

## WING MOVEMENTS AND LIFT REGULATION IN THE FLIGHT OF DESERT LOCUSTS

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### Summary

1. We simultaneously recorded lift/body weight, flight speed, body angle and 12 variables of wing movement for locusts performing tethered long-term flight with low movement scatter. The movements of the forewings and hindwings were recorded in three dimensions by means of miniature induction coils.

2. By adjusting the body angle, we could reproducibly manipulate lift generation as a consequence of induced changes in the wings' movement patterns. We were therefore able to analyse various relationships between the movement patterns and lift.

3. The most prominent variations of kinematic variables were observed for the forewing movements. The relative lift and the steady angle of pitch were positively correlated but there was a negative correlation between relative lift and pitching amplitude. We found no correlation between relative lift and flapping amplitude. Our results seem to correspond to a new theory about unsteady aerodynamics of oscillating aerofoils.

4. We sometimes observed variations in lagging.

5. The forewing downstroke was delayed by 0–8ms following the hindwing downstroke. Relative lift was positively correlated to this delay.

### Introduction

In locust flight, lift production depends on the body angle (Zarnack and Wortmann, 1989). Changes of lift originate in changes of the movement patterns of the wingbeat. Little is known of the quantitative influence of the relevant kinematic variables of wing movements, especially those of the hindwings, on lift production although there are several hints about the importance of pronation and flapping amplitude. In this second part of our investigations (cf. Zarnack and Wortmann, 1989), it was our intention to study these relationships by applying a method which combined inductive wingbeat recording and force measurements.

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### Materials and methods

Adult *Schistocerca gregaria* Forskål were obtained from the colony in the First Zoological Institute of the University of Göttingen, Germany. We used 20 individuals, each of which was flown in straight flight for at least 45min, and often for as long as several hours.

#### *Recording of the wingbeat*

In wind-tunnel experiments, the main features of which have already been described by Zarnack and Wortmann (1989), desert locusts performed long-term flight. We could record the relative lift ( $I_{rel}$ ) (see below), flight speed ( $v$ ) and body angle ( $\beta$ ), because the animals were fixed to a system of force transducers. Using two miniature induction coils on each of the four wings (Schwenne and Zarnack, 1987), we recorded the wing movements in three dimensions (Koch, 1977; Koch and Elliott, 1983; Zarnack, 1978). We fixed the miniature coils (18  $\mu$ m diameter copper wire, 80 turns, coil diameter 1mm) to the wings near their articulations. One coil was fixed flat on the wing surface to define the normal vector of the wing plane ( $\mathbf{n}_f$  and  $\mathbf{n}_h$ , where f and h refer to forewing and hindwing, respectively). The other coil was perpendicular to the first and pointed to the wing-tip (see Schwenne and Zarnack, 1987), thus defining the wing-tip vectors  $\mathbf{wt}_f$  and  $\mathbf{wt}_h$ . The eight coils therefore generated eight three-dimensional vectors. All vectors have a length of 1 (i.e. they are unit vectors).

Owing to the constraints of the data acquisition system, we could not record all eight vectors (i.e. 24 vector components) simultaneously, but had to confine our recordings to the four vectors of the forewing and hindwing on one side of the body.

#### *Steadiness of the flight performance*

Generally, flight was steady at a mean speed of about  $3 \text{ ms}^{-1}$ . The steadiness of flight was also indicated by steady lift production and by consistent wing movements. To observe the latter during flight, we simultaneously monitored four pairs of two vector components on an oscilloscope in the  $x,y$ -mode by means of a special multiplexer. The eight vector components were generally  $n_x$  and  $n_y$  ( $x$ - and  $y$ -components of the normal vectors) and  $wt_x$  and  $wt_z$  ( $x$ - and  $z$ -components of the wing-tip vectors) of two wings, usually the left and right forewings. The oscilloscope thus showed the projections of two normal vector paths on the  $x,y$ -plane and of two wing-tip paths on the  $x,z$ -plane (similar to the paths shown in Fig. 1B,D). Sometimes we used  $n_x$  and  $n_y$  of all four wings.

Only during flight sequences with very steady movement patterns was data acquisition activated, each time lasting for 12s. In this time interval, there was generally only a very small scatter of wingbeat (compare Fig. 4D with Fig. 4F).

#### *Mathematical treatment*

The cyclic movement of each wing is the result of three independent rotatory, generally non-harmonic, oscillations (Zarnack 1972, 1982): (i) pitching, i.e. rotation around the wing's longitudinal axis (pronation and supination), indicated by the  $x$ -component of the normal vector ( $n_x$ ); (ii) flapping (i.e. up and down movement), indicated by the

$z$ -component of the wing-tip vector ( $wt_z$ ); (iii) lagging, i.e. forward and backward movement, indicated by the  $x$ -component of the wing-tip vector ( $wt_x$ ).

The methods of kinematic analysis have already been described (Zarnack, 1972, 1983, 1988; Schwenne and Zarnack, 1987). We will usually present the data as parallel projections (i.e. time-independent trajectories) of the three-dimensional vector paths (e.g. Fig. 1B–E). In order to demonstrate phase relationships between the movements of different wings, we will also use the time functions of the vector components (e.g. Fig. 5Aii–Dii). Finally, we will show characteristic correlations between kinematic variables and lift.

## Results

In locusts, the movements of all four wings can vary greatly (Schwenne and Zarnack, 1987; Schwenne, 1990). To minimize problems of data interpretation, we analysed only flight sequences with steady wing movements, as shown for the left wings in Fig. 1. In this flight sequence, the movement patterns as well as the relative lift ( $l_{rel}$ ; the quotient of absolute lift and body weight) were reproducible even after the long flight (Fig. 1F,  $83\text{min} < t < 152\text{min}$ ), although the individual had, in the meantime, been subjected to various tests with other body angles that had induced changes in lift production (see below).

It was our intention to investigate functional relationships between changes of the wing movement patterns and relative lift ( $l_{rel}$ ). Therefore, we induced changes in lift generation by imposing different body angles ( $\beta$ ) on the flying locust (Zarnack and Wortmann, 1989).

### *Movement variations of a single wing*

These results are demonstrated using long-term flight data from one individual, some of which have already been published (Zarnack and Wortmann, 1989, Fig. 3iii). Fig. 2 shows movements of the left wings during single wingbeat cycles at different values of  $\beta$ ,  $l_{rel}$  and  $v$ . Actual values are given in Table 1. The upper rows contain the projections of the normal vectors ( $\mathbf{n}_f$ ) and ( $\mathbf{n}_h$ ) on the  $x,y$ -plane and the lower rows contain the projections of the wing-tip vectors ( $\mathbf{wt}_f$ ) and ( $\mathbf{wt}_h$ ) on the  $x,z$ -plane. Arrows indicate the sense of circulation. For further explanation of data representations see Zarnack (1972) or Schwenne and Zarnack (1987).

During the flight, only the forewing movement patterns changed greatly, especially their pitching (Fig. 2A–D and I–L). The pitching angle  $\alpha$  was calculated from  $\alpha = \arcsine(n_x)$ . The relative lift ( $l_{rel}$ ) was positively correlated to both the minimum angle of pitch ( $\alpha_{min}$ ) and the steady angle of pitch  $\alpha_s = (\alpha_{max} + \alpha_{min})/2$ , but was negatively correlated to the pitching amplitude  $\alpha_o = |(\alpha_{max} - \alpha_{min})/2|$  (Fig. 3A). Changes in the flapping amplitude  $\eta_o = |(\eta_{max} - \eta_{min})/2|$  occurred often but were not correlated to lift production [Fig. 3B, where  $\eta = \arcsine(wt_z)$ ]. A description of Fig. 3C will be given below.

Some individuals (Fig. 4) showed further remarkable variations of forewing lagging because of variations in the phase angles  $\kappa$  (between flap and pitch) and  $\sigma$  (between lagging and pitch; see Discussion). In Fig. 4, 20 wingbeat cycles are superimposed. Note

the small scatter of the movements of both wings in Fig. 4A,B,D,E and the relatively great scatter of the forewing movements in Fig. 4C,F.

Generally, the movement patterns of the hindwings remained almost constant. Sometimes, however, remarkable changes in the wing-tip path did occur (Fig. 5B,D).

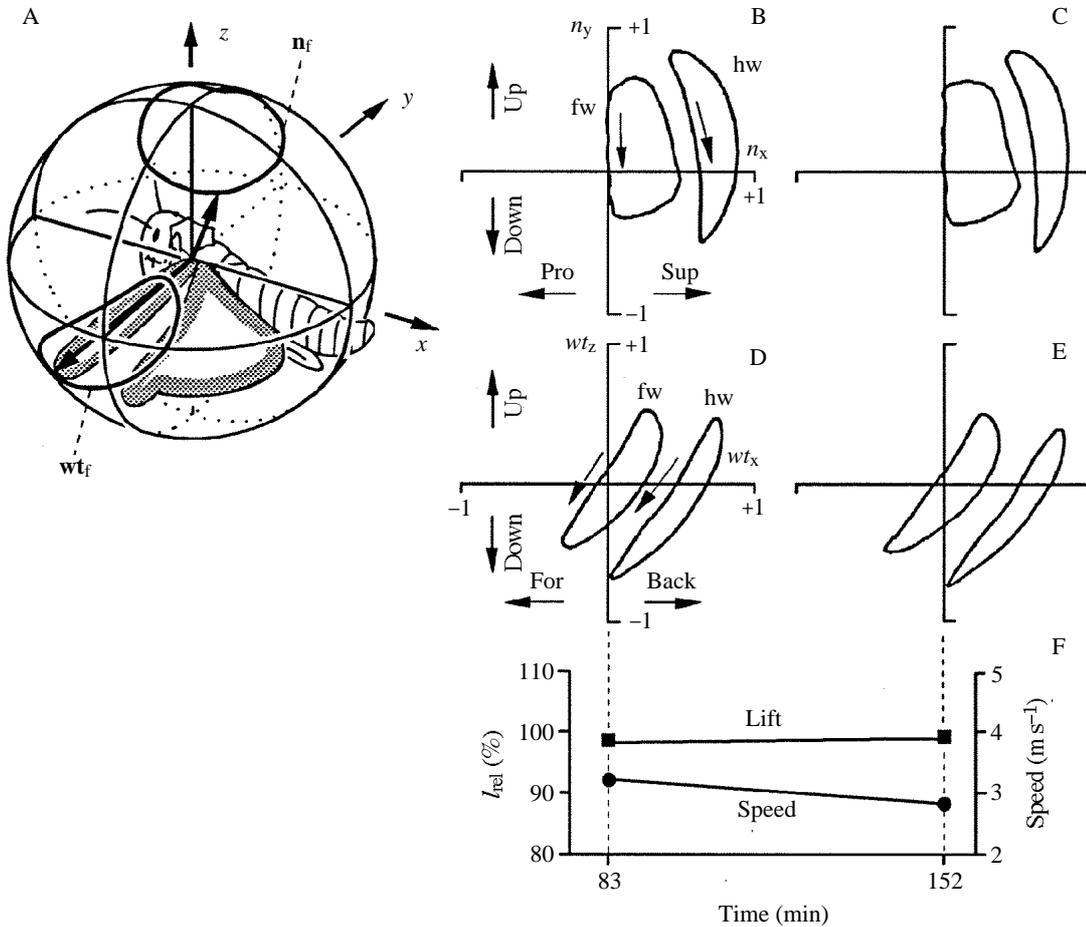


Fig. 1. Relationships between movement patterns of the left wings, lift and flight speed at different times during a continuous flight. The one cycle in each diagram (B-E) represents a coherent series of many very low scattering cycles (see also Fig. 4). (A) Orientation of the locust with respect to the coordinate system ( $x$ ,  $y$ ,  $z$ ; space fixed). The trajectories of the normal vector ( $\mathbf{n}_f$ ) and the wing-tip vector ( $\mathbf{wt}_f$ ) of the left forewing are also shown. (B,C) Projections of the paths of the normal vectors onto the horizontal plane ( $x,y$ -plane) at 83min (B) and 152min (C) into the flight. (D,E) Projections of the wing-tip vectors onto the median plane ( $x,z$ -plane) at 83min (D) and 152min (E) into the flight. All vectors are unit vectors and are always related to the space.  $n_x$  and  $n_y$  indicate the  $x$ - and  $y$ -components of the normal vectors,  $wt_x$  and  $wt_z$  indicate the  $x$ - and  $z$ -components of the wing-tip vectors. Arrows near the traces indicate the sense of circulation. Back, backward; down, downstroke; for, forwards; fw, forewing; hw, hindwing; pro, pronation; sup, supination; up, upstroke. (F) Lift and speed plotted against time. The relationships between the projections and the diagram are indicated by dotted lines. For further explanation see the text.

Phase relationships between forewing and hindwing movements

We observed varying phase relationships between the movements of the forewing and hindwing of the same body side (Fig. 5) which correspond to previously described changes in the relative coordination of the muscles of these wings (see Discussion).

The delay  $\Delta t = t_{S,F} - t_{S,H}$  between the beginning of the forewing downstroke ( $t_{S,F}$ ) and the hindwing downstroke ( $t_{S,H}$ ) changed within the range 0ms to almost 8ms. The

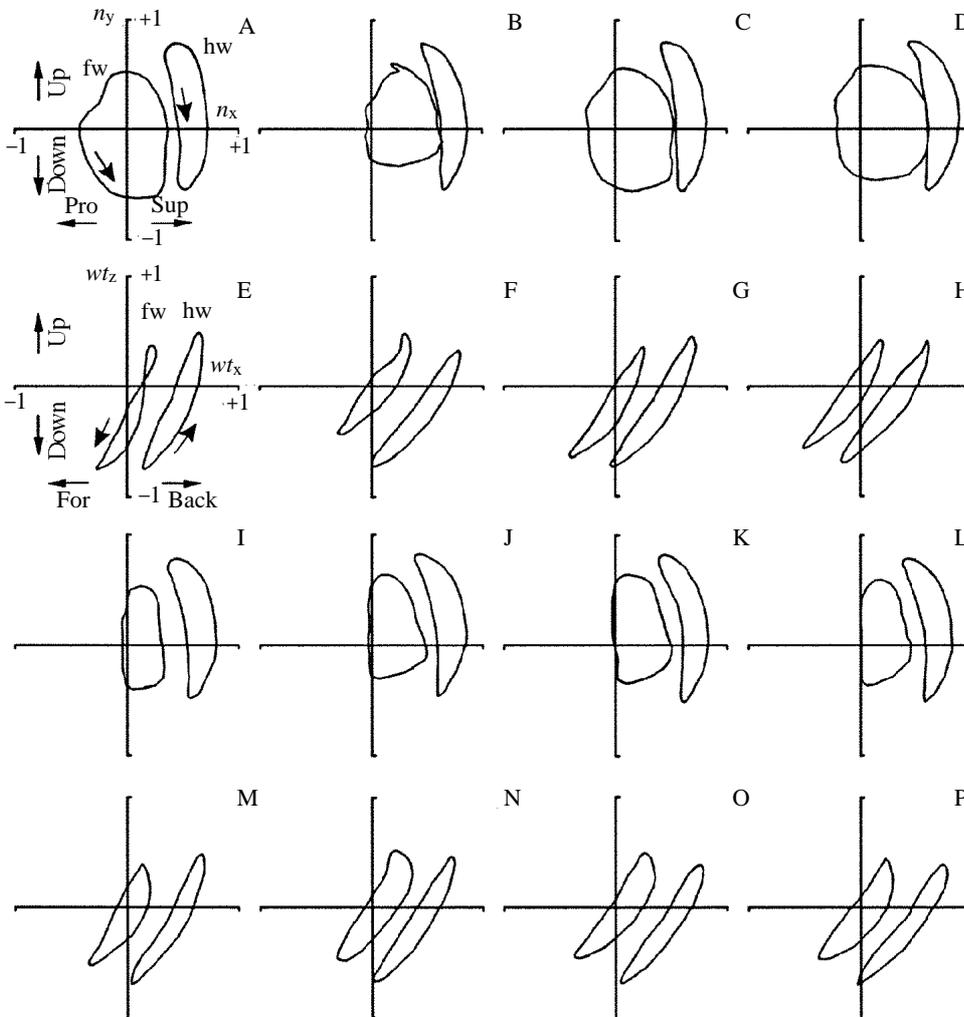


Fig. 2. Dependence of the movement patterns of the left wings on the relative lift ( $l_{rel}$ ), body angle ( $\beta$ ) and flight speed ( $v$ ). The upper rows (A–D, I–L) show the projections of the paths of the normal vectors of the left wings (cf. Fig. 1B,C), whereas the lower rows (E–H, M–P) show the projections of the paths of the wing-tip vectors of the left wings (cf. Fig. 1D,E).  $n_x$  and  $n_y$  indicate the  $x$ - and  $y$ -components of the normal vectors;  $wt_x$  and  $wt_z$  indicate the  $x$ - and  $z$ -components of the wing-tip vectors. Arrows near the traces indicate the sense of circulation. For further explanation, see Fig. 1 and text.

Table 1. Values of relative lift ( $l_{rel}$ ), body angle ( $\beta$ ) and flight velocity ( $v$ ) for the corresponding parts of Fig. 2

Fig. 2	$l_{rel}$ (%)	$\beta$ (degrees)	$v$ (m s <sup>-1</sup> )
A, E	59	7.5	2.7
B, F	67	25	2.1
C, G	83	16	2.5
D, H	84	21	2.3
I, M	89	13	3.0
J, N	89	18	2.9
K, O	98	19.5	3.2
L, P	101	21.5	3.1

forewing usually started the downstroke several milliseconds later than the hindwing, resulting in a positive  $\Delta t$ . Small squares on the trajectories in Fig. 5Ai–Di indicate the start of the forewing downstroke. The delay ( $\Delta t$ ) is indicated by the labelled arrows in Fig. 5Bii, Dii.

The relative lift was 95% when  $\Delta t$  was approximately 6ms (Fig. 5Ci,ii, Di,ii, F). But when forewing and hindwing started the downstroke at the same time ( $\Delta t$  of approximately  $-0.5$ ms),  $l_{rel}$  was 65% (Fig. 5Ai, Bi,ii). We found a positive correlation between  $l_{rel}$  and  $\Delta t$  (Fig. 3C) when all the data of this flight sequence lasting 150min were analysed (cf. Zarnack and Wortmann, 1989, Fig. 3iii).

The cycle duration ( $T_{cyc}$ ) did not change when  $l_{rel}$  changed (Fig. 5E), whereas the quotient of downstroke duration to upstroke duration ( $q_{df}$  and  $q_{dh}$ ) varied for both wings (Fig. 5G,H). Note that the forewing quotient  $q_{df}$  is smaller at the higher value of lift than at the lower one, whereas the hindwing quotient  $q_{dh}$  changed in the opposite way.

### Discussion

In desert locusts that performed straight flight of at least 45min duration, combined measurements of lift, flight speed, body angle and wing movements were made for the first time. We induced variations of lift mainly by adjusting the body angle (cf. Zarnack and Wortmann, 1989) in order to analyse the relationships between lift and the kinematic variables of the wingbeat. Similar studies have previously been undertaken using photogrammetrical methods (Weis-Fogh and Jensen, 1956; Zarnack 1969, 1972, 1983; Cloupeau *et al.* 1979; Dreher and Nachtigall, 1983; Zanker and Götz, 1990). In the following, we will discuss first some features of our methods and then the results.

#### *Method of wingbeat recording*

The electromagnetic method of movement recording had three major advantages over photographic methods: (i) there was no flight distortion by intermittent light or light flashes; (ii) many movement components could be monitored simultaneously on an oscilloscope; and (iii) electrical movements could be recorded continuously for several hours. This allowed the great individual variation of flight performance to be

observed, and the special flight state of an individual could be taken into account during data acquisition. Consequently, it was not necessary to average kinematic data originating in different flight behaviours. Thus, we could achieve relatively clear results (see Fig. 3).

A disadvantage of our data acquisition system was that we could only record four of the eight vectors simultaneously. We were, therefore, not able to analyse the movements of both sides of the body at the same time.

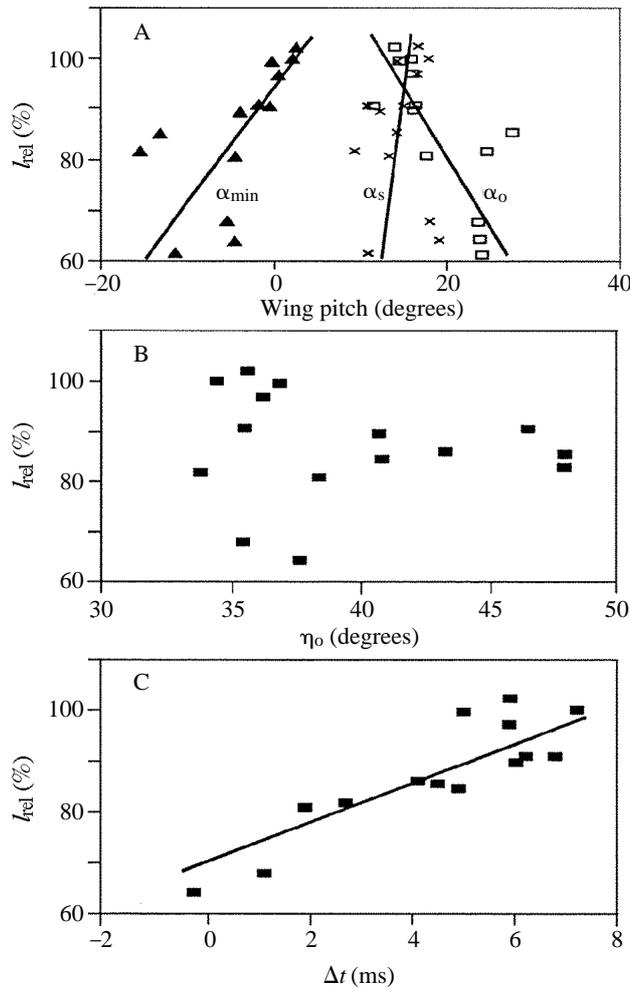


Fig. 3. (A) The dependence of wing pitch on relative lift ( $l_{rel}$ ). Minimum angle of pitch ( $\alpha_{min}$ ), triangles; steady angle of pitch ( $\alpha_s$ ), crosses; pitch amplitude ( $\alpha_o$ ), squares. (B) The dependence of  $l_{rel}$  on the flapping amplitude ( $\eta_o$ ). (C) The dependence of  $l_{rel}$  on the delay of the forewing downstroke ( $\Delta t$ ). When  $\Delta t$  is positive, the hindwing starts the downstroke before the forewing.  $N$  is approximately 200 for each value. The standard deviations are negligible in every case because of the generally small scatter (cf. Fig. 4).

*Results of single wing movements*

Variations in forces and torques are generally related to changes in several kinematic variables in arbitrary combinations (Thüring, 1986; Waldmann and Zarnack, 1988; Schwenne and Zarnack, 1988, 1989; Schwenne, 1990; Reuse, 1991; Wortmann, 1991). In this first quantitative study of the influence of wing movements on lift production, we cannot show all possible correlations that may occur. We have analysed only very steady flight sequences in which (i) changes of lift correspond clearly to changes of one rotative degree of freedom, e.g. pitching, or (ii) in which only a few kinematic variables changed simultaneously, e.g. pitching and the phase relationship between forewing and hindwing movements.

In the flight sequence lasting 150min (approximately 180000 wingbeat cycles), the variation of lift originated less in the variation of hindwing movement variables than those of the forewings. Most prominent were changes in pitching. These findings

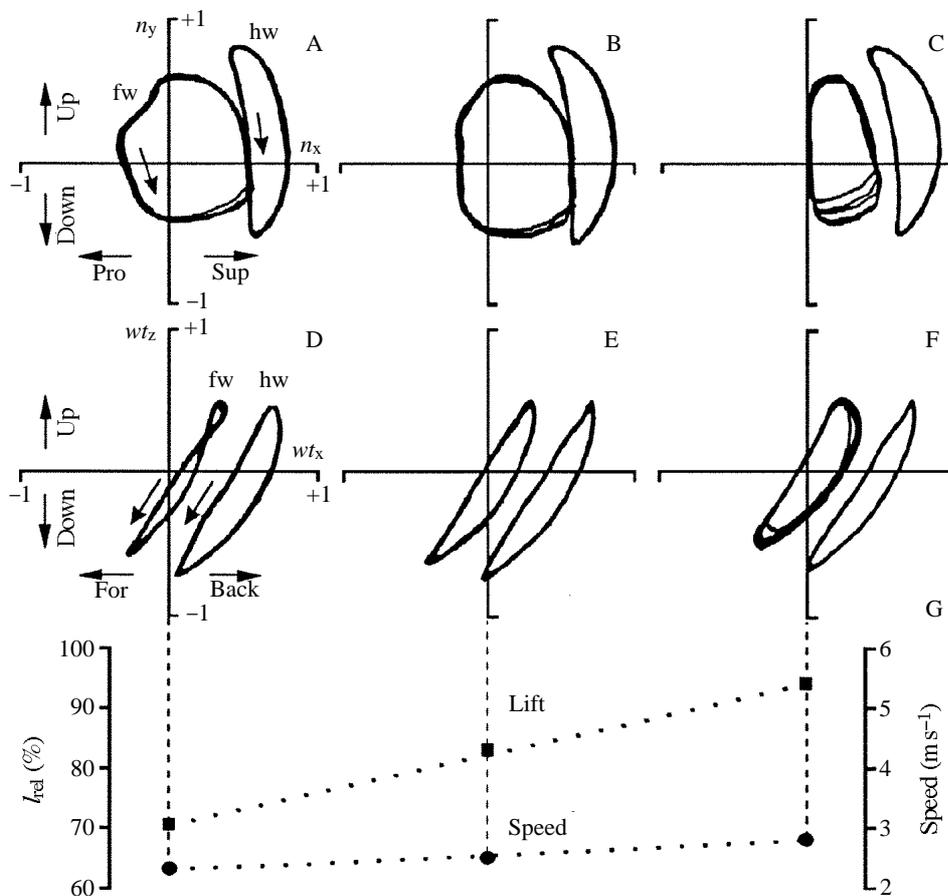


Fig. 4. Dependence of lagging on relative lift and speed. The projections of the paths of the normal vectors (A-C) and of the paths of the wing-tip vectors (D-F, cf. Fig. 1) of the left wings are shown at three values of lift. Twenty cycles of wingbeat are superimposed in each diagram. For further explanation, see Figs 1 and 2 and the text.

correspond to previous reports (Weis-Fogh, 1956; Jensen, 1956; Wilson and Weis-Fogh, 1962; Gettrup and Wilson, 1964; Zarnack, 1969, 1982, 1988). We observed a correlation between lift ( $l_{rel}$ ) and the steady angle of pitch ( $\alpha_s$ ) as well as between  $l_{rel}$  and pitching amplitude ( $\alpha_o$ ) (Fig. 3A); however, the gradients have different signs.

#### *Lift and steady angle of pitch*

There is a more-or-less additive effect of steady and unsteady aerodynamics according to Send's (1992) theory about unsteady aerodynamics (see below). The steady angle of pitch ( $\alpha_s$ ) is the fundamental variable of pitch that affects lift production (Send, 1992, equation 67). The more-or-less linear relationship between  $l_{rel}$  and  $\alpha_s$  (Fig. 3A,  $\alpha_s$ ) is independent of the changing body angle because (i) Table 1 shows, in successive pairs of rows, almost the same  $l_{rel}$  at different body angles ( $\beta$ ); (ii) Fig. 4Giii in Zarnack and Wortmann (1989) shows no linear relationship between these variables. Our result is, therefore, compatible with Send's theory. Note, however, (i) that in our experiments the lift originated from four wings, and (ii) that the reduced frequency ( $\omega^*$ ) is in the range of about 0.15 (forewing) and 0.35 (hindwing) (Zarnack *et al.* 1990). Unsteady aerodynamics should therefore be applied.

#### *Lift and pitching amplitude*

Surprisingly, a decrease of lift was correlated with an increased pitching amplitude. This also seems to be compatible with Send's theory, some features of which will be described here for the convenience of the reader. Extensive explanations and biological applications of the theory will be given by the author himself (W. Send, manuscript in preparation).

Send's linear theory of unsteady aerodynamics offers time-dependent solutions of the powers, forces and moments as well as of the aerodynamic coefficients of lift,  $C_L$ , and drag,  $C_D$ , etc. The theory is based on the kinematics of a rigid body, e.g. an aerofoil or an insect's wing, oscillating in three dimensions: pitching, flapping and lagging. This is an adequate kinematic description of insect flight.

The solutions depend on the reduced frequency  $\omega^*=2fc/2v$  (where  $c$  is the chord length of the wing,  $f$  is the beat frequency and  $v$  is the flight speed) and on eight additional kinematic variables in the case of real harmonic oscillations:

$$\alpha(t) = \alpha_s + \alpha_o \cos(\omega t), \quad (\text{pitching})$$

$$\eta(t) = \eta_s + \eta_o \cos(\omega t + \kappa), \quad (\text{flapping})$$

$$\varphi(t) = \varphi_s + \varphi_o \cos(\omega t + \sigma), \quad (\text{lagging})$$

(where  $\alpha_s$  is the steady angle of attack;  $\eta_s$  and  $\varphi_s$  are the coordinates of the centre of oscillation;  $\alpha_o$ ,  $\eta_o$  and  $\varphi_o$  are the amplitudes;  $\kappa$  and  $\sigma$  are the phase angles relative to pitching; and  $\omega=2\pi f$ ). Higher harmonics can be taken into account.

These nine variables have different aerodynamic effects. In other words, the aerodynamic powers, forces and moments in each dimension of the movements of a single wing are influenced by eight (disregarding  $\omega^*$  and higher harmonics) independent kinematic variables. One should therefore consider at least 32 independent kinematic

variables (not to mention the different and varying wing shapes) when analysing locust flight. Such an analysis has been carried out on roll manoeuvres (Wortmann, 1991).

High power occurs only when the phase angles  $\kappa$  and  $\sigma$  are approximately 90 degrees (Figs 7 and 8 in Send, 1992). These values are always met in the flight of locusts (e.g. Zarnack, 1972, 1982, 1983, 1988; Schwenne and Zarnack, 1987; Waldmann and Zarnack, 1988; this work, Fig. 5Ai, Di), of Diptera (e.g. Fig. 25 in Nachtigall, 1966; Fig. 6 in Zanker, 1990) and of other insects and birds.

Send (1992) pointed out that only a motion of combined flapping and pitching results in thrust, whereas a simple flapping oscillation has no propulsive effect. This implies that a

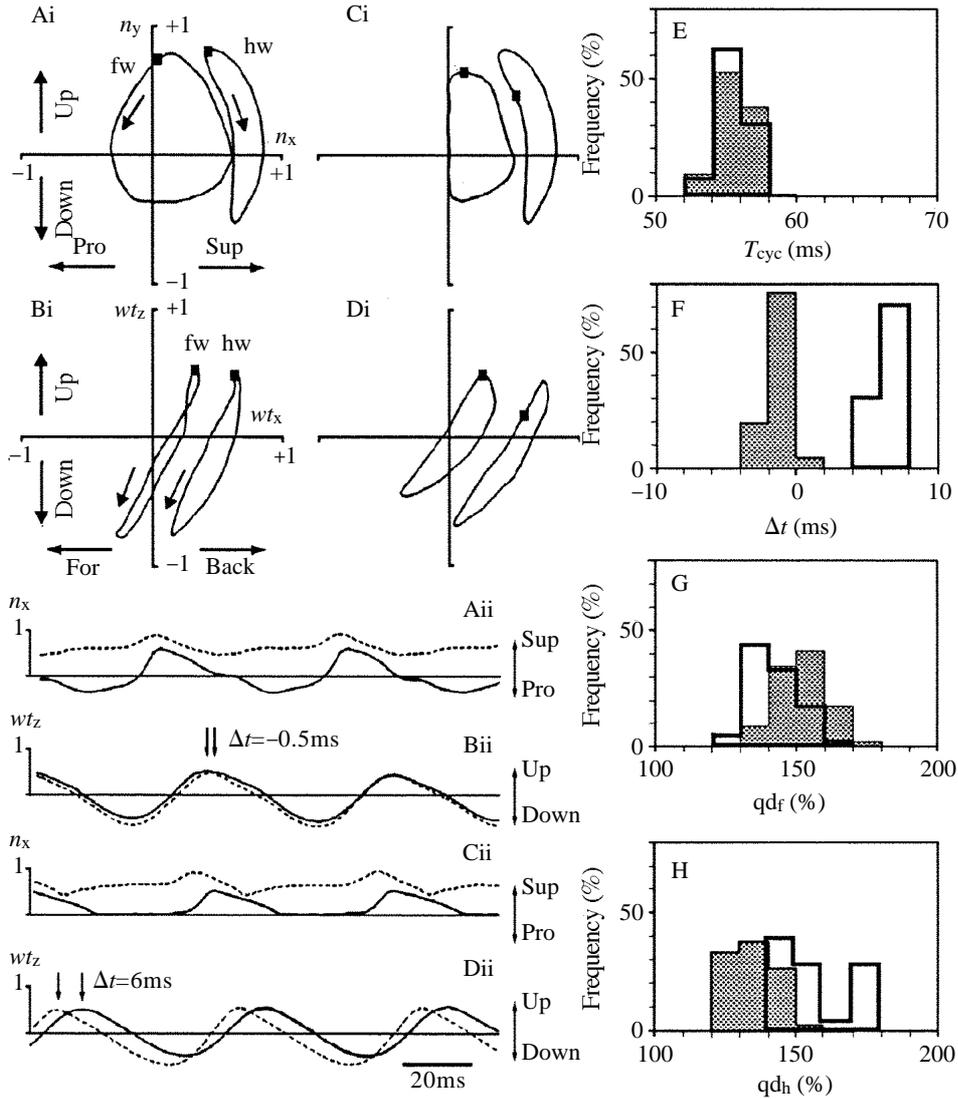


Fig. 5

realistic aerodynamic interpretation of the separate downstroke and upstroke is impossible (W. Send, personal communication), although the vector fields of the kinematic velocities are very different because of the superposition of the translatory and the three-dimensional rotative movement (Zarnack, 1969, 1975). Furthermore, the absolute flapping amplitude is not relevant to lift production (Send, 1992). Our experiments did not show any correlation between lift and flapping amplitude (Fig. 3B). We sometimes found a greater flapping amplitude at a lower lift (approximately 70%) (Fig. 4A,D) than at a greater lift (approximately 95%; Fig. 4C,F).

How could Send's theory explain our finding that a decrease of lift was correlated with an increased pitching amplitude? According to him, the increase in power depends on an increased quotient of flapping amplitude to pitching amplitude, among other parameters (Figs 6–8 in Send, 1992). We have found that the flapping amplitude usually remained almost constant, so the quotient grew because of a decreasing amplitude of pitching. Therefore, our negative correlation between lift and  $\alpha_0$  seems to be compatible with Send's theory.

#### *Further results of single wing movements*

In roll manoeuvres, changes in the forewing movements are most frequent, but Wortmann (1991) has also found long sequences of roll manoeuvres that depend mainly on changes in pitching of one hindwing. A slight increase in lift caused by increasing wingbeat frequency has been reported (Weis-Fogh, 1956, p. 484), but we could find no such correlation in our experiments because the distribution of  $T_{\text{cyc}}$  was the same when  $l_{\text{rel}}$  was approximately 65% and when it was 95% (Fig. 5E).

#### *Phase relationship between forewing and hindwing movements*

According to electrophysiological investigations (Wilson and Weis-Fogh, 1962; Zarnack and Möhl, 1977; Zarnack, 1982, 1988; Schmidt and Zarnack, 1987; Waldmann and Zarnack, 1988) and kinematic studies (Zarnack, 1983), the forewing starts the

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Fig. 5. Time relationships between movements of the forewing and hindwing at different values of relative lift ( $l_{\text{rel}}$ ).  $\Delta t$  is the delay between the start of the forewing downstroke ( $t_{\text{S,F}}$ ) and the start of the hindwing downstroke ( $t_{\text{S,H}}$ ):  $\Delta t = t_{\text{S,F}} - t_{\text{S,H}}$ . When  $\Delta t > 0$ , the hindwing leads the forewing. (Ai–Di) Projections of the paths of the normal vectors (Ai,Ci) and the paths of the wing-tip vectors (Bi,Di) of the left wings. Small squares on the traces indicate the same point in time for the four traces in Ai and Bi and for the four traces in Ci and Di. Thus, a delay  $\Delta t$  of approximately 6ms is visible in the pair Ci, Di. (Ai–Di) Time functions of wing pitch (represented by the component  $n_x$ ) and flapping (represented by the component  $wt_z$ ) at a relative lift ( $l_{\text{rel}}$ ) of 65%, body angle ( $\beta$ ) of  $18^\circ$  and flight speed ( $v$ ) of  $2.3 \text{ ms}^{-1}$  (Aii,Bii) and at a ( $l_{\text{rel}}$ ) of 95%, ( $\beta$ ) of  $18^\circ$  and ( $v$ ) of  $2.9 \text{ ms}^{-1}$  (Cii,Dii). Arrows indicate a  $\Delta t$  of approximately  $-0.5 \text{ ms}$  (synchronous downstroke) in Bii and a  $\Delta t$  of approximately 6ms (delayed forewing downstroke) in Dii. Solid lines represent forewing data and dotted lines represent hindwing data.  $n_x$  and  $n_y$  indicate the  $x$ - and  $y$ -components of the normal vectors,  $wt_x$  and  $wt_z$  indicate the  $x$ - and  $z$ -components of the wing-tip vectors. (E–H) Frequency histograms ( $N=210$ ) of cycle duration ( $T_{\text{cyc}}$ ) (E), delay ( $\Delta t$ ) (F), quotient of downstroke duration to upstroke duration ( $q_{\text{d}_f}$ ) of the forewing (G) and  $q_{\text{d}_h}$  of the hindwing (H). Solid outlines represent data at the higher lift (95%); stippled areas represent data at the lower lift (65%). For further explanation, see Fig. 1 and the text.

downstroke after the hindwing (Wortmann and Zarnack, 1987). The delay ( $\Delta t$ ) varied, depending on lift, within the range 0ms to almost 8ms (Fig. 3C), i.e. a corresponding phase angle would change in the range  $0^\circ$  (at  $I_{rel}$  of approximately 70%) and  $60^\circ$  (at  $I_{rel}$  of approximately 100%).

The changing delay ( $\Delta t$ ) corresponds to a varying gap between both wings of one side during the downstroke (Fig. 5Di). The gap was smallest at low lift production. The gap influences the aerodynamic flow. The idea that locusts could steer by adjusting this gap as has already been discussed (Zarnack, 1983). Until now, however, we have had no aerodynamic explanation for the phenomenon.

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