

ON THE SO-CALLED CONSTANT-LIFT REACTION OF MIGRATORY LOCUSTS

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Summary

1. Locusts were fastened to a force transducer in front of a wind tunnel to measure their lift and thrust during tethered flight heading into the wind. The thrust measurement was used to adapt the wind speed to the flight speed of the animals. Thus, the locusts could choose their flight speed freely in the range 0.5–7 m s⁻¹.

2. At light intensities of about 0.02 lx (twilight), the locusts generally produced a maximum lift greater than 100% of their body weight.

3. A miniature motor mounted on the force transducer could alter the body angle of the locusts without further interference. Lift was found to be influenced by body angle. No 'constant-lift reaction' evoked by exteroceptive information of the aerodynamic flow was found.

4. Flight speed was almost independent of the imposed body angle.

5. Generally, a flight speed of about 3 m s⁻¹ was necessary for level flight. There was no further correlation between lift and flight speed.

Introduction

The aerodynamic forces and torques produced in flight are difficult, if not impossible, to measure in free-flying animals. These parameters, together with physiological information, are therefore often recorded during tethered flight. An early example of such an investigation is the study by Marey (1869, cited by Kresling, 1985) of pigeons attached to an aerodynamic balance.

Flight performance can clearly be affected by tethering. Thus, whereas locusts must produce lift as great as their body weight to achieve level flight, this has been observed only in some studies of tethered locusts (Weis-Fogh, 1956*a*; Zarnack, 1969, 1972; Cloupeau *et al.* 1979; Wortmann and Zarnack, 1987) but not in others (Gewecke, 1975; Dreher and Nachtigall, 1983; Krüppel and Gewecke, 1985). One way in which tethering affects flight performance is by reducing the degrees of freedom of movement. For example, a tethered animal cannot control its body angle relative to the line of flight. The relationship between lift and body angle has therefore been given special attention. Weis-Fogh (1956*b*, p. 573) concluded that

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the 'desert locust is provided with a mechanism which keeps the lift constant and independent of the body angle when this angle varies between 0 and 15°'. This 'constant-lift reaction' (Wilson and Weis-Fogh, 1962, p. 648) has been investigated further (Gettrup and Wilson, 1964; Gettrup, 1966).

In this paper we have measured flight parameters in locusts during tethered flight under experimental conditions which allowed the locusts to choose their flight speed over a wide range, under different levels of ambient illumination. We have studied the effect of visual input upon lift production, and re-examined the constant-lift reaction. During these experiments, wing movements were recorded using an electromagnetic method (Schwenne and Zarnack, 1987). The relationship between these movements and the forces produced will be described in a future publication (M. Wortmann and W. Zarnack, in preparation).

Materials and methods

Adult *Schistocerca gregaria* (F.) were obtained from the colony in the First Zoological Institute of the University of Göttingen.

The locusts were fixed ventrally to an aerodynamic force transducer, inside a light-proof Faraday cage, in a laminar airstream (Fig. 1). The force transducer measured lift (l) and thrust (th). The laminar airstream had a diameter of 150 mm (achieved with a nozzle 180 mm in diameter) and a temperature of 28°C. Wind speed (v) generally had an initial value of 2 ms⁻¹, and was then adjusted automatically depending upon the degree of measured thrust, so that the thrust was balanced by the drag. In this way, the animals could choose flight speeds in the range 0.5–7 ms⁻¹, and they flew for several hours under these closed-loop conditions.

On each side of the locust, parallel to the wind, was a rigid artificial horizon (made of black and white paper). The interior of the Faraday cage was illuminated by a small lamp. The intensity of light was measured by a sensor and was adjustable between 0.02 and 30 lx.

Wing movements were continuously recorded using an inductive technique (Schwenne and Zarnack, 1987) which had essentially no effect upon the observed results (see Discussion). The movements will be described in a forthcoming study (M. Wortmann and W. Zarnack, in preparation). Two miniature probing coils (Koch, 1977, 1980) connected to a probe amplifier, were mounted on each of the four wings. The locust was surrounded (outside the artificial horizon) by three pairs of field coils c_x , c_y and c_z , 360, 380 and 400 mm in diameter, respectively. Each pair was fed by a separate amplifier to produce an electromagnetic field in one of the three dimensions, thus inducing a voltage in the probing coils. Each pair of probing coils was arranged on the wing such that the three voltages induced in one of them described the normal vector of the wing, and those induced in the other described the wing-tip vector.

The resultant number of movement coordinates to be recorded was 24 (8×3), of which we could record simultaneously. For data acquisition, the signals from tl.

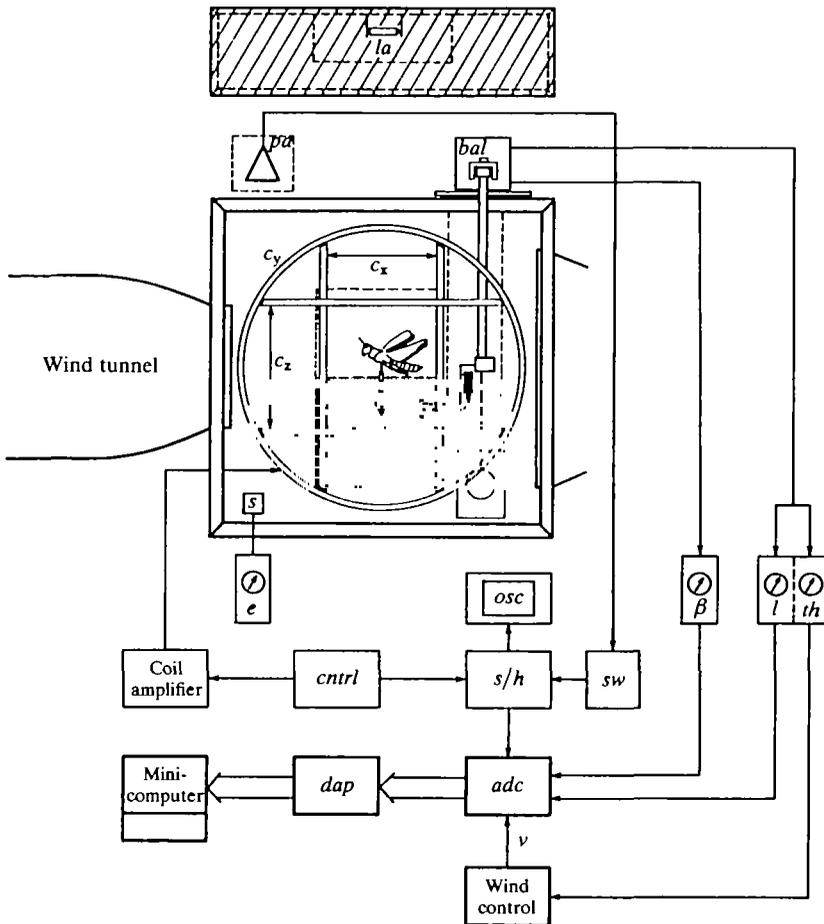


Fig. 1. Experimental apparatus. *adc*, analog-to-digital-converter; β , body angle; *bal*, force transducer; *cntrl*, control circuit; c_x , c_y and c_z , three pairs of field coils; *dap*, data acquisition processor interfacing to a minicomputer; *e*, light intensity; measured by a lightmeter; *l*, lift; *la*, lamp; *osc*, oscilloscope; *pa*, eight-probe amplifier; *s*, light sensor; *s/h*, special amplifiers selecting the vector components from the probe signals; *sw*, switch; *th*, thrust; v , wind speed. Connection of the wind controller to the fan not shown. For further explanation see text.

two probing coils of two wings were selected by a switch. We used the complete data from different pairs of wing in four basic combinations: from fore- and hindwing of the left or right side, and from forewings or from hindwings. Using special amplifiers controlled by an electronic circuit (for further details, see Zarnack, 1978), the resulting 12 coordinates were extracted from the four signals from the selected four probing coils. Usually eight motion coordinates were monitored simultaneously upon an oscilloscope.

The 12 motion coordinates, as well as lift (*l*), thrust (*th*), body angle (β), and wind speed (v), were digitized and processed by a special processor (Zarnack,

1982) for data acquisition with a minicomputer (Nova 4C and Eclipse S/250, Data General).

The force transducer measuring lift and thrust (Fig. 2) was an improved version of the aerodynamic balance used by Zarnack (1969). Because of the Cardan joint, the beam could swing horizontally (axis a_2) and vertically (axis a_1), allowing the

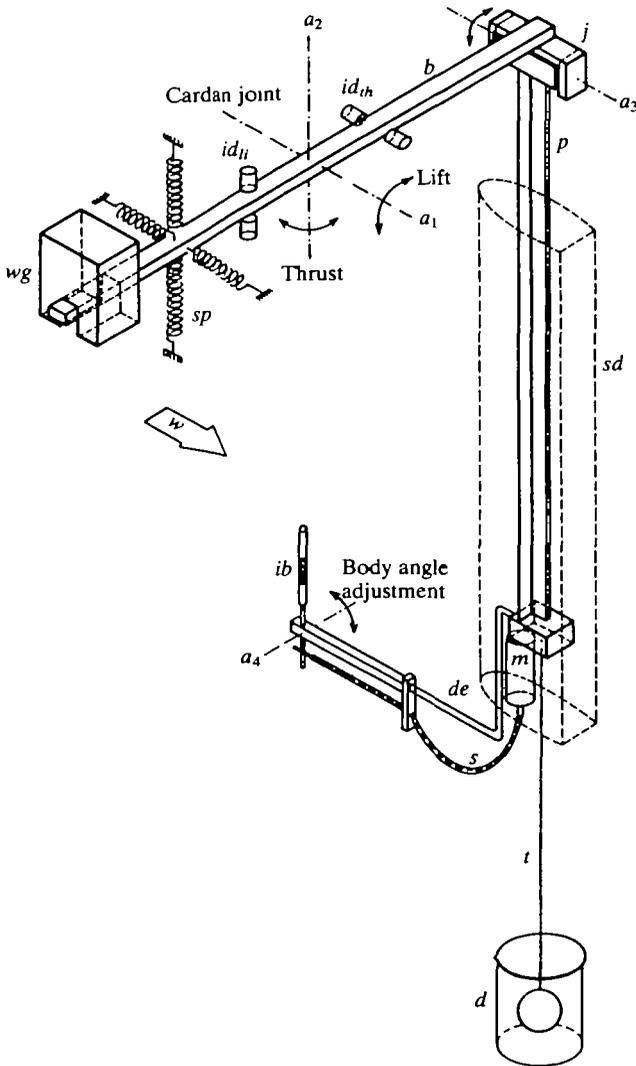


Fig. 2. Details of the aerodynamic force transducer, measuring lift and thrust. a_1 , a_2 , a_3 , a_4 , axes; b , beam; d , brass sphere in an oil bath; de , derrick; ib , insect holder with sensor coil; id_{ii} , pair of inductive displacement transducers for lift measurement; id_{th} , pair of inductive displacement transducers for thrust measurement; j , joint; m , miniature motor and gear; p , pendulum; s , flexible shaft; sd , aerodynamic shield; sp , soft springs; t , thread; w , wind direction; wg , brass weight to compensate the weight of the pendulum. For further explanation see text.

animal to make linear displacements independently in both directions. The displacements depended on lift and thrust. In the horizontal direction, the maximum displacement was 4 mm. In the vertical direction, the displacement was 6 mm for an animal of 20 mN that produced 100% relative lift.

Two pairs of soft springs kept the beam at the zero position. Near the Cardan joint and without contact with the beam, the displacements were measured independently in both directions by means of inductive displacement transducers (Tr 5, Hottinger Baldwin), for lift and thrust measurements.

At one end of the beam, a pendulum was connected with a joint, the axis (a_3) of which was parallel to the horizontal axis of the Cardan joint. At the other end of the beam, a brass weight was used to counterbalance the weight of the whole pendulum. The force transducer was at balance with no animal in position. A derrick was mounted at the lower end of the pendulum. An insect holder with a sensor coil supported the animal ventrally. The connection between the locust and the force transducer was made with a small screw glued to the sternum with cyanoacrylate glue and a mixture of beeswax and resin. The attached screw was mounted to the rod.

The inclination of the insect holder was adjustable between -27° and $+27^\circ$ by a flexible shaft driven by a combined miniature motor (type 1212, Faulhaber) and gear (1130:1, type 121, Faulhaber). Thus, the body angle of the animal, i.e. the angle (around axis a_4) between the wind direction and the long axis of the body, could be varied without disturbing the flight. The inclination of the insect holder was also recorded inductively by means of the electromagnetic fields used for recording wing motion. The absolute error of the body angle was about $\pm 3^\circ$, mainly caused by differences in the attachment of the body to the screw.

The oscillations of the whole force transducer [frequency of 0.5 Hz, logarithmic decrement of 1.35 (lift) and 1.12 (thrust)] were critically damped in orthogonal directions by a brass sphere (diameter 32 mm) in an oil bath. To avoid interference between lift and thrust measurements due to damping, the sphere was connected with fine thread to the end of the pendulum.

To minimize the parasitic drag of the structure of the force transducer, all parts of the device exposed to the wind, except the derrick, insect holder and flexible shaft, were surrounded by an aerodynamic shield. The shielded transducer had a parasitic drag that was similar in value to that of the locust, so it was necessary to calibrate for the parasitic drag (depending on the actual wind speed) of the device without animal.

Analysis of flight sequences was made only for very persistent fliers in the posture of long term-flight (Weis-Fogh, 1956a) during which the aerodynamic drag of the animal is minimal.

Results

There were great individual differences in flight performance, resulting in a

large variation of all parameters recorded. The range of behaviour can be seen from the data for three individuals (Figs 3i,ii,iii, 4i,ii,iii).

Flight performance

Locusts in the typical long-term flight posture flew continuously for at least 90 min. Different flight modes could be induced artificially by altering the imposed body angle (see below), resulting in descending, level or ascending flight. Many animals tended to increase their lift slowly without external influence during the course of the experiment.

At the end of the observation time, the animals were still able to perform level or ascending flight, i.e. they produced lift of at least 100 % of their body weight. One animal produced a maximum lift of about 200 % (not shown) 1 day before the recording (Fig. 3ii) was made. Thus, we assume that the flight performance of the animals was not influenced by fatigue. Both constancy and changes of flight parameters over 90 min of flight are shown (Fig. 3).

Lift

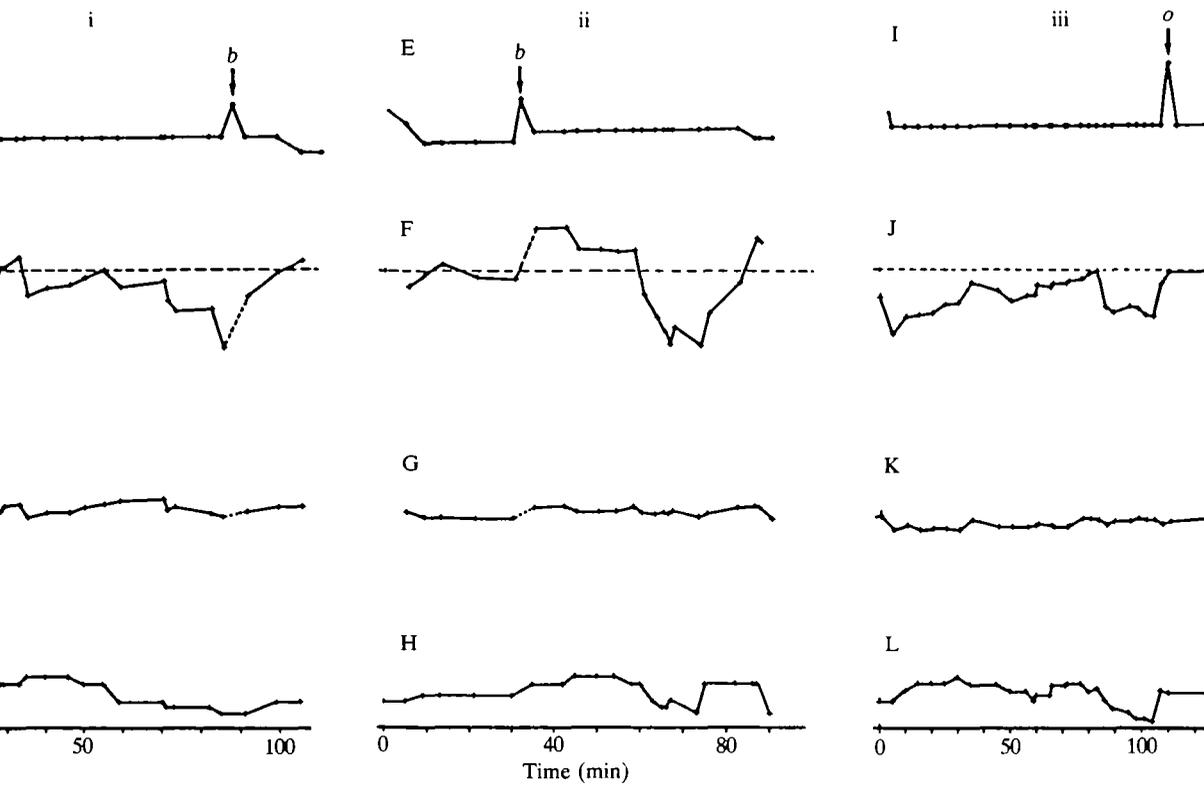
In earlier studies on the interdependence of wing motion and aerodynamic forces, high light intensities were needed for photography. Using the miniature coils, we could record wing motion over a wide range of light intensities. Usually lift increased when the animal was exposed to twilight. At light intensities less than 0.1 lx, the lift was often greater than 100 % of body weight, when the body angle was adequate.

To avoid 'on'-effects (which were generally not observed), a few minutes (equivalent to more than 2000 wing beats) were allowed to elapse between adjustment of the imposed body angle and the measurement of lift values. To avoid phenomena similar to adaptation, we generally used randomized series of body angle values.

In spite of miniature coils on the wings, the relative lift (l_{rel}) was generally rather constant, when the body angle (β) was constant (Fig. 3). Whenever β was varied, there was a change in l_{rel} : l_{rel} could be manipulated between 20 and 150 % by adjusting β between 0 and 25° (Fig. 3). At lower or higher body angles, the animals interrupted flight.

In addition to these general results, there was occasionally a large increase in l_{rel} from 55 to 130 % within 10 min even though β was constant (Fig. 3F,H, observation time about 80 min); decrease in lift also occurred at constant β . Consequently, only a vague relationship between lift and body angle was found (see below).

Since the relative lift was often fairly constant when the body angle remained constant, we tried to characterize l_{rel} as a function of β for comparison of our results with those of Weis-Fogh (1956b, p. 567). Regardless of the temporal relationships, the mean values and standard deviations of l_{rel} were calculated and plotted against β (Fig. 4A,D,G). The dotted curves indicate smoothing lines of quadratic form. (An unsuccessful test was made using a sine function near 90°.)



simultaneous recording of light intensity (e) (top row), relative lift (l_{rel}) (second row), flight speed (v) (third row) and immersion (β) (bottom row) of three individuals. Measurements taken at 2- to 3-min intervals. b , flight interruption; o , change in light intensity.

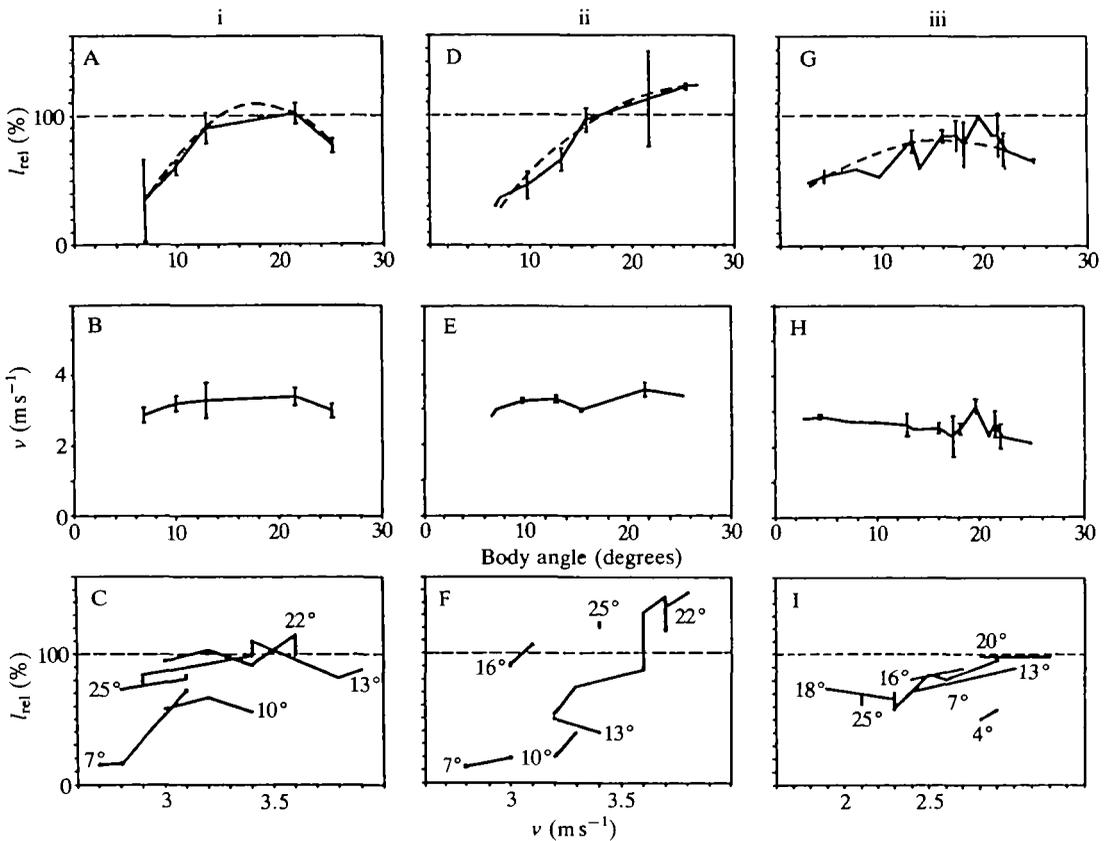


Fig. 4. Relationships between relative lift (l_{rel}) and body angle (β) (top row), between flight speed (v) and body angle (β) (second row), and between relative lift (l_{rel}) and flight speed (v) (bottom row) of three individuals. The imposed body angles are indicated in C, F and I.

The characteristic curves are not similar. In the first experiment (Fig. 4A), lift increased ($\beta < 14^\circ$), remained rather constant ($14^\circ < \beta < 22^\circ$), and then decreased ($22^\circ < \beta$). In the second experiment (Fig. 4D), there was a fairly steady increase in lift. In the third experiment (Fig. 4G) there were only small variations in lift. This result resembles to that of Weis-Fogh (1956b, Table IV,3). But in our experiment the lift was greatly influenced by β (Fig. 3J,L), even when β was varied in the middle range of $15^\circ \pm 5^\circ$ (Fig. 3J,L, observation time about 70 min). This will be discussed in detail below.

The relationship between flight speed and body angle

Flight speed (v) was fairly constant and independent of body angle β (Figs 3, 4).

The relationship between lift and flight speed

In Fig. 4C,F,I, the single values of relative lift depending on flight speed at a

given imposed body angle are connected. In the second experiment (Fig. 4F), at $\beta=22^\circ$, eight pairs (l_{rel} , v) have been measured, 60 %, 3.2 m s^{-1} ; 73 %, 3.4 m s^{-1} etc. These points are connected and the actual value of the body angle is indicated.

For level or ascending flight, a speed of at least 3 m s^{-1} seemed to be necessary (Fig. 4C,F,I) if the body angle was in the range 12° – 22° . Weis-Fogh (1956a, Fig. II,6) found comparable values of about 3.5 m s^{-1} .

Discussion

Migratory locusts are able to fly continuously for several days (Rainey, 1985). We will first discuss two requirements necessary for such long-term flight: (i) long-term production of sufficient lift and (ii) regulation of lift, especially the constant-lift reaction. Finally, our results will be compared with those found in other insects.

Lift production

Migratory locusts must be able to produce a lift at least equal to their body weight. This has been demonstrated in many wind tunnel experiments (Weis-Fogh, 1956a; Zarnack, 1969, 1972; Cloupeau *et al.* 1979) and was confirmed in the present study for long periods of flight, e.g. 30 min (Fig. 3F). Surprisingly, some experiments have shown lift values below body weight (Gewecke, 1975; Dreher and Nachtigall, 1983; Krüppel and Gewecke, 1985). How can one explain the discrepancy between these results?

To measure forces during flight, the experimental animal has to be tethered to some kind of support, which affects sensory feedback loops. For instance, in tethered flying locusts, the latency (i.e. the time interval between onset of a disturbance and the animal's response) of roll manoeuvres is several seconds when visually induced by a simple artificial horizon (Wilson, 1968; Schmidt and Zarnack, 1987). However, the latency is greatly reduced, to less than 0.5 s (Zarnack, 1988), when the tethered locust flies in a flight simulator with a quick servo system similar to that used by Götz (1987).

The influence of experimental aerodynamic conditions on lift

Relatively low lift values have been observed with isometric measurements, in which the animal could not move its body (Gewecke, 1975; Dreher and Nachtigall, 1983; Krüppel and Gewecke, 1985). In our experiments and those of Weis-Fogh (1956a, Fig. II,25), vertical displacements were possible (owing to the mobility of the force meter) without changing the aerodynamic environment, because wind speed was constant over the laminar windstream cross-section. The rate of change of the vertical displacement (Fig. 1) was at most 0.0025 m s^{-1} , i.e. about 0.1 % of the flight speed. It is questionable whether such a low speed can be perceived by the animal through its aerodynamic senses. Thus, we exclude an aerodynamic reason for the high lift values found in our experiments.

The influence of visual input on lift

Visual input has an important influence on lift production (*o* in Fig. 3). Weis-Fogh (1956a, p. 499) suggested that low light intensity was responsible for steady flight. Gewecke (1975, p. 93) supposed that the constant visual information is partly indirectly responsible for insufficient lift production in experiments measuring isometric lift. In our experiments, high values of lift were only achieved at low light intensities of about 0.02 lx, i.e. twilight (Siebeck, 1976). At this light level, the artificial horizon is the only part of the experimental apparatus visible to a human observer, whereas under brighter light the wind tunnel nozzle, stands and parts of the field coils are also visible.

When the animal moves up or down in the apparatus, its visual input changes, since the horizon remains still in space. The perceivable light decreases generally with the square root of the distance between the light source and the observer. At very low light intensities only neighbouring objects will be visible, so the ratio of apparently moving to apparently immobile parts of the optical environment (pattern) is greater than that at high light intensities. Therefore, during vertical movements of the animal, the changing visual input may be sufficient to maintain visual control at low light intensities, but not at high light intensities.

The relationship of body angle to lift regulation, the constant-lift reaction

To maintain horizontal balance, the animal has to avoid rotations about the pitch and roll axes, so we examined the effect of pitch and body angle on lift regulation. Rotations about the roll axis have little influence on the aerodynamic flow relative to the animal (Waldmann and Zarnack, 1988) but act on the lift. A change in the animal's pitch angle divides the aerodynamic force into lift and thrust components, and also changes the aerodynamic flow around the animal. Therefore, it is possible to perceive pitch and body angle by mechanoreceptors, e.g. hairs on the head which are sensitive to the aerodynamic flow (Weis-Fogh, 1949; Smola, 1970; Bacon, 1983).

Weis-Fogh reported that lift was independent of body angle (1956b, p. 567, Table IV,3, four mean values without standard deviation) and concluded that 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°' (Weis-Fogh, 1956a, p. 460). He compared the phenomenon with a 'servo-mechanism', which should be controlled by campaniform sensilla at the wing base (Weis-Fogh, 1956b, p. 582). Wilson and Weis-Fogh (1962) and Gettrup and Wilson (1964) investigated further this 'control reaction' and 'reflex' (Gettrup, 1966).

In our experiments, flight performance varied with time and from animal to animal. Only data from continuous flight sequences were evaluated, because after interruption the resumed flight often showed remarkably altered lift (*b* in Fig. 3A,E), although the body angle remained unchanged.

Weis-Fogh stressed 'that it was impossible to influence the lift significantly by

changing the body angle between 0° and 15 to $20''$ (Weis-Fogh, 1956a, p. 469). In contrast, we found that in the range 0° – 26° lift was influenced by the body angle (Fig. 3).

Since our experimental apparatus does not influence the aerodynamic flow (except for the stimulus, the imposed body angle), we conclude that there is no reflex, control reaction or servo-mechanism evoked by any extero- or proprio- (mechano-) receptor which keeps the lift constant and is elicited by the aerodynamic flow. This was the assumption of Weis-Fogh (1956b, p. 581).

Our experiments and those of Weis-Fogh (1956a, pp. 468, 499; except for photography) used very low light intensities, presumably perceivable by the animals. Therefore, it seems to be rather unlikely that there is a constant-lift reaction based on visual input. However, this cannot be excluded.

Detailed comparison of our experiments and those of Weis-Fogh

How can we explain the discrepancies between our results and those of Weis-Fogh? Neglecting temporal relationships, he calculated mean values and standard deviations of all lift data of the actual body angle (Weis-Fogh, 1956b, p. 567, Table IV,3). Thus, to compare our results with his we did the same (Fig. 4A,D,G). The only difference between our evaluation and that of Weis-Fogh is that we treated the individual data separately, whereas he mixed the data from all individuals. We have found in some cases, but only when disregarding the time dependence, that lift seems to be fairly independent of body angle (compare Fig. 4A, $14^\circ < \beta < 22^\circ$, and Fig. 4G).

Obviously, the mean values (Fig. 4A,D,G) do not reflect the animal's behaviour, since even in the third experiment (Fig. 3J,L), with the smallest variation of mean lift values, the lift changed during the course of the experiment, whenever the imposed body angle was changed.

The basic assumptions in calculating the mean values are that the lift is (i) constant at a constant body angle and (ii) independent of time. We can see that both necessary conditions are not met. (i) In the third experiment, the response was tonic, i.e. at constant body angles, lift remained constant for several minutes (Fig. 3J,L, observation time about 70, 110 min). Despite the tonic response, at different observation times, the lift often had different values at the same body angle, resulting in a large standard deviation of the mean lift at a particular body angle (Fig. 4G). (ii) In the first and second experiments, the lift increased both slightly and greatly and even decreased at a constant body angle (Fig. 3B,F). Therefore, in our opinion, a time-independent evaluation is not valid for a reflex where time-dependence is decisive.

We think that a servo-mechanism or control reaction (here the constant-lift reaction) must be provable in each individual. We have never found evidence for a servo-mechanism. Weis-Fogh based his conclusion (1956b, p. 573, see Introduction) on the following findings: '... the preferred relative lift varies from individual individual and from one flying to the next with the same locust...' (p. 566), the 'preferred relative lift of the individuals varied from 55 to 150 % of their basic

weight, but the mean lift... of the total material was about 100 %' (p. 567), the relative lift '... was 70 to 162 % respectively' (p. 569). Yet, he calculated the mean relative lift at four body angles from the data for different individuals because '... none of the deviations from the chosen average lift of an individual during an experiment exceeded $\pm 10\%$. In fact, the deviation was less than $\pm 5\%$ in 113 of 118 cases' (Weis-Fogh, 1956*b*, p. 566). In contrast, in the three experiments presented here, the lift of an individual varied between 20 and 110 % (Fig. 3B), 20 and 140 % (Fig. 3F) and 30 and 100 % (Fig. 3J). Moreover, individual variations of up to 200 % were also observed. With regard to this great variability, we conclude that such an analysis of the data, disregarding temporal relationships, is inadequate.

Of course, there are experimental differences, which could further explain the different results concerning the constant-lift reaction. (i) Our wind tunnel provided a continuous speed control, activated by the locust in a feedback loop. This increased the locust's drive to fly. Weis-Fogh (1956*a*) used a speed control in discrete steps of 0.1 m s^{-1} . (ii) We attached the animal at the sternum, while Weis-Fogh used a tergal-abdominal attachment (Weis-Fogh, 1956*b*, p. 503). (iii) Weis-Fogh (1956*a,b*) and Gettrup and Wilson (1964) adjusted the body angle manually. In our experiments the body angle was adjusted by remote control (Fig. 2). This avoided interruptions of continuous flight. A complete series of body angles can be imposed during one continuous flight bout, because the animal does not fatigue. (iv) We used intact animals, whereas Weis-Fogh had cut away the tarsi. The miniature coils we attached to the wings of the locusts in the present experiments seemed to account neither for excessive lift production nor for the influence of the body angle on lift control. This was shown by omitting the coils in control experiments with five locusts.

Obviously, we have used more 'natural' experimental conditions than former authors were able to apply. Therefore, we assume that our results are representative of a more natural flight condition, and are not artefactual.

Variations of speed, thrust and lift

Flight speed (v) (Figs 3, 4) varied independently of the body angle between about 2 and 6 m s^{-1} (not shown). We were not able to measure the total drag (the sum of the static and dynamic terms) and thrust, but we can estimate their variance because the static drag is proportional to v^2 and the animals were generally flown at a steady speed. In this case, thrust equals drag.

Speed must be at least 3 m s^{-1} to generate a relative lift of 100 % (Fig. 4C,F,I). There is no further dependence between lift and speed and, consequently, between lift and thrust (see above). Therefore, locusts are able to vary lift and thrust, and consequently speed, independently and widely. These results are in agreement with those of Weis-Fogh (1956*a*).

Lift generation by locusts is influenced by body angle. In other insects further aerodynamic forces also depend on body angle. For instance, in bees, lift correlated with increasing body angle and flight speed is correlated with decreasing

body angle (Nachtigall *et al.* 1971; Esch *et al.* 1975). In *Drosophila*, both body angle and movement of the imposed optical pattern act on the magnitude, but not on the elevation, of the average force produced relative to the body axis during free flight as well as during tethered flight (David, 1978; Götz and Wandel, 1984).

We conclude that locusts do not control lift only through body angle. At a constant body angle and an almost constant speed, locusts are able to increase the relative lift from 55 to 130% (e.g. Fig. 3F,G, observation time 75–85 min). As mentioned above, this is not the case in *Drosophila*. The great scatter of the lift values at a given imposed body angle shows that locusts are able to generate the same lift at different body angles. But, in our opinion, this finding is not sufficient to prove the existence of a servo-mechanism that keeps the lift constant regardless of body angle.

If the pattern of wing movement is constant relative to the body, a change of the body angle would directly influence the static angle of attack, resulting in a changing relative lift, partly explaining our observation that lift can be manipulated by adjusting the body angle. As we discussed above, lift can vary in spite of a constant body angle. Thus, other factors must also influence lift. Nevertheless, we have been able to use this phenomenon to study relationships between wing motion and generated aerodynamic forces (M. Wortmann and W. Zarnack, in preparation).

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