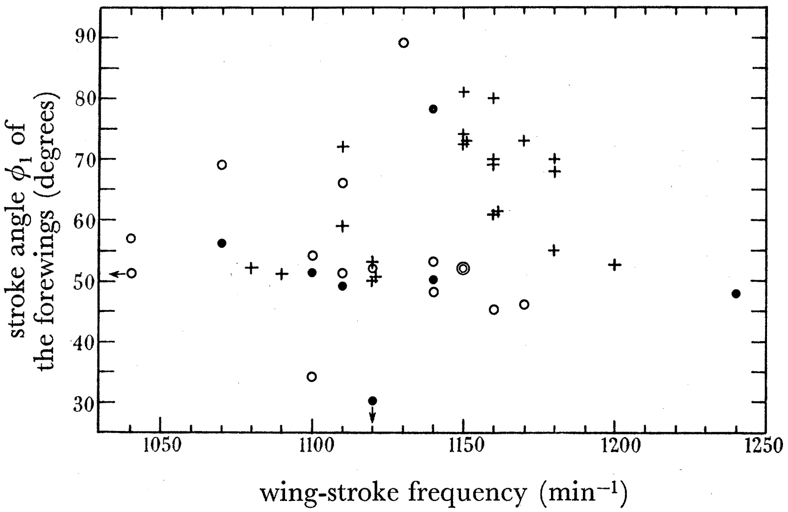

FIGURE II, 14. No correlation was observed between the wing-beat frequency and the stroke angle of the forewings.

	s.d. in degrees	
	ϕ_1	ϕ_2
● at 95 and 100% lift	12	4
○ at 105 and 110% lift	10	2
+ at 115 and 120% lift	16	3

The power necessary to overcome the extra-to-wing drag is small (about 2 %) compared with the metabolic rate and little energy can be saved by improving the shape of the body. In fact, the body is far from being streamlined.

The wing-stroke frequency varied both with the size of the individuals (maximally 15 %) and with the lift produced (maximally 8 %). It could be described by a simple formula. Otherwise, its constancy is more striking than its variations. Since the stroke angles were even more constant and practically independent of the lift, the general picture of the most conspicuous wing movements is that of little alteration and considerable independence of the aerodynamic forces produced.

5. ANGULAR MOVEMENTS OF ENTIRE WINGS

The velocity of a wing element through the air is the sum of the velocity of the body of the locust and of the velocity of the element relative to the body. In locusts the two vectors are of the same order of magnitude. The latter term is proportional to the angular velocity of the wing, $\omega = \mathrm{d}\gamma'/\mathrm{d}t$. The wind forces acting on the element are approximately proportional to the square of the resultant velocity, and the power for driving it through the air is proportional to this velocity to the third power. The inertial torque Q_i about the fulcrum (part I) due to the mass of the wing is proportional to the angular acceleration $\mathrm{d}^2\gamma'/\mathrm{d}t^2 = \mathrm{d}\omega/\mathrm{d}t$, and these moments can be two or three times as big as the aerodynamic torques. These facts show how important it is to get an accurate estimate of the variation of γ' with time.

(*a*) *Data* (table II, 6)

Twenty-one stroboscopic slow-motion films taken from behind (along the x-axis) were analyzed. The locusts flew under standard conditions apart from the white flashes and the noise from the flash lamps. Each film comprised four or five apparent wing strokes derived from about 80 or 90 single beats (see p. 468 and appendix D). γ was measured and recalculated to γ' so that the positional angle (ordinate) could be plotted against time (abscissa) on graph paper. The average values from the right and left wings were used. The two sides seldom differed significantly in the hindwings, but the values from the forewings were discarded in four films on account of asymmetry. In order to analyze the graphs nine parallel rulers were arranged at fixed relative distances and laid parallel to the time axis, the distance between the two flanking rulers corresponding to the stroke angle (= double amplitude). In a complete wing stroke the rulers would intersect each curve at seventeen points whose relative amplitudes were known. The abscissa of each point was estimated as a percentage of the duration of a complete cycle. Since the hindwings moved in the most regular manner, the starting point was chosen as the middle position during their upstroke. For each film the results are given as the average of three to five apparent strokes.

TABLE II, 6. MATERIAL AND FLIGHT DATA IN TWENTY-ONE SLOW-MOTION FILMS COMPARED WITH NORMAL FLIGHT

The right-hand column gives the mean values (92 % of lift) found in all experiments performed under standard conditions, i.e. the *normal* values. The asterisk indicates that the figure deviates significantly from the normal.

8 female + 9 male *Schistocerca*	size (cm³)	standard $v = 54{\cdot}1$ cm³
volume index, av.	56·7	
volume index, min.	32·8	
volume index, max.	86·2	

average in films	found in films (%)	normal values
relative lift, av.	92	—
relative lift, min.	65	—
relative lift, max.	150	—

	mean	s.d.	mean	s.d.
flying speed (m/s)	3·4 ± 0·1	0·5	3·4 ± 0·1	0·5
body angle, B (degrees)	7·2 ± 0·6	3	7·1	3 to 4
*stroke angle, ϕ_1 (degrees)	85 ± 2	9	68 ± 3	12
stroke angle, ϕ_2 (degrees)	109 ± 1	6	109 ± 2	8
middle position, $\gamma'_{\mathrm{av.1}}$ (degrees)	97 ± 2	8	91 ± 2	9
*middle position, $\gamma'_{\mathrm{av.2}}$ (degrees)	98 ± 1	5	89 ± 2	5

* Wing-beat frequency N is increased by 6 % ± 1·4 % (s.d. = 6 %) compared with the normal.

Table II, 6 shows the means of the other flight parameters in the twenty-one films. The locusts varied in size from very small males ($v = 32{\cdot}8\ \text{cm}^3$) to the largest females ($v = 86{\cdot}2\ \text{cm}^3$), but their mean volume index was near to the standard index. The relative lift varied from 65 to 150 %, i.e. 2·3 times, with an average value of 92 %. The mean values of only three flight parameters (marked with an asterisk) differed significantly from those found under standard conditions. The stroke angle ϕ_1 and the middle position $\gamma'_{\text{av.}2}$ hardly affect the flight significantly, because the forewings only deliver one-third of the aerodynamic work and because the hindwings retained a normal stroke angle in spite of the increase in middle position. But the wing-beat frequency might be a factor of importance. The normal frequency for each individual at the given lift was calculated from equation (II, 5) on p. 482. The mean percentage increase was 6 % above the normal, but since the scattering was large (s.d. = 6 %) and since the data include values from 903 (8 % below the normal) to 1210 (13 % above the normal) strokes per minute, the mean relation between amplitude and time was likely to show an increased scatter rather than a systematically altered shape.

(*b*) *Positional angle and time* (figure II, 15)

In figure II, 15 the found mean values of γ' in films have been plotted against the time given as a percentage of the duration of a complete wing stroke. The curve starts when the hindwings are in the mean position on the upstroke. The standard deviations of the mean time readings are given as horizontal lines, and the distances enclosed by the arrow-heads indicate the standard errors of the mean.

The regularity of the wing stroke is surprising. In spite of great variations in animal size and in flight performance the standard deviation did not exceed 4·4 % in the hind-

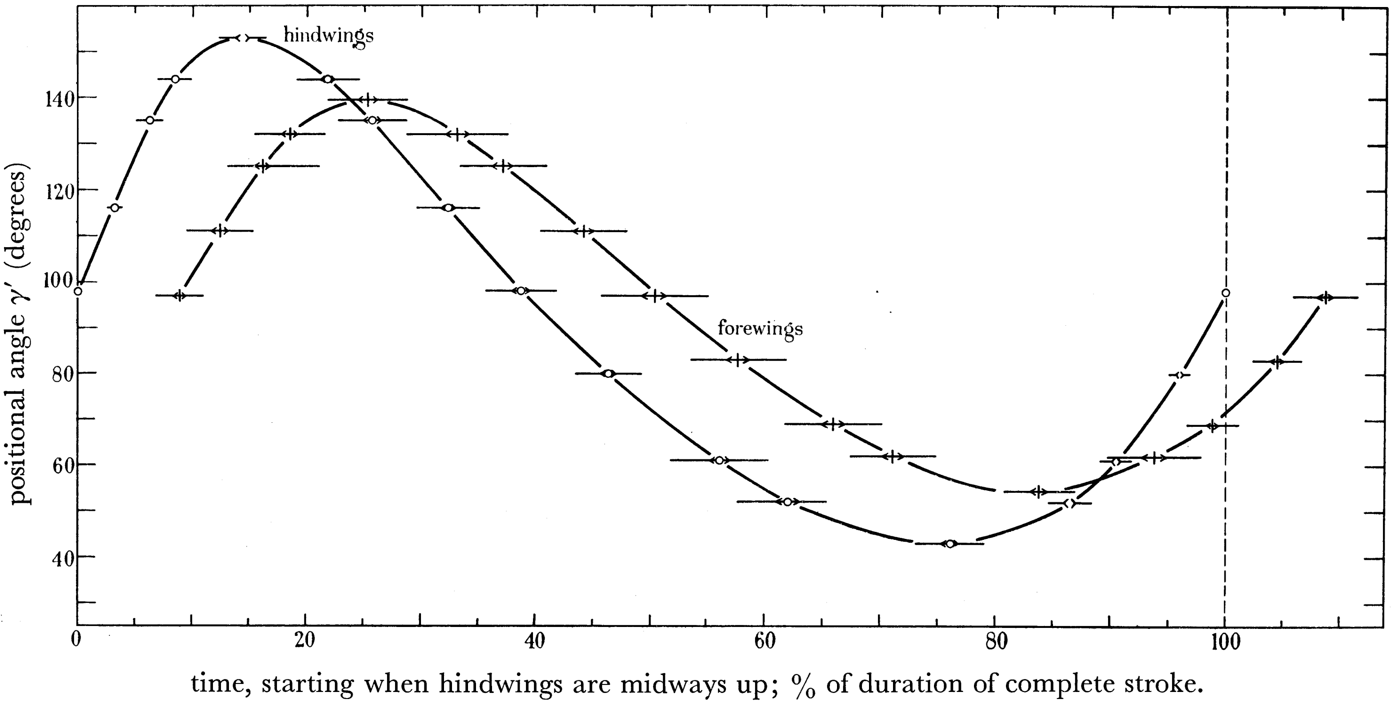

FIGURE II, 15. The variation with time of the positional angles. Average of twenty-one films from seventeen individuals; the standard deviations (bars) and the standard errors (arrow-heads) are indicated. ○, hindwings, γ'_2; +, forewings, γ'_1.

wings and 4·6 % in the forewings. The average mean curve could be drawn through points the standard error of which was 1 % or less. The results therefore made possible a detailed analysis of the time parameters of the wing beat.

(*c*) *Conclusions*

Some fundamental general conclusions are obvious from figure II, 15. (1) The variation of γ' with time is not a simple sinusoidal function. The upstroke of the hindwings lasted 38 % of the total period, that of the forewings 42 %. A detailed analysis is given on p. 495. (2) On an average the forewings were 9 % out of phase (behind) the hindwings, but the time functions of the wings differed somewhat. (3) The relative position of the two curves was as regular as was the shape of the single curves. The coupling between the wings must therefore be very strong whether it be of mechanical, neurological or of combined origin. Some features of the mechanical coupling will be discussed separately (in part VI). (4) As has been demonstrated in dragonflies (Chadwick 1940), the phase difference between the locust wings will reduce the effect of the wake of the forewings on the flow over the hindwings. In locusts the phase difference is smaller than in dragonflies, but the difference in stroke angle compensates for this. In fact, the mutual aerodynamic effect between the locust wings is small, as estimated from the mutual influence upon the circulation Γ about the wings (see part III).

A further discussion of the angular movements is found on p. 493.

6. FLIGHT PERFORMANCE AND TEMPERATURE

In *Drosophila*, Chadwick (1953) showed that there is a distinct correlation between stroke frequency and air temperature. But the flies were tethered and the frequency was the value read 1 or 2 s after the start. The experiments could therefore not be taken as representing natural, continuous flight, and they are not supported by the following observations on flying desert locusts.

The relevant data are derived from observations in the simple pendulum (appendix A), from roundabout experiments (Krogh & Weis-Fogh 1952; Weis-Fogh 1952), and from experiments with the compound flight balance. It must be remembered that the average speed in the wind tunnel was 3·5 m/s against 3·0 m/s in the roundabout, so that the speeds in figures II, 16 to II, 18 should not be directly compared with those observed in the wind tunnel. In all cases the locusts were shielded from radiant heat, so that the results show the relationship between flight and the temperature of the ambient, streaming air. The effect of thermal radiation was studied separately (Weis-Fogh & Muus, unpublished). The humidity was controlled and adjusted so that the difference in water-vapour pressure inside and outside the working locust was approximately the same at all temperatures ($D = 26$ mm Hg, see figure II, 19 and p. 492).

In roundabout experiments with several locusts flying at the same time, the number of animals which did not fly was counted every 5 min and calculated as a percentage of the maximum possible. This is the *degree of truancy* (Krogh & Weis-Fogh 1952).

(*a*) *Lower limit for flight* (figure II, 16)

From 15 to 17° C a suspended *Schistocerca* would start to flap its wings when stimulated to fly. The initial frequency was as low as 600 to 750 strokes per min, but in males it could be increased to 950/min during the first 3 to 5 min on account of the heating up of the thorax. Then the locust would stop. The 'flying' locusts could not lift their own weight.

Prolonged roundabout experiments showed that *Schistocerca* could start at normal flying speed and metabolic rate (Weis-Fogh 1952) when the air temperature was increased to about 22° C. But figure II, 16 shows that the speed, which increased during the first minutes, soon dropped to about 2·3 m/s, where it would remain (experiment I) if the temperature was not increased (experiments II and III). The low percentages of truancy written below the curves show that the decrease was caused by a decreased average performance of the individuals and not because some of them did not continue to fly. At the low temperature, the degree of truancy was normally small. When the roundabout experiments were performed at 25° C the flying speed (3 m/s) and the endurance were normal (Weis-Fogh 1952). It was concluded that the lower temperature limit (air temperature) for flight at average intensities was 22 to 24° C when thermal radiation was of no significance.

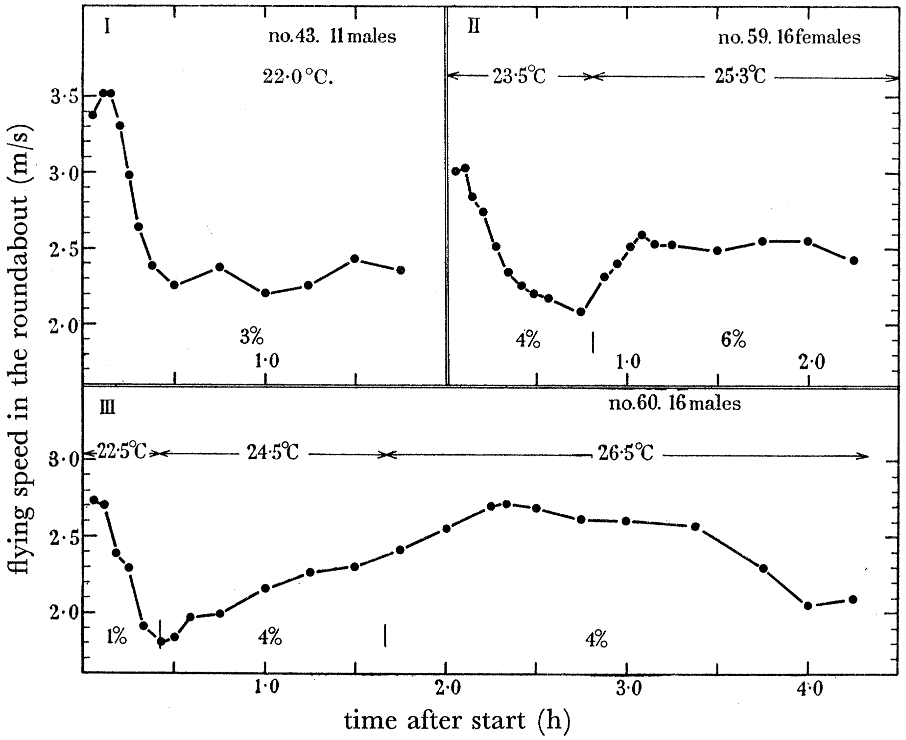

FIGURE II, 16. Roundabout experiments with flocks of *Schistocerca gregaria below* the optimum air temperature, i.e. below 25° C. The speed is an indicator of the power output and averages 3 m/s under optimum conditions (Weis-Fogh 1952). The degree of truancy is shown below the curves (in percentage).

(*b*) *Upper limit for flight* (figures II, 17 and II, 18)

At 40 to 42° C the locusts would start to fly upon stimulation; initial stroke frequencies up to 1500/min (males) have been recorded. But within the first minute both speed and frequency decreased to subnormal values and the insect stopped, invariably 'panting' violently, there being 120 to 150 deep respiratory movements per minute, or about twice the frequency observed *during* normal flight (Weis-Fogh, unpublished). The reaction could be considered as a reaction to overheating, since the increase in pterothoracic temperature often amounted to 5° C in the course of the first minute after the start.

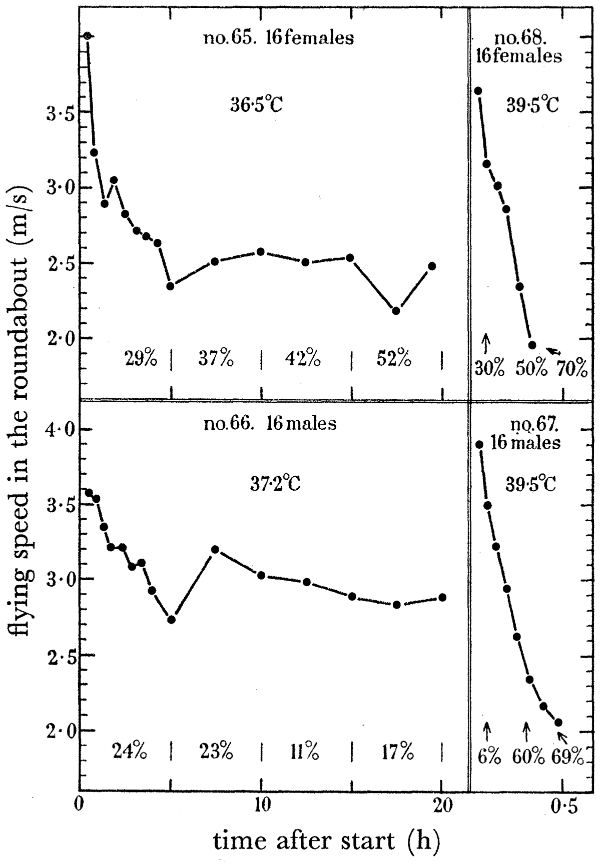

FIGURE II, 17. Roundabout experiments with flocks of *Schistocerca gregaria* at air temperatures *above* the optimum, i.e. above 35° C. See legend to figure II, 16.

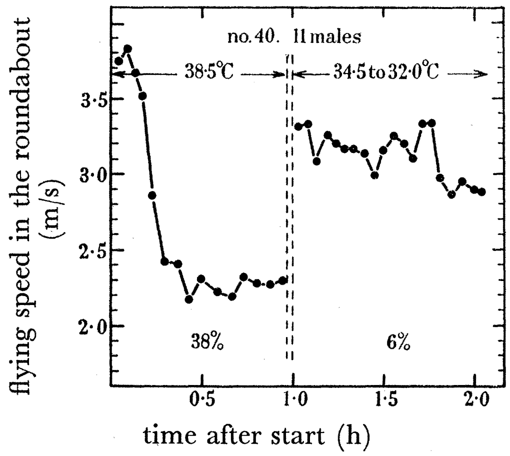

FIGURE II, 18. Roundabout experiments with a flock of male *Schistocerca gregaria* at air temperatures first above and later within the optimum range. See legend to figure II, 16.

A series of experiments with the roundabout showed that the upper limit for sustained flight was about 37 to 38° C. Figure II, 17 demonstrates that neither males nor females could fly continuously at 39·5° C, more and more individuals ceasing to fly. At 37° C the performances were sometimes normal (no. 66), although the percentage of truancy used to be large at temperatures above 35° C (no. 65). The experiment in figure II, 18 was started at 38·5° C, but after 58 min the air temperature was lowered to 34·5° C in 4 min and further down to 32·0° C in the course of the next 20 min. The locusts immediately responded by increasing the flying speed to 3·2 m/s and the truancy became negligible until the roundabout was stopped. In the absence of heating radiation the upper temperature limit for continuous flight was therefore about 37° C. An increased evaporation rate due to dryer air may increase the limit by maximally $1\frac{1}{2}$° C (Weis-Fogh & Muus, unpublished).

(*c*) *Optimum temperature range* (figure II, 19)

It has previously been demonstrated that the flying speed in the roundabout is the same at 25, 30 and 35° C (table 11 in Weis-Fogh 1952), indicating that the metabolic rate is independent of temperature. In order to analyze this result further, eight males and four females from the same batch were selected. Each individual was made to fly for 30 min in the flight balance at three different temperatures, the females on 3 succeeding days and the males in the course of 7 days. The speed, the lift and the stroke frequency were measured at regular intervals, so that three to six sets of readings from each individual were obtained during each of the time intervals 0 to 5, 5 to 10, 10 to 20 and 20 to 30 min after the start. The mean values from the eight males are seen in figure II, 19 as white circles connected by curves and with the standard error indicated as vertical bars. The means from the four females are indicated by ♀. The mean temperatures (26·2, 30·7, 35·5° C) are given above the curves together with the relative humidity. During normal flight at 30° C and 65 % r.h. the increase in pterothoracic temperature at 100 % of lift was 6·8° C (Weis-Fogh & Muus, unpublished). This figure should be added to the air temperature to give the temperature of the flight muscles. At 35·5° C air temperature it thus amounted to about 42° C, the air in the tracheoles being supposed to be saturated with water vapour at this temperature. The maximum differences D between the vapour pressures inside and outside the locust varied only from 26 to 28 mm Hg at the used combinations of temperature and humidity, so that differences in evaporation rate could not have influenced the results. A discussion on the relationship between evaporation and ventilation will appear elsewhere.

From figure II, 19 it is seen that neither the flight performance expressed as lift and speed nor the stroke frequency varied significantly, even during the first 5 min of heating up the thorax. There is an indication of a relatively decreased performance at the high temperature, but the differences are not significant. The decrease in lift and speed during the first half-hour of flight is normal for flight in the laboratory and has been discussed previously (Weis-Fogh 1952). At 26° C the frequency increased during the first 1 or 2 min, whereas this was not the case at 35° C, but the later decrease in both cases cancelled the difference so that the averages were identical.

(*d*) *Conclusions*

From the roundabout experiments and from figure II, 19 it is concluded that flying between 25 and 35° C is independent of temperature as regards metabolic rate, flight performance and the stroke frequency. The latter parameter was chosen because a temperature-dependence should have been easy to detect. The optimum temperature range for flight extends over about 10° C. The temperature-dependent processes must therefore be so regulated or arranged that the net result is a temperature independence.

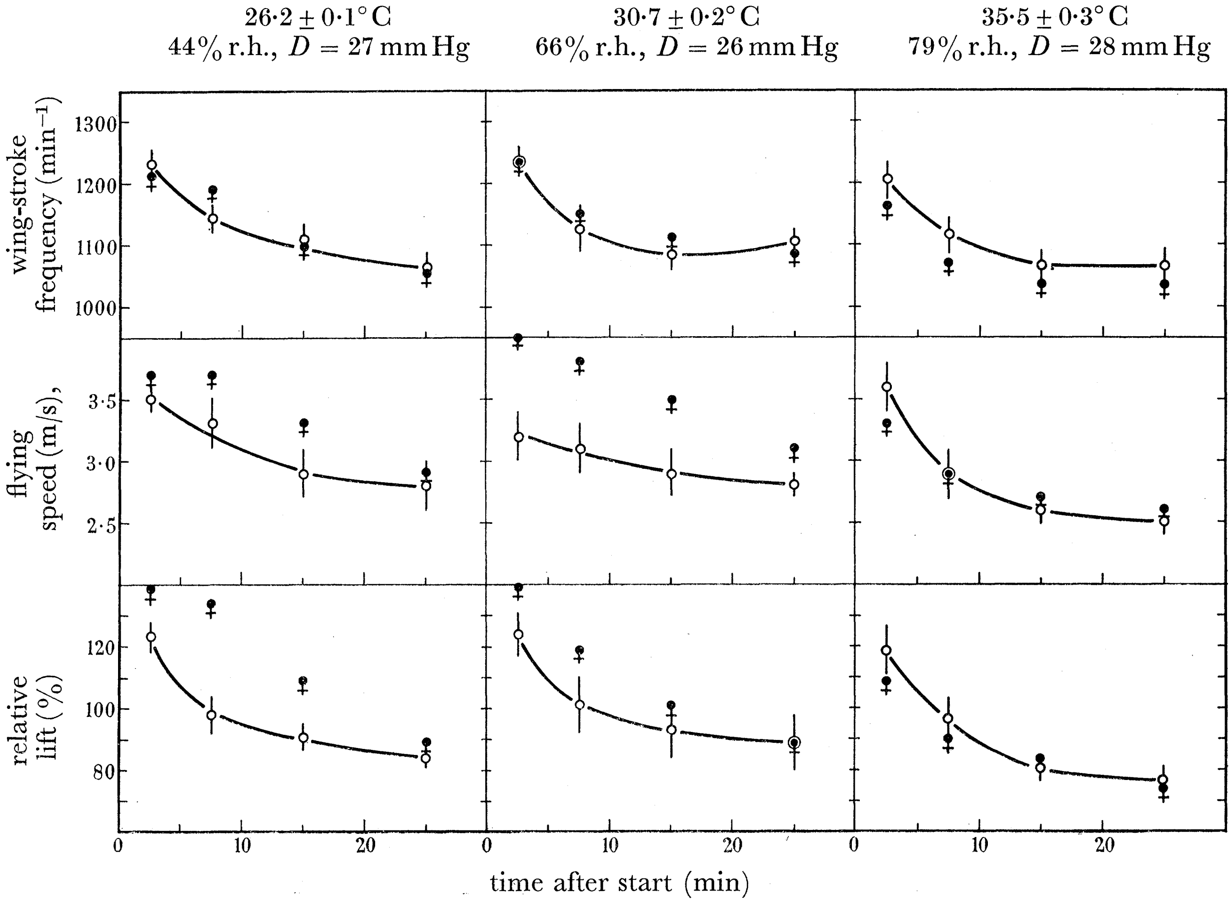

Figure II, 19. Average flight performances in the flight balance of the *same* eight male *Schistocerca gregaria* (open circles) at three different air temperatures (26·2, 30·7 and 35·5° C) under constant conditions for evaporation (*D* varied from 26 to 28 mm Hg). Similar averages for four female individuals are indicated by ♀. The flight was independent of the air temperature within the range *ca.* 25 to 35° C.

7. Standard wing stroke

The three preceding sections show that both pairs of wings move in a very regular manner in space and time and that the flight performance and the frequency are practically unaffected by variations in the air temperature within the range 25 to 35° C. It was therefore reasonable to assume that the other time parameters of the stroke were also indifferent to such changes in temperature. This being the case, investigations on the flight processes could be very much simplified by studying an average wing stroke.

(*a*) *Standard stroke* (figure II, 20)

The standard stroke was defined as the average stroke of a *standard Schistocerca* which lifted its basic weight ±10% and flew with a forward speed $v = 3{\cdot}5 \pm 0{\cdot}1$ m/s at a body angle $B = 7 \pm 1°$. In this case the stroke parameters amounted to:

$$N = 1040 \text{ strokes/min},$$
$$b_1 = 33 \pm 1°,$$
$$b_2 = 29 \pm 1°,$$
$$\phi_1 = 68 \pm 2°,$$
$$\phi_2 = 110 \pm 1°.$$

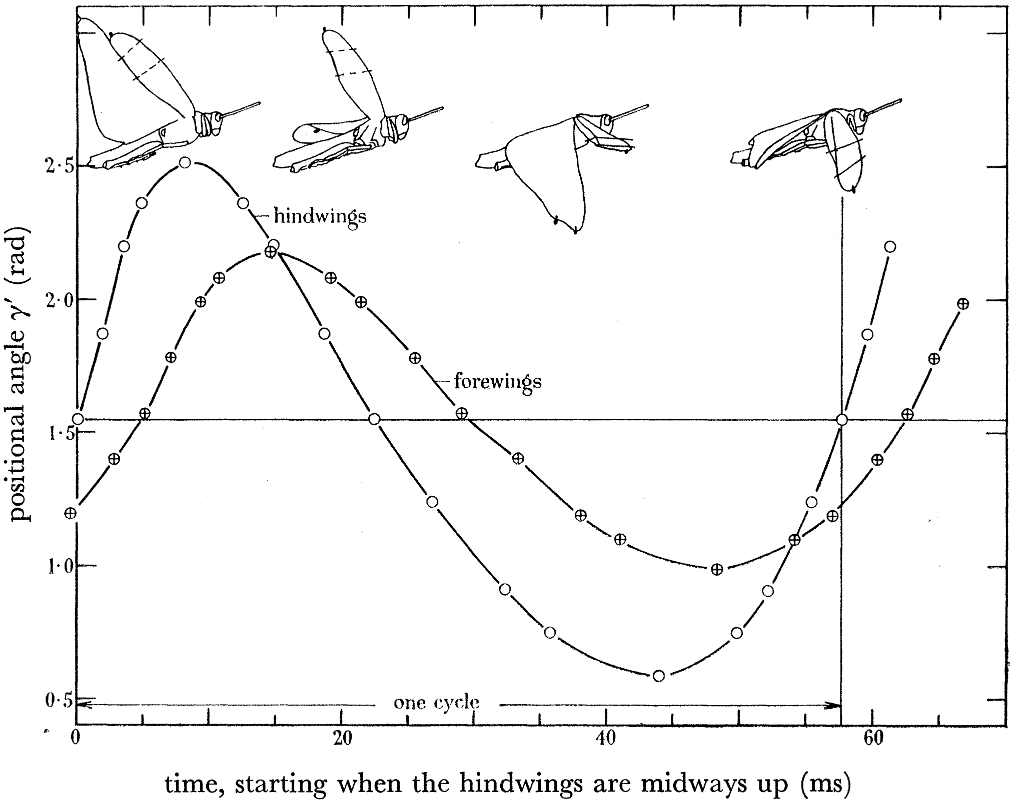

FIGURE II, 20. The standard wing stroke of *Schistocerca gregaria*. The radius of the markings is equal to the standard error of the mean readings along *both* axes. Typical wing positions are shown above the curve and were drawn from slow-motion films, the abscissa referring to a point midways between the two pairs of wings. The cross-lines on the forewings are thin hairs which indicate the twisting of the wing plane; flap of the forewings is seen. The wing tips are marked by black dots. See also figure II, 15. The small degree of scatter is most striking. ○, hindwings, γ_2'; ⊕, forewings, γ_1'.

The angular movements were calculated from N, ϕ and the relative time measurements given in figure II, 15. The resulting standard curve is shown in figure II, 20, which represents an important result of the kinematic analysis. The standard errors along both axes are shown by the radius of the circular markings. The ordinate shows the positional angle γ' in radians and the abscissa the corresponding time in ms, beginning when the hindwings pass the middle position on the upstroke. The forewings are represented by crosses and the hindwings by circles. The sketches visualize four characteristic phases of the stroke, drawn from a slow-motion film. The torsions and other deformations of the wing planes are indicated, as is also the flap at the rear edge of the descending forewings which is discussed in parts III and VII.

The probable deviations from the curves drawn through the points were small enough to allow a detailed analysis of their shape. The results of the variations of $d\gamma'/dt$ and $d^2\gamma'/dt^2$ with time will be given in part VI in connexion with the discussion on the kinetic energy and the inertial torque of the wings.

(*b*) *Comparison with harmonic motion* (figure II, 21)

In the case of a simple harmonic motion

$$\gamma' = \tfrac{1}{2}\phi \sin\frac{2\pi t}{t_0} + \gamma'_{\text{av.}}, \qquad \text{(II, 6)}$$

where t_0 is the duration of the stroke, i.e. $t_0 = 1/n$, where n is the frequency in c/s. However, it is obvious from figure II, 20 that the functions deviate considerably from a sinusoidal oscillation. An approximation to a sinusoidal oscillation could be established by considering the movement of each wing as composed of two simple functions. If the upstroke lasts the fraction a of the total stroke cycle, t_0 becomes

$$\text{for upstroke:} \quad t_0^u = \frac{2a}{n}, \qquad \text{(II, 7)}$$

$$\text{for downstroke:} \quad t_0^d = \frac{2(1-a)}{n}. \qquad \text{(II, 8)}$$

The formulas of approximation then become

$$\text{upstroke:} \quad \gamma' = \left[\tfrac{1}{2}\phi \sin\frac{\pi n t}{a} + \gamma'_{\text{av.}}\right] \text{rad}, \qquad \text{(II, 9)}$$

$$\text{downstroke:} \quad \gamma' = \left[\tfrac{1}{2}\phi \sin\frac{\pi n t}{1-a} + \gamma'_{\text{av.}}\right] \text{rad}, \qquad \text{(II, 10)}$$

where $a_1 = 0{\cdot}416$ and $a_2 = 0{\cdot}378$. If the calculated functions are adjusted to coincide with the found relations at the best defined points of the curves, i.e. when the ascending wings passed the middle position and ω was maximum, the thin curves in figure II, 21 result. If a simple harmonic motion was applied, only the most crude calculations could be performed. Equations (II, 9) and (II, 10) describe the angular movements fairly well and could be used for simple aerodynamic calculations (cf. part IV), but they deviate too much from the true relationship to make possible estimates of the kinetic energy of the wings and of the inertial torques with respect to the fulcrum. For those purposes the experimentally found curve has to be used.

(*c*) *Conclusions*

The fact that the measured stroke parameters did not vary to any extent compared with the very considerable variations in the lift shows that the variable parameter must be something else. The only complex of factors which has not been investigated and which would be able to alter the flight resultants profoundly in spite of constancy of the remaining parameters, is the function between wing torsion and time $\theta = \theta(r, t)$. In other words, the sequence of variation of the angles of attack can, by exclusion of other factors, be regarded as the main parameter determining the aerodynamic result. The aerodynamic machine of locusts can therefore be considered as *analogous* to a variable-pitch propeller.

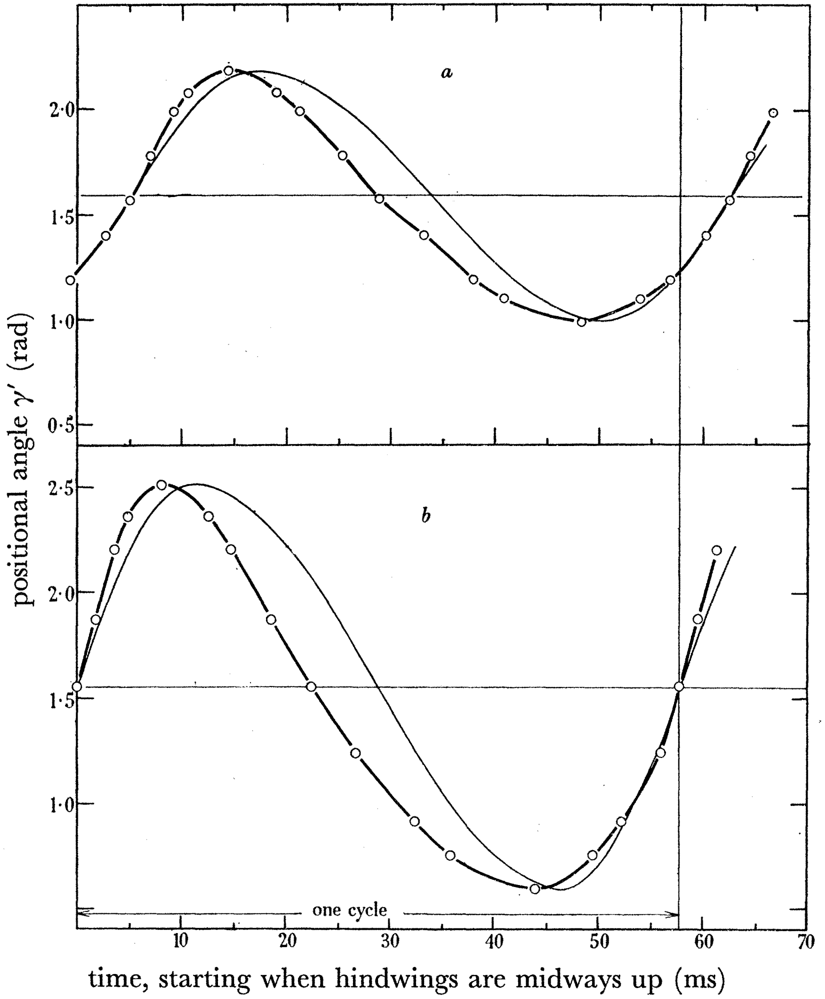

FIGURE II, 21. The observed variation of the positional angle of (*a*) forewings (γ'_1 heavy curve) and of (*b*) hindwings (γ'_2 heavy curve) during a standard stroke as compared with the sinusoidal oscillation (thin curves) mentioned in the text. The horizontal line shows the average positions, $\gamma'_{\text{av.}\,1}$ and $\gamma'_{\text{av.}\,2}$ respectively.

8. DISCUSSION

(*a*) *Natural flight*

In most respects the locusts used have previously been shown to resemble natural migrants (Weis-Fogh 1952). A comparison with observations in nature might indicate to what extent the experimental results can be considered consistent with natural flight.

Lift

During prolonged performances in the wind tunnel, the relative lift ranged from 35 to 175 %. At the start it sometimes exceeded 200 %. The low values may be of biological interest during descents from high altitudes or during periods of vertical atmospheric convection which considerably influence migrations in East Africa (Rainey & Waloff 1951). High lift is of course necessary for pregnant females and during periods of climbing. The result in figure II, 5 indicates that in the laboratory locusts produce lifting forces of the same magnitude and range as one would expect to find in nature.

Speed

In the wind tunnel the lifting force never reached 100 % at speeds below 2·5 m/s, the average speed being 3·5 m/s, s.d. = 0·5 m/s. At 140 % relative lift the average air speed increased only to 3·7 m/s. It was concluded that the average speed during *steady*, *horizontal* flight in nature would probably range between 3·5 and 4·2 m/s (from 7·8 to 9·4 m.p.h.) and would not vary much in full migrants compared with sexually mature locusts. During intensive *continuous* flying the speed sometimes averaged 4·5 m/s (10·1 m.p.h.), while the *initial* speed and lift (possibly attempted climbing) was generally higher and averaged 4·7 m/s (10·5 m.p.h.) and 136 % respectively. The maximum speed observed is 5·5 m/s (12·3 m.p.h.). The average figures are lower than those published from direct measurements in nature, namely, 4·9 m/s or 11 m.p.h. (Waloff & Rainey 1951). In a later paper Rainey (1951) estimated the air speed of migrating individuals to between 7 and 11 m.p.h. According to these authors (1955, personal communication) it is 'unlikely that the individual locusts whose air speed we have estimated in nature had been in continuous flight for more than a few minutes prior to the observation, as all swarms observed exhibited characteristic intermittent flight'. There is therefore hardly any difference between the flying speed in the experiments reported here and the air speed of natural migrants. Wootten & Sawyer (1954) found that the speed of *Schistocerca* flying in a wind tunnel varied between 2·5 and 6·5 m/s with an average of 3·2 m/s. The body angle was not read; it might be larger than 7°, since the suspending hook was situated well in front of the centre of gravity.

Air temperature

In the absence of radiant heat, the thoracic temperature corresponded to the air temperature plus an amount due to the metabolism of the wing muscles; at normal lift and flying speed this increase was 6 to 7° C. Under the present experimental conditions evaporation remained nearly constant and heat exchange by radiation was negligible. Any alteration in air temperature should therefore produce a similar alteration in the thoracic temperature. It was therefore surprising to find that neither the flight performance nor the wing-stroke parameters were influenced to any measurable extent when the air temperature was altered between 25 and 35° C. At 15 to 17° C a suspended *Schistocerca* would start to beat its wings at subnormal frequencies (600 to 750 min^{-1}) when stimulated, but normal continuous flight performances did not take place below 22 to 24° C. The upper limit for sustained flight was 35 to 37° C, although *short* bursts could be induced up to 40 or 42° C, followed by prolonged periods of violent 'panting', apparently to cool the thorax by means of evaporation. This 'panting' was only seen after flight at high temperatures.

When compared with observations in nature, two factors should be remembered. The effect of thermal radiation must be estimated during normal flight and not from the temperature of settled locusts. In flight the radiation could increase the temperature by only 3 or 4° C at an intensity in the infra-red (high absorption coefficient) corresponding to 1 cal cm^{-2} min^{-1} (Weis-Fogh & Muus, unpublished). In other words, in sunshine the air temperature at which flight can take place may be lowered by approximately this amount. Secondly, in the laboratory *Schistocerca* could *start* normal flight at 22° C, but the flight soon became subnormal. This means that with some heating by radiation, rolling and intermittent migration (Gunn, Perry, Seymour, Telford, Wright & Yeo 1948) might well take place at 20° C. In sunshine where basking locusts can obtain much higher excess body temperature than in flight, take-off must be possible at still lower temperatures, but resettling (and reheating) must then be frequent, since the new temperature equilibrium of flight will be approached quickly and be fully established within about 5 min (Weis-Fogh & Muus, unpublished).

Waloff & Rainey (1951) concluded that in nature the minimum *thoracic* temperature for forced flight was 20° C and that *thoracic* temperatures well above 25° C were necessary for sustained flight. They concluded (p. 17) that 'sustained flight has been recorded in the absence of sunshine only at air temperatures above 23° C by day, and at air temperatures of 25° C or over by night'. Fraenkel (1929) mentions that 25° C is the lower limit for the air temperature. Gunn *et al.* (1948) did not measure thoracic temperatures higher than 41° C in desert locusts caught in flight. Again, these observations fit well with the present experimental results.

In *S. gregaria* we therefore have to consider a locomotor system which normally functions at the same rate in spite of alteration in temperature of the flight muscles amounting to not less than 10° C, i.e. the range within which sustained continuous flight is possible. This finding is surprising and must be explained as the result of the interaction of several factors some of which are temperature-dependent (activity of the nervous system; speed of contraction etc.) and some of which are not (elasticity of the cuticle). From a biological point of view this relative independence on temperature can be considered as an advantage for the species, since the necessary mechanical aerodynamic work for flight is practically unaffected by normal changes in temperature. The success of locusts as migrants might to some extent be due to this ability to keep their flight performance constant under conditions which otherwise would influence a poikilothermal animal. Finally, it should be stressed that the relative temperature-independence makes the factors involved in migration simpler to analyze, a possibly variable factor proving in fact to be constant.

Humidity

The water-vapour deficit between the air inside the thorax (saturated at 7° C above air temperature) and the ambient air was kept constant at about 27 mm Hg in all experiments reported here. According to calculations supported by analyses of the water and fat content after prolonged flight (Weis-Fogh 1952), the amount of water evaporated approximately corresponded to the amount produced by oxidative processes. In fact, in the course of 5 and 9 h of flight respectively, the hydration of the non-fatty dry matter of two flocks of *Schistocerca* had remained nearly constant or improved slightly. In the flight balance the water economy was therefore hardly influenced by the air temperature or by the duration of flight. It was repeatedly observed that an increase in water-vapour deficit tended to increase the degree of truancy and to decrease the endurance, but otherwise the experiments did not give information about the behaviour of flying locusts exposed to different conditions for evaporation. The effect upon the heat balance is certainly small (Weis-Fogh & Muus, unpublished).

Sound stimuli

High-pitched sounds produced by a file against metal or by the shutter of a camera immediately intensified the flight but only for a short time (cf. Williams 1933). If the supra-oesophageal ganglia were severed, however, the effect lasted several minutes apparently with little or no adaptation. There was no indication of any response to the noise from the beating wings of other individuals. Bilateral cauterization of the tympanal organs produced no effect. Low-pitched sounds like the voice of man were also without effect. The sound pattern therefore hardly influenced the flight.

Visual stimuli

Many sudden alterations in visual pattern could induce a short intensification of the flight, but no lasting response was observed. This was also found by Wootten & Sawyer (1954). It should be noted that illuminating the locust with short-wave ultra-violet light invariably disturbed and usually inhibited flight. Records of the track of fluorescent markings on the wings therefore had to be abandoned.

Flight was most steady in subdued white or in red light. It could be argued that this is an unnatural situation, but night flying has often been observed in nature and no lower light threshold for flight is known to exist. It was found that flight in subdued light brought the experimental insect into the state of monotonous and steady flight activity which characterizes migrations in general (Fraenkel 1932). It appears that flight itself, once brought about, tends to reduce the level of environmental stimuli necessary for its continuation.

(*b*) *Comparison with other animals*

Endurance

In the compound balance flight could continue for several hours. After the initial burst of activity, a decrease in intensity (lift, speed and frequency) was observed followed by an increase to a steady level; this was also observed in roundabout experiments (Krogh & Weis-Fogh 1952; Weis-Fogh 1952). In conformity with other insects (Williams, Barness & Sawyer 1943; Wigglesworth 1949; Hocking 1953; Sotavalta 1954), the endurance then largely depends on the amount of fuel reserves. Neural fatigue is probably not significant.

Drag

The aerodynamic power used to overcome the extra-to-wing drag could maximally amount to 4% of the metabolic rate and during normal, horizontal flight it did not reach 2%. Hocking (1953) has recently studied the body resistance in several insects, and he considered it an important factor in the energy account. His figures are of the same order of magnitude as those found here. He also claimed that the body of the honeybee contributes to the lift by as much as one-third of the weight of the insect. According to his figures this means that the lift coefficient should range from 0·4 to 0·7, which is a very peculiar result for a barrel-shaped structure and finds no parallel in locusts (part III).

Stroke frequency

Wootten & Sawyer (1954) suspended *Schistocerca* from a loop fixed to the pronotum. As is discussed in appendix A, this type of suspension should be avoided as far as possible because the posterior shield-like reduplication of the pronotum may interfere with the movements of the forewings. By increasing the freedom for yawing, rolling and pitching, they observed better performances and higher wing-stroke frequencies (from 1320 to 1440/min) than with rigid pronotal suspensions (from 1040 to 1200/min). The high frequencies were within the range which we observed in exceptional cases. The lower values correspond to the normal range in this study when the lift was 100 % or more, i.e. during good performances. An increase in frequency from 1040 to 1320/min will double the important inertial work (see table II, 5). There is no doubt that, at a given performance, reduction of N to the lowest possible value will be an advantage; the high stroke frequencies cannot, therefore, be taken as an indicator for improved conditions for flight. It should be noted that the average speed in this study was 3·5 m/s against 3·2 m/s in the case of Wootten & Sawyer in spite of the increased frequency.

At a given lift, the stroke frequency varied with the size in the same way as assumed by Sotavalta (1947, 1952), namely, $N \propto l^{-\frac{2}{3}}$, where l is the length index. But *N also* varied with the relative lift (in percentage; equation (II, 5)). Chadwick (1953; see also part I) has reviewed the literature on the regulation of the initial frequency in *Drosophila* performing tethered flapping under various external conditions, *inter alia* variations in the density ρ of the air. Under these conditions, both N and ϕ decreased when ρ was increased (Chadwick & Williams 1949; Chadwick 1951). It was concluded that increased aerodynamic 'loading' caused a reduction of the main stroke parameters. This is of course intelligible if the muscle system was working near to its maximum power output as was often the case in *Schistocerca* during the first minutes of flight (Weis-Fogh 1952). It is highly doubtful, however, whether the statement is valid during continuous performances which only rarely take place at maximum power (as will be shown in part VIII). In any case, increased lift and thrust simply mean increased aerodynamic loading; in *Schistocerca* this *additional*, *reflexly controlled* loading was correlated, not with a diminished, but with an increased stroke frequency. This is the relationship found in propellers, and it seems likely that Chadwick's statement only holds for flight under special conditions; it must also be remembered that the true, forced change in aerodynamic loading was unknown in *Drosophila*.

Angular movements

The movements of the forewings vary more than those of the hindwings; the forewings seem to regulate the flight. Any change in illumination, noise, air currents, etc., immediately resulted in small changes of ϕ_1 and $\gamma'_{\text{av.}\,1}$ on one or both sides, but had only a small effect on the hindwings (see also legend to figure II, 14). Such regulatory movements may of course exert a considerable influence upon the sense and magnitude of the system of torques responsible for stability, as has been demonstrated in *Muscina* (Hollick 1940), but they will hardly change the power output significantly if lift and speed remain constant.

Wing twisting

Chadwick (1951, 1953) arrived at the conclusion that a major factor in the regulation of the initial flight performance of *Drosophila* is the 'sine of the angle of attack'. '$\sin \alpha$', however, is a colligative, non-specific expression (see part I, p. 454). Apart from the influence which the alterations of Reynolds's number may or may not have exerted in his experiments, the term covers variation of the wing twisting $\theta = \theta(r, t)$ and the induced wind velocity w (*Drosophila* performed tethered flapping). We must therefore conclude that the twisting is an important factor in the regulation of the flight in both types of insects. In locusts it is the *main* parameter.

9. Appendices

A. *Pendulum and suspension* (figures II, 22 and II, 23)

Pendulum

The locust was suspended from the lower free end of a vertical pendulum. The thrust produces a torque about the horizontal axis of pivoting of the pendulum. When this torque balances that due to the body resistance plus the drag of the suspending bar, the pendulum is in equilibrium, i.e. vertical, and the wind speed corresponds to the flying speed. Figure II, 22 shows the arrangement used for estimating the relations between the flying speed and the drag. The suspending bar (*a*) has a streamlined cross-section, the leading edge being a stainless steel cannula. The transverse horizontal bar (*b*) to which it is attached rests upon a fixed stand (*c*) and is provided with an iron core (*d*). An electric current through the coil (*e*) produces a torque tending to turn the pendulum and the locust up against the wind from the tunnel (*f*). At all wind speeds the current in the coil can be adjusted so that the torque equals that due to the drag of the bar alone but in the opposite sense. (*g*) points then at zero. By switching on and off the current the apparent drag of a flying locust can then be altered suddenly and the corresponding alterations in speed be read. The sensitivity and the zero position of the pendulum can be adjusted by means of the jockey weights at (*h*); the oscillations are damped by a vane-in-oil dash pot (*i*). When compensation is used, the extra-to-wing drag can be estimated from the torque necessary to bring the pendulum back to zero by placing known weights on the pan (*j*) connected to it by a nylon thread over a nearly frictionless pulley.

Suspension

The posterior shield-like reduplication of the pronotum of grasshoppers can exert a considerable pull upon the base of the forewings (La Greca 1948); the pronotum is furthermore free to pivot round an axis situated 15 mm in front of the centre of gravity (part VII). In pronotal suspension, any force not exactly balanced by the drag and the gravitational pull therefore exerts a torque about this 'artificial' axis and might, in addition, press the edges of the shield against the wing base. Suspension from the pronotum, which was used by us for studies on the flight metabolism (Krogh & Weis-Fogh 1951; Weis-Fogh 1952) as well as by Wootten & Sawyer (1954), was thus abandoned for investigations on the flight mechanics.

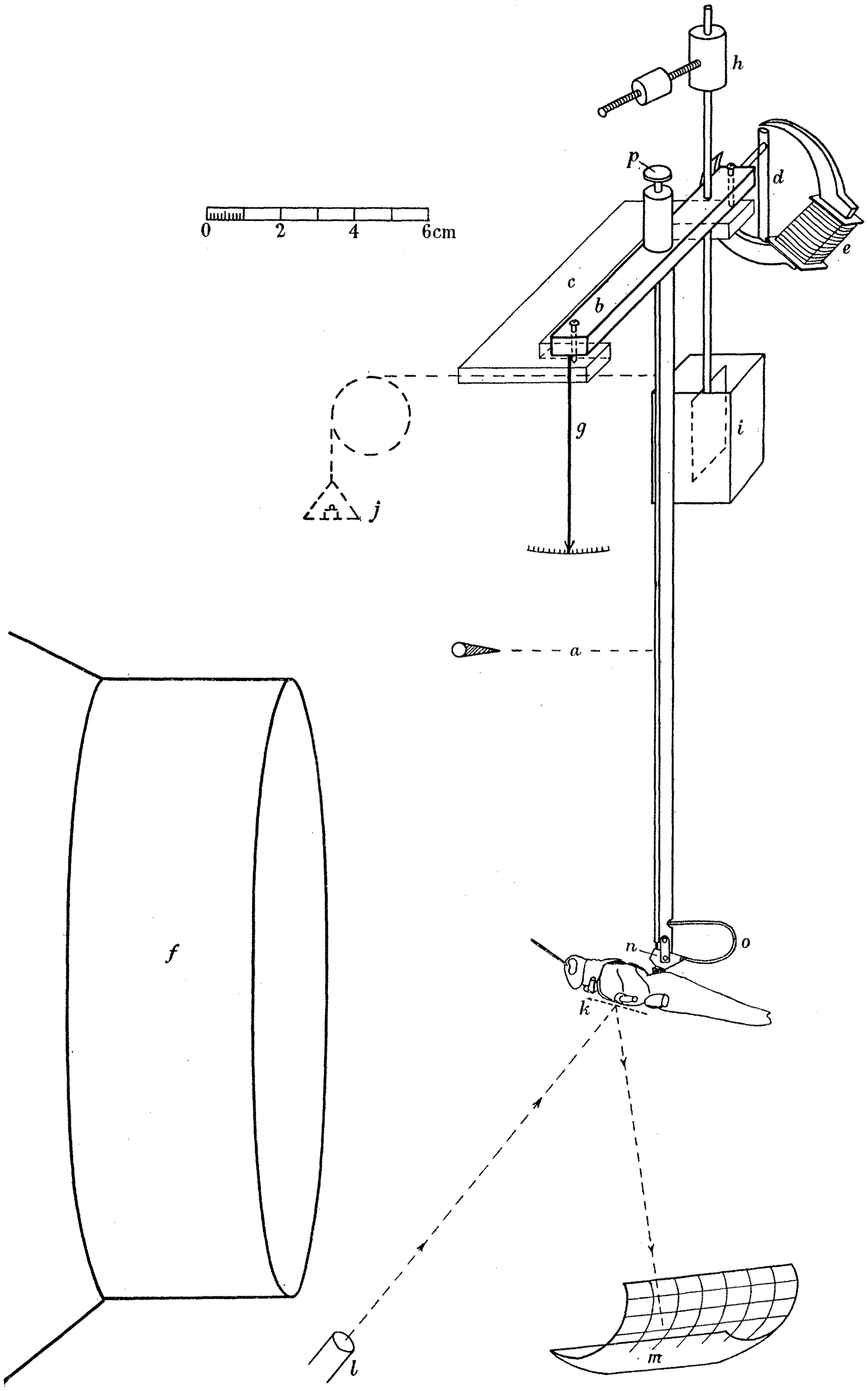

Figure II, 22. The locust is suspended from the first abdominal tergum (suspension type (1)) to a simple adjustable pendulum; it faces the horizontal wind from the orifice of the tunnel (*f*). The drag of the suspending bar (*a*) is compensated by passing current through the electromagnet (*e*). The body angle is adjusted by means of the screw (*p*). The light from the lamp (*l*) is reflected from the mirror (*k*) on to the screen (*m*) and indicates both the *mean* body angle and the pitching *during* a stroke. The pan (*j*) was only used when estimating the extra-to-wing drag.

The ideal would be to study natural flight with no restriction of freedom. However, in wind-tunnel experiments those rapid movements of the locust relative to the air must be prevented which in free flight are partly compensated by the simultaneous alteration of the direction of the path through the air. This applied to yawing and, to some extent, to pitching.

As to yawing of a suspended locust, the rotations would only correspond to the natural ones provided the axis of rotation coincides with that in free flight. The natural yawing axis is unknown and is not likely to be constant. It was therefore concluded that a suspension which prevents rotations about a vertical axis is to be preferred and that the relatively free type used by Wootten & Sawyer (1954) is less suited for wind-tunnel investigations.

In order to study the *pitching* movements, the sternum of the locust was provided with a minute mirror (figure II, 22, *k*), and light from the source (*l*) was reflected upon the screen (*m*) so that the alterations of the body angle could be studied in various types of suspension. When the bar was fixed to the pronotum, the deflexions of B varied about 10° *during* each stroke and decreased during the downstroke; this showed that the lift acted behind the pronotal axis of pivoting. In free flight the lift may attack in front of the centre of gravity, resulting in an increase of B during the downstroke. At least, such movements were seen when suspension type (1) (see below) was used, the deflexions amounting to 3 or 4°. Furthermore, in a suspension in which the locust could pitch rhythmically about an axis situated 5 mm vertically above the centre of gravity, B varied by a similar amount but the sense was not constant. Since the flying speed was found to be identical in the two latter cases, freedom to pitch was not considered essential.

The tergal, abdominal suspension, type (1), consists of the suspending bar in figure II, 22, *a* provided with a movable end-piece (*n*) for adjustment of the body angle. The spring (*o*) serves to press (*n*) against the tip of a rod gliding inside the leading edge (cannula) of (*a*); by means of the screw (*p*) the body angle can be adjusted without any direct interference with the flying locust. The first abdominal tergum is in rigid connexion with the pterothorax and, taking no part in the rhythmical movements, a small saddle of dentist's cement ('Model Kryptex') is moulded to fit the tergum of each individual and fixed to it by means of adhesive wax (beeswax + resin). In this way the locust is suspended above the centre of gravity, and neither the movements of thorax and wings nor the heat balance are interfered with; the body angle could be controlled and the pitching observed. The method has the disadvantage of being laborious, the locusts must be narcotized (CO_2 in air) and, moreover, the attachment of the saddle sometimes damaged the aorta. It was especially used for studying the relationship between flying speed, drag and body angle.

The sternal suspension of type (2), figure II, 23 *A*, consists of a slender bar (*a*) with streamlined cross-section (*b*); it is clamped to the compound flight balance. The leading edge is a stainless steel cannula (diameter 0·9 mm) soldered to a narrow fan of phosphor bronze; below the fan, the cannula is bent backwards, turned downwards so that it follows the curvature of the abdomen and bent forwards again, ending in a small suction cup (*c*) which is provided with a sharp-edged rubber rim (*d*, hatched). The bottom and the sides of the cup are sheltered by a streamlined plastic cover (outlines) designed so as to reduce its drag to an insignificant amount. The suspension bar (*a*) therefore represents the only drag in addition to the extra-to-wing drag, but it is so small that no compensation was found necessary (cf. p. 477). In order to fix the cup, the plastron of the locust is provided with a *thin* amount of adhesive wax so that its surface becomes smooth. The rubber tube at the top of the bar is connected to a vacuum pump, the plastron is sucked against the cup, the tube clamped at (*f*), and the bar with the locust is ready for being placed on the balance. The locust is suspended from the only part of the pterothorax which does not undergo deformations during flight; it is completely undamaged and the same individual can be used many times; all movements are unhampered; the animal is easy to observe. The suspension is light and its drag small. It was used for all standard experiments with the compound flight balance.

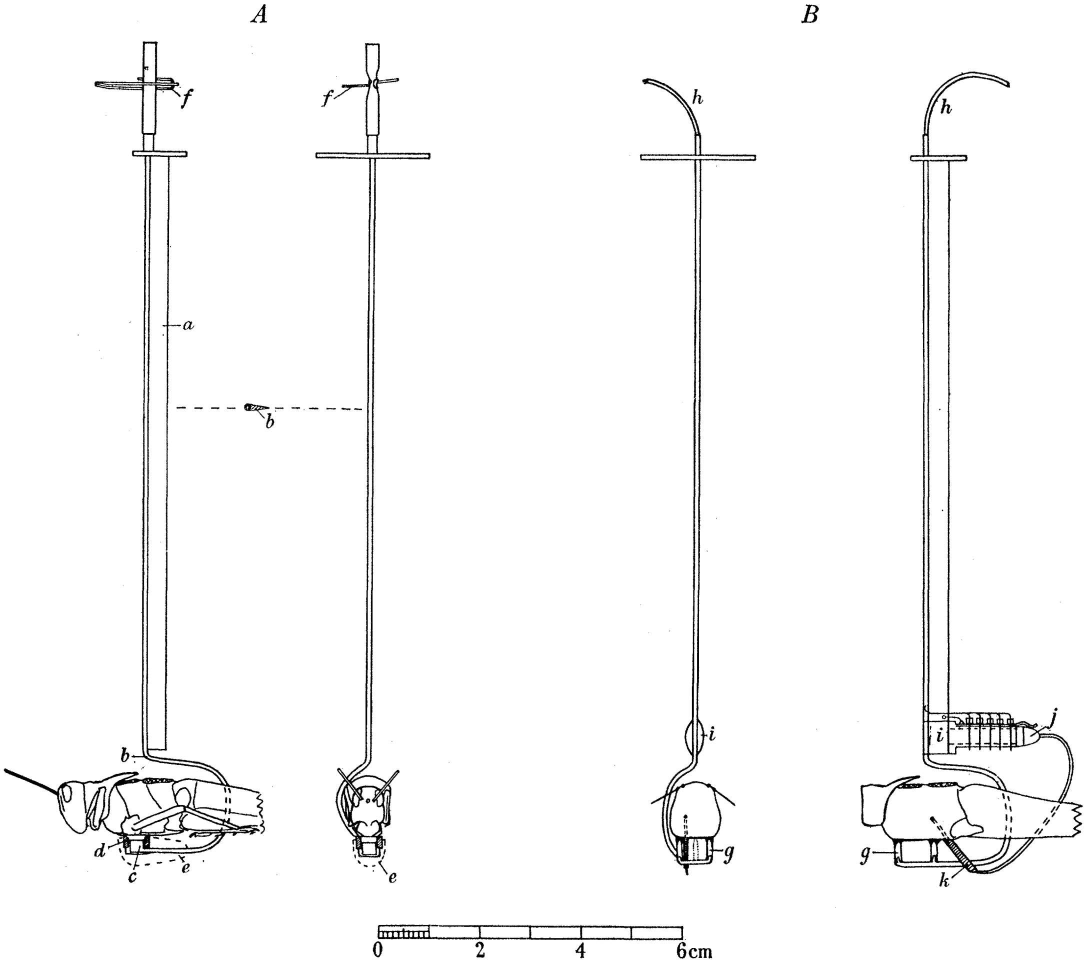

FIGURE II, 23. Sternal suspension of *Schistocerca*. *A*, suspension type (2); side and front view of a locust sucked to a streamlined bar (*a*) of low drag; the suction cup (*c*, *d*) was connected to a vacuum pump via the hollow leading edge of the bar (cannula), ending in the rubber tube at the other end. The cup is sheltered by the cover (*e*, broken lines), practically eliminating its drag. *B*, suspension type (3); a locust is fixed with wax to three plastic pegs (*g*) so that the thorax is freely exposed to the air; a thermistor (*k*) is placed into the pterothorax for temperature measurements; it is fed via (*h*), (*i*) and (*j*).

The sternal suspension of type (3) is seen in figure II, 23*B*. The suction cup is replaced by three small plastic pegs (*g*) to which the plastron is glued by means of wax (black). The thermal conditions are practically the same as in free flight and are discussed in part VIII. The suspension was used for measurements of the thoracic temperatures, minute thermistors being used. The isolation wires (*h*) for the thermistors were drawn through the cannula and soldered to a streamlined plug-socket (*i*) fitted for a five-way plug (*j*). One of the five thermistors (*k*) is seen inserted between the working flight muscles. The technique is further described in part VIII. Although bigger than in (2), the drag of this suspension did not necessitate any compensation either.

B. *Flight balance* (figures II, 24 to II, 26)

The flight balance consists of a pendulum and of the balance proper. Care was taken to make it sufficiently big to permit direct readings and to make all movable parts as light and stiff as possible.

The pendulum (figure II, 24) has a supporting bar (*a*) which rests (pointed steel pins (*b*)) on the steel cups (*c*) soldered to the one end of the balance beam. The plastic tube (*d*) is suspended from (*a*) by means of two steel tubings (*e*); at each end it has miniature ball-bearings (*f*) for the horizontal axle (*g*) whose centre line is normal to the centre line of the wind tunnel (orifice indicated by broken circle). The end away from the air jet has a circular core (*h*), two-thirds of which consist of iron and the remaining of brass (dotted). The torque developed by sending current through the two aluminium coils (*i*) turns the

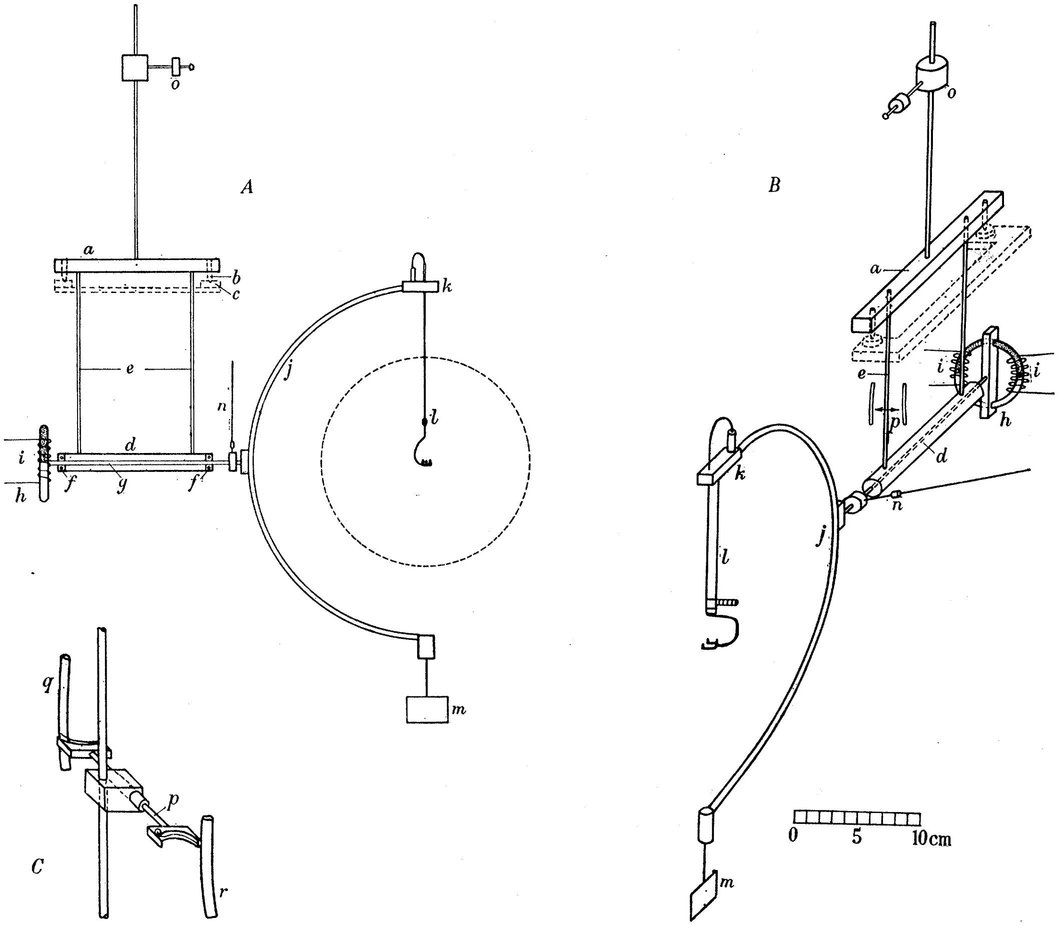

Figure II, 24. Diagram of the compound pendulum from the flight balance. *A*, front view; the circular outlet of the wind tunnel is shown by broken lines. *B*, perspective view. *C*, details of the contact unit placed at (*p*) in *B*.

axle in the desired direction. The other end of (*g*) carries a semicircular bow (*j*) to which the suspending bar (*l*) is attached by means of an adjustable clamp (*k*). The lower end of the bow is provided with a plate for damping (*m*). The entire turning device (*g* to *n*) is centred so that the extension of (*g*) passes through the centre of gravity of the locust. Furthermore, the pointer (*n*) with the jockey-weight can adjust the position of the centre of gravity of the turning device. Before flight the two centres were brought to coincide so that the equilibrium was neutral. The pointer directly shows the body angle with an accuracy of ±1° on a scale (figure II, 27, *b*). The locust chooses *B* when the electric current is switched off, while the observer can adjust it to any desired value by passing currents through the coils. On account of the neutral equilibrium, the deflexion of the pendulum only depends upon the thrust and drag of the locust. Its sensitivity is adjusted by jockey-weights (*o*) so that a distinct deflexion from the zero position is seen when the wind speed is altered by 0·1 m/s during steady-state flight.

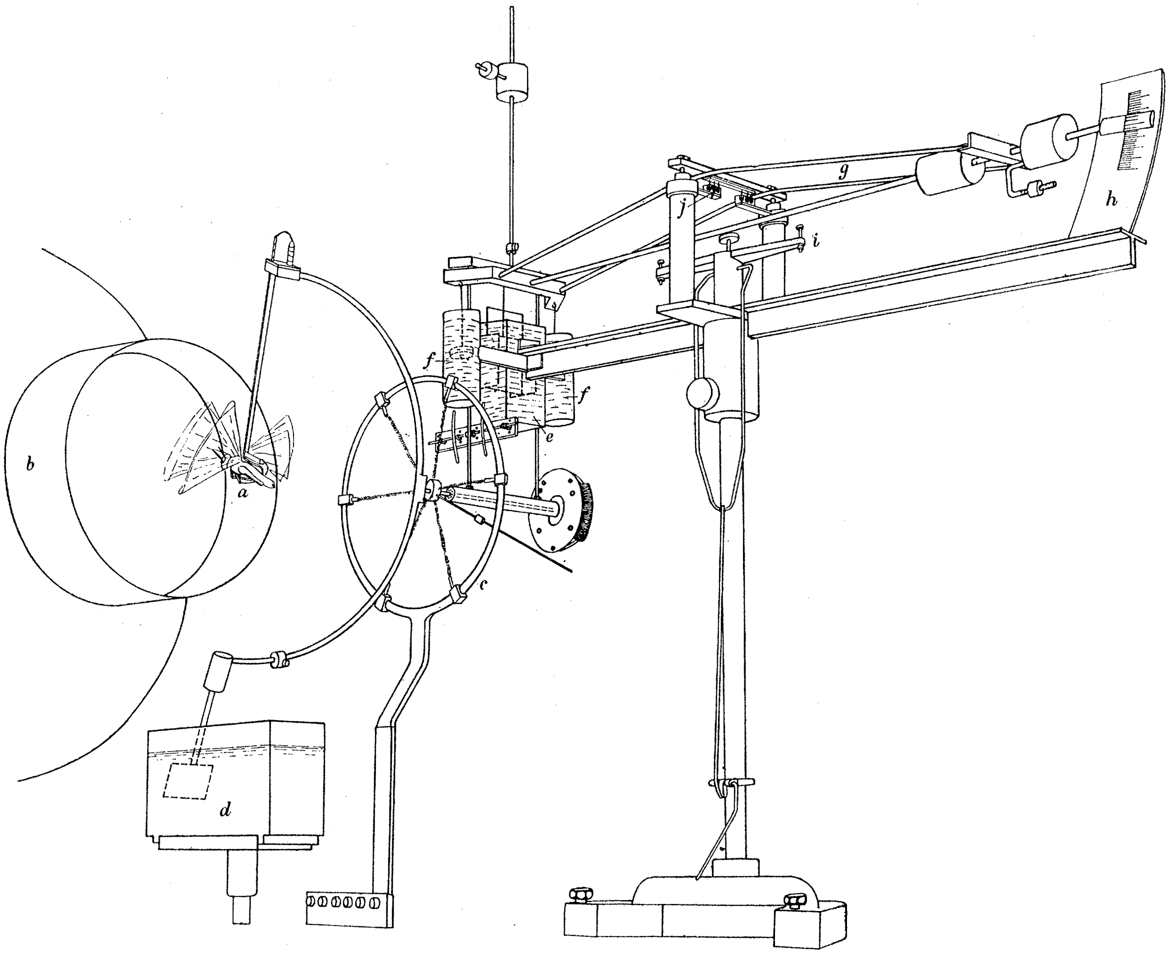

FIGURE II, 25. The compound flight balance with a flying *Schistocerca gregaria* suspended according to type (3).

Any alteration in the flying speed must immediately be compensated by a similar alteration of the wind speed; the adjustment of the wind tunnel was therefore made automatic. The pendulum has a small sliding piece of steel tubing (*p*) which is provided with a concave contact unit at each end (see sketch at lower left corner). When deflected

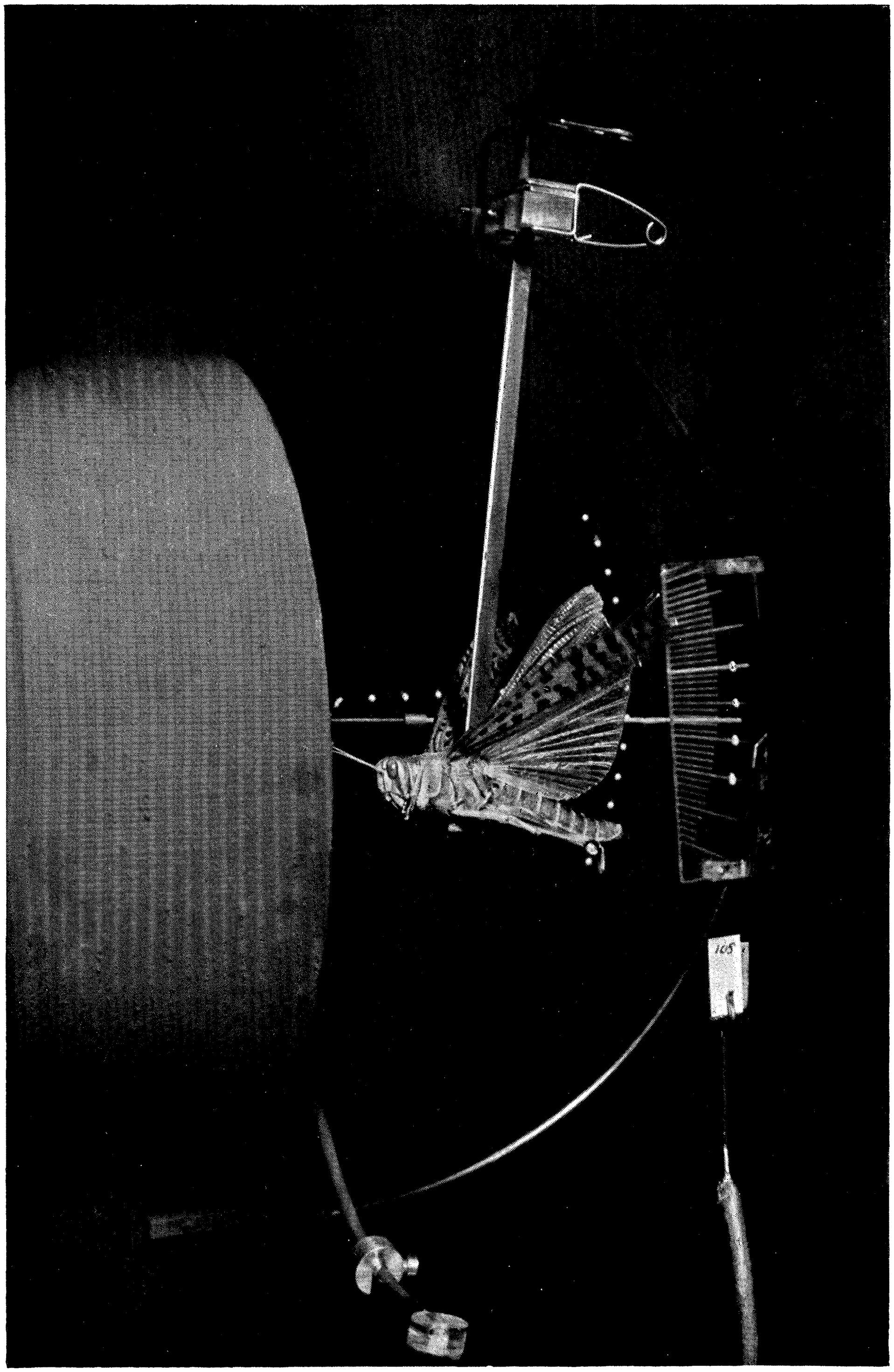

Figure II, 26. Flash exposure of *Schistocerca gregaria* (10^{-4} s) flying in front of the tunnel, suspended from the compound flight balance according to type (2). The scale to the right-hand side indicates the body angle (7°).

from the zero position, contact is obtained with either of the properly curved, polished, steel tubings, (*q*) and (*r*). A servo-mechanism then changes the gear of the air compressor of the tunnel to its new equilibrium position. The short, nearly frictionless sliding of (*p*) is sufficient to prevent the system from oscillating. Actually, tiny springs made of 0·05 mm platinum-iridium wire serve as contactors; when one of them touches the steel tube it short-circuits the grid and the cathode of a triode which controls one of the two relays of the servo-motor. By means of a simple mechanical clutch the automatic control of the tunnel gear can be altered to hand control; this was often found convenient under special circumstances.

The entire balance is seen in figure II, 25. The locust (*a*) flies against the wind from the tunnel (*b*) with a thermistor inserted in the thorax. The ring (*c*) carried six thin (0·09 mm) loosely coiled copper wires for the five thermistors so that the pendulum and the turning device are free to move. No part of the balance is exposed to wind except for the suspending bar. The turning is damped by the dash pot (*d*), whereas the complicated fan in (*e*) damps both the main movements of the pendulum and the small twistings of the beam of the balance (*g*). The up and down movements are damped by the freely suspended weights in (*f*). The average lift is read on the scale (*h*) with an accuracy 30 mg, i.e. within 1·5 % of the body weight. The balance is clamped by means of (*i*). A system of small mercury cups with platinum wires (cf. *j*) transmits the currents for the coils and the servo-mechanism. Originally, a third system was also present which automatically would adjust the body angle until a given lift resulted. However, it did not work because of the active regulation of the lift described in part IV. Figure II, 26, plate 9, is a flash photograph (10^{-4} s) of a *Schistocerca gregaria* flying against the wind from the tunnel (left). It is attached to the balance by means of suspension type (2).

C. *Measurements of stroke parameters* (figure II, 27)

The *wing-stroke frequency* was measured by means of a General Radio Co. 'Strobotac'. When frequently calibrated it works with an accuracy within 1 %. It was provided with a red glass filter to avoid strong light. The *stroke-plane angles* were estimated with an accuracy of about 2° by means of a simple protractor ((*a*) in figure II, 27). The *body angle* was read on the scale (*b*) as mentioned in appendix B. The camera (*c*) was provided with a lens of aperture *f*/3·5. Even in the subdued light a fairly bright picture of the flying locust is formed so that the *extreme wing positions* can be read directly by means of the special protractor (*d*); its four nylon indicator threads can be adjusted independently of each other and move in the focal plane. Ground glass was not necessary and would absorb light. A complete reading consisted of four positions from the forewings and four from the hindwings. The accuracy is 1°.

D. *Slow-motion films*

Illumination and flying

Two high-intensity lamps for continuous flashing (General Radio Co. 'Strobolux') were both triggered from the stroboscope. The flash duration is 10^{-5} s. The locust was suspended from the compound flight balance. By means of the stroboscope, the flash frequency was adjusted to about 5 % below the instantaneous wing-beat frequency so that the movements appeared to be slow. The flight could thereby be observed and the parameters measured as during normal experiments. The spectrum of stroke parameters was read immediately before and after an exposure. Each film strip took 3 to 4 s and represents 60 to 80 *true* wing strokes distributed over three to five *apparent* strokes. The unavoidable noise from the flash lamps caused some trouble because it sometimes increased the intensity of flight for a short time. However, this difficulty was partly overcome by extending the period of flashing beyond the time of exposure.

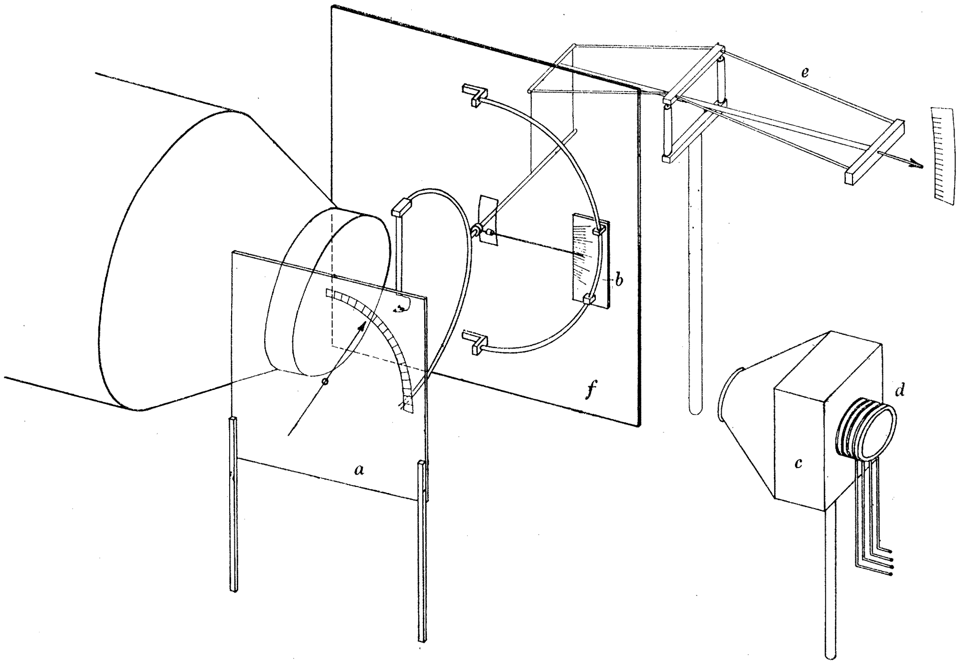

FIGURE II, 27. Diagram of the arrangement for measuring stroke-plane angles (*a*), body angle (*b*), and the extreme wing positions (*c* and *d*). The flight balance is indicated (*e*) together with a black screen (*f*).

Camera

The small flash duration (10^{-5} s) made a revolving diaphragm as well as the discontinuous film movement of an ordinary camera superfluous. A drum camera taking a 1 m strip of normal film (35 mm) was therefore used. Even with two lamps triggered simultaneously the flash intensity was the critical factor and influenced the entire technique. With the locust viewed from the side (along the *y*-axis), the curvature of a point upon the moving wing is opposite the curvature of the film strip on the drum. With focal opening 2·0, as was generally used, and a 15 times decrease in size from object to image, the part of the object in focus is a cylindrical shell which is only 15 mm thick; this estimate is based on an average grain size of $\frac{1}{50}$ mm. The lens must be focused at a point about 35 mm from the fulcrum and towards the camera. Only in that case will a section of the wing situated 45 mm from the fulcrum be in focus throughout the wing stroke. These features determine the limits of focusing which must be done with an accuracy of $\pm 0{\cdot}02$ mm as referred to a point on the film emulsion.

The film used is Ilford's HP-X, designed for X-ray screen photography. It is fast and has a very uniform emulsion. The lens is a 25 mm coated 'Switar' with maximum aperture $f/1{\cdot}4$. In order to focus the image exactly, the lens is replaced by a micrometer caliper accurate to 0·01 mm. The caliper is slightly pushed against the film, the film drum is then removed and replaced by a small focusing microscope also brought into contact with the caliper. By replacing the caliper with the lens, focusing can be done with sufficient accuracy.

The lens is provided with an electromagnetic shutter and the camera is driven by an electric motor with a stabilizing rotary gear pump (oil) and a potentiometer for fine regulations of the speed. The speed of revolution is adjusted to the flash frequency, i.e. to the wing-stroke frequency. The relays for the shutter also operated a small glow discharge tube (220 V, 50 c/s) for time tracings at the margin of the film.

The axis of the camera pointed horizontally towards the origin of the co-ordinate system. In about forty films the animal was viewed from behind (along the x-axis) and in the remaining sixty films from the side (along the y-axis). The films were used partly for determining the variations of γ' with time and partly as a basis for the detailed aerodynamic analysis in part III. The wings were marked with pieces of thin hair provided with minute balls of white paint so as to give distinct contrast at any position. Between the balance and the animal was placed a screen covered with black velour (figure II, 27, f). All other parts within the nearest field of view were likewise blackened.

The flight technique is illustrated in a 16 mm film which also shows the wing movements and the resulting forces in slow motion (Martin Jensen & Weis-Fogh 1953).

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Part I. Weis-Fogh, T. & Jensen, Martin 1956 Basic principles in insect flight. A critical review.

Part III. Jensen, Martin 1956 The aerodynamics of locust flight.

Part IV. Weis-Fogh, T. 1956 Notes on sensory mechanisms in locust flight.

The following Parts are being prepared:

Part V. Jensen, Martin Strength and elasticity of locust cuticle.

Part VI. Weis-Fogh, T. Wing movements and elastic deformations in flying locusts.

Part VII. Weis-Fogh, T. Functional anatomy of the wing system of the desert locust (*Schistocerca gregaria*), including the tracheal system.

Part VIII. Weis-Fogh, T. Lift and metabolic rate of flying locusts.

Part IX. Jensen, Martin & Weis-Fogh, T. The energetics of locust flight.

Part X. Jensen, Martin & Weis-Fogh, T. General discussion of locust flight.

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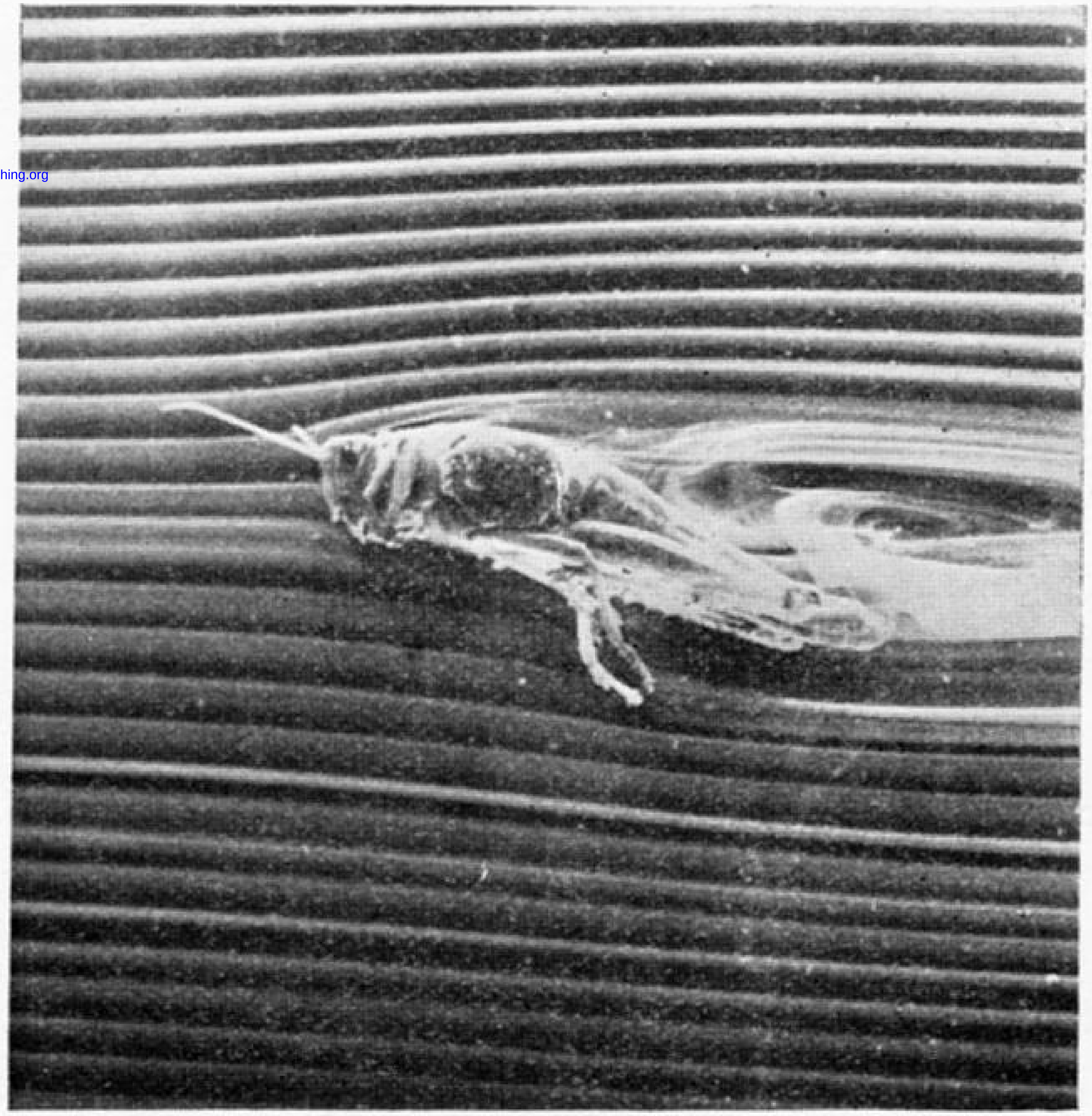
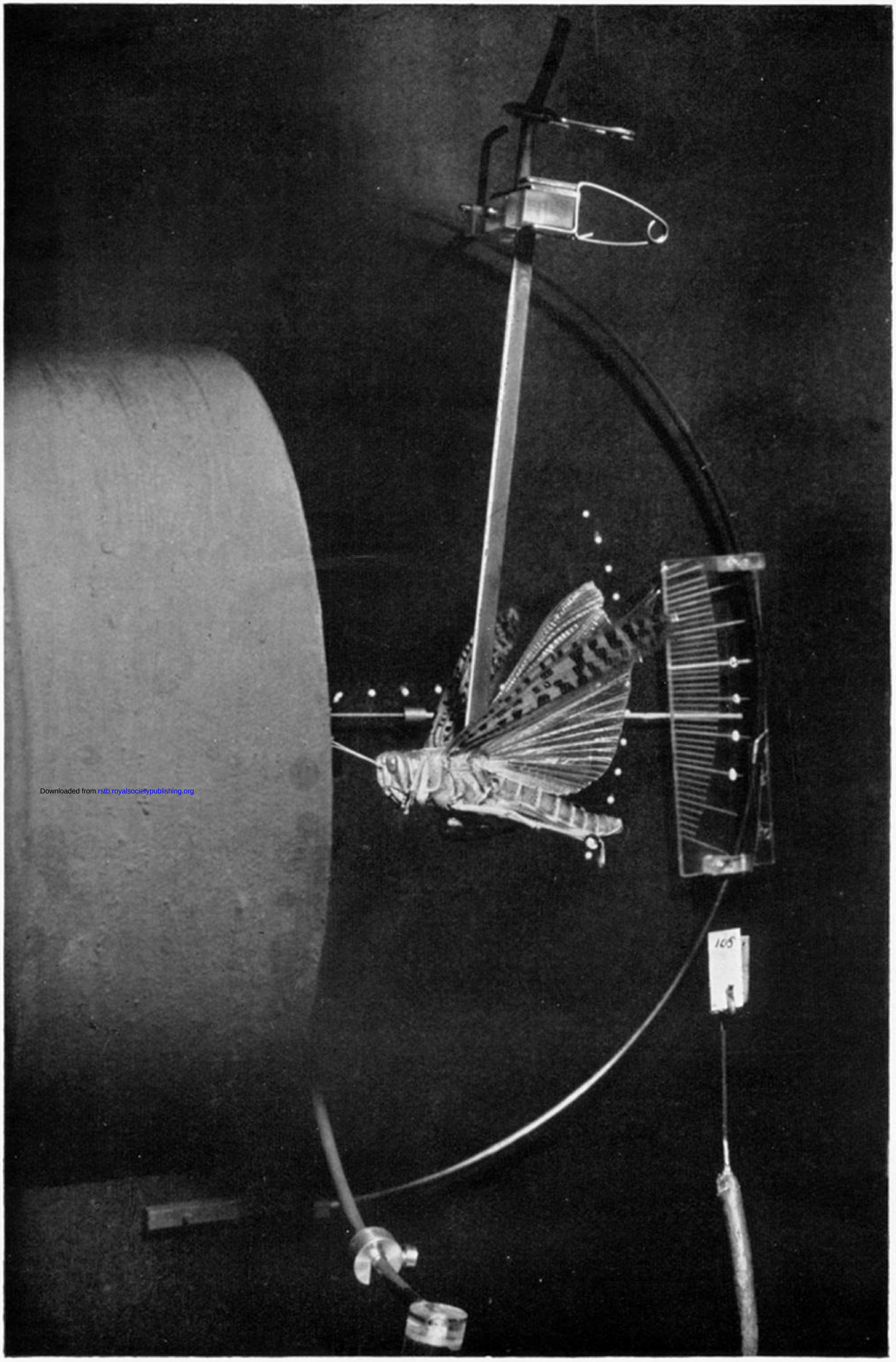


IGURE II, 10. Photograph from a wind tunnel with body and legs of a *Schistocerca gregaria* arranged in complete flight posture (apart from the middle legs which ought to be stretched more backwards). The flow is indicated by two-dimensional smoke patterns; in the undisturbed stream they run parallel and horizontal. The streaming behind the thorax is always turbulent when $B > -10°$; in this photo $B = 14°$.



GURE II, 26. Flash exposure of *Schistocerca gregaria* (10^{-4} s) flying in front of the tunnel, suspended from the compound flight balance according to type (2). The scale to the right-hand side indicates the body angle (7°).