

RELATIONSHIPS BETWEEN BODY MASS, MOTOR OUTPUT AND FLIGHT VARIABLES DURING FREE FLIGHT OF JUVENILE AND MATURE ADULT LOCUSTS, *SCHISTOCERCA GREGARIA*

HANNO FISCHER^{1,*} AND WOLFRAM KUTSCH²

¹*School of Biology, Division of Biomedical Sciences, Bute Medical Building, University of St Andrews, Fife KY16 9TS, Scotland* and ²*Fachbereich Biologie, Universität Konstanz, 78457 Konstanz, Germany*

*e-mail: hf4@st-andrews.ac.uk

Accepted 23 June; published on WWW 22 August 2000

Summary

Little information is available about how the adult locust flight system manages to match the aerodynamic demands that result from an increase in body mass during postmoult maturation. In *Schistocerca gregaria* of both sexes, flight variables, including flight speed, ascent angle and body angle, were investigated under closed-loop conditions (i.e. during free flight) as a function of adult maturation. Motor patterns were examined by telemetric electromyography in juvenile and adult mature animals of both sexes. Functional relationships between particular flight variables were investigated by additional loading of the animals and by reductions in wing area. The results indicate that an increase in flight speed as the flight system

matures enables it to match the aerodynamic demands resulting from increases in body mass. Furthermore, the data suggest that this postmoult increase in flight speed is not simply a consequence of the increase in wingbeat frequency observed during maturation. The instantaneous body angle during flight is controlled mainly by aerodynamic output from the wings. In addition, the mean body angle decreases during maturation in both sexes, and this may play an important part in the directional control of the resultant flight force vector.

Key words: locust, free flight, postmoult maturation, flight behaviour, telemetry, *Schistocerca gregaria*.

Introduction

During flapping flight of insects such as locusts, the functional task of the flight motor system is the generation of a motor pattern providing an aerodynamic output sufficient to support the body weight during flight. The pattern for alternating wing depression and elevation during flapping flight is generated by a neuronal oscillator (e.g. Wilson and Weis-Fogh, 1962; Delcomyn, 1980; Robertson and Pearson, 1985; Stevenson and Kutsch, 1987) that is controlled by sensory information from wing-related or head-located sense organs (e.g. Wendler, 1974; Gewecke, 1975; Möhl, 1985; Pearson and Wolf, 1987; Reye and Pearson, 1988; Wolf and Pearson, 1988; Fischer and Ebert, 1999).

In locusts, the hemi-metabolous development to the imago involves five non-flying larval stages and is characterised not only by an increase in body length but also by a large increase in body mass (Phipps, 1950; Cheu, 1952). After final ecdysis, the adult juvenile locust continues accumulating body mass up to maturation; however, there is no further increase in body size. Furthermore, the body mass of adult mature locusts exhibits considerable fluctuations, in particular for females after oviposition. However, as reported from field studies, locusts are capable of free flight from the second day of adult life and maintain this flight capability throughout the complete

adult life span, apparently independent of age and body mass (Kennedy, 1952). This suggests that the motor output of the adult locust flight system is somehow adjusted to the developmental stage during adult ontogeny, i.e. to the required increase in lift production during flight that is demanded by an increasing body mass. In previous studies involving animals flying either tethered or suspended on a flight balance, changes in particular flight variables, such as wingbeat frequency and flight speed, were observed to change coincidentally with adult age (Kutsch, 1971, 1973; Gewecke and Kutsch, 1979; Kutsch and Gewecke, 1979).

There is, however, little information about (i) how the motor output of the locust flight system depends on body mass, (ii) which free-flight variables are influenced by the body mass and change accordingly as body mass increases, and (iii) how, in terms of behaviour, the locust flight system might 'balance' a large increase in body mass such as that observed during adult maturation.

To understand more about the functional implications of such morphological changes in relation to motor output and flight behaviour in maturing adult locusts, we investigated changes in flight variables in relation to body mass during adult maturation. We manipulated, reproducibly, the body mass of

individuals and investigated the resulting changes in motor output and flight variables under free-flight conditions. Functional relationships between particular flight variables that changed during maturation were also investigated after partial wing reductions.

Materials and methods

Animals and flight conditions

All experiments were carried out using male and female desert locusts *Schistocerca gregaria* Forskål. The animals were bred at 42 °C and 70 % relative humidity in crowded colonies of both sexes. Maturation occurred on average 18 days after final ecdysis (determined by observations of copulating pairs). Individual flight sequences were investigated in a room measuring 10 m × 5.5 m × 2.2 m at a temperature of 34 °C. The average illumination of the room was 4500 lx. After an initial warming to 40 °C, each animal was placed on a platform. For the majority of animals, flight activity started either with the animal jumping spontaneously or with a jump in response to hand-clapping or to a short puff of wind to the cerci. When jumping could not be elicited, flight was initiated by launching the animal vertically into the air (speed at release from the hands 2–3 m s⁻¹). To avoid any residual effects of the jump and the launch during the observations, the platform and the point of launch were 5 m in front of the observation area (see also Fischer and Kutsch, 1999).

Telemetric electromyography

For acquisition of electromyographs (EMGs) during free locust flight, one-channel radiotelemetry was used. The mass of the device was 0.3 g including the power supply. For a detailed description of the transmitter, attachment of the device to the animal and the receiver system used, see Fischer (1998) and Fischer and Ebert (1999). The metathoracic subalar wing depressor muscle (M129, muscle nomenclature according to Snodgrass, 1929) was recorded using low-resistance electrode wires (Manganin, Dillenburg, Germany; 50 µm in diameter).

Morphological variables

The individual body length (in mm) was measured and the individual body mass m (in g) was determined before or after flight by weighing. The term m^* indicates the body mass including any additional loading (see following section) and/or the mass of the transmitter. For each individual investigated, the wing area A_w (in cm²) was measured by weighing the clipped wings after the experiments. The remaining wing area, after partial reduction of the fore- and the hindwing as well as of both wings, was determined in a similar manner after the flight experiments. After determining the body mass of freshly killed individuals, the proportion of the flight muscle mass (as a percentage of the body mass) was determined by the mass difference between the isolated pterothorax, including the flight musculature, and the mass of the same thorax after maceration in KOH. For additional loading of the animals, small lead balls (Fischerei Zubehör, Germany) were flattened

and fixed onto the pronotum of the experimental animal using beeswax.

Video recordings

The free-flight sequences of individual male and female locusts were recorded using a stationary video camera (Panasonic NV-MS4EG; frame frequency 50 Hz, shuttering time 1 ms). If telemetric EMG recording was performed synchronously, the EMGs were displayed on an oscilloscope (Tektronix D11) and stored on tape (Racal Store 4DS). The oscilloscope screen was filmed by a second video camera (Revue Video 8, frame frequency 50 Hz, frame interval 20 ms). The video outputs of both cameras were mixed online by a Panasonic digital mixer (WJ-AVE5) and recorded on a video master tape.

In a different approach, the flights of 12-day-old adult females were recorded by digital high-speed video (maximum frame frequency 500 Hz, shuttering time 750 µs; Weinberger Systems, Switzerland) for resolution of the instantaneous forewing angle of attack α (in degrees) in relation to the longitudinal body axis (in degrees). In accordance with Wolf (1990), the values obtained were transformed with reference to the parallax (for a description of the measurement errors, see Fischer, 1998).

Data evaluation

The video recordings were screened on a 27 inch Sony Trinitron colour video monitor. Flight variables were acquired by frame-by-frame analysis (Panasonic digital video recorder AG7355) of the continuous displacement of the body silhouettes transferred to overhead transparencies (for methods, see Baker and Cooter, 1979; Baker et al., 1981). For a detailed evaluation of the measurement errors with respect to silhouette length and flight variables, see van der Wall (1996). All variables are considered as 'instantaneous' flight variables since they were constant within the given frame interval.

Free-flight variables

The following behavioural variables were investigated during free translatory movement of an animal: (a) ascent angle (χ) with respect to the horizontal (degrees) (i.e. vertical flight path); (b) body angle (ϕ) with respect to the horizontal (degrees) and (c) flight speed (v , m s⁻¹). According to Fischer and Ebert (1999), flight capability is defined as the ability to maintain continuous level flight (i.e. $\chi \geq 0^\circ$), indicating that a particular animal is able to generate sufficient lifting power to support its body weight. During free flight, the aerodynamic output of the flight system is dependent on the ascent angle χ and can be monitored as the instantaneous effective lifting power P_{EL} (in W), calculated as:

$$P_{EL} = mgv \sin \chi,$$

where m is the body mass (in kg), g is the gravitational constant (9.81 m s⁻²), v is the instantaneous flight speed and χ is the instantaneous ascent angle. Instantaneous wingbeat frequency (f_{WB} , in Hz) was calculated from the cycle lengths (in ms) by

evaluating telemetric EMG recordings (see Fig. 1C). The stroke plane inclination of the wings was evaluated from high-speed video recordings and determined by superimposing body silhouettes of consecutive frames. The instantaneous forewing angle of attack (α) was determined from the wing profiles by spatial geometry after Wolf (1990, 1993).

Statistical analyses

Data analysis and statistical procedures were computer-aided (software KaleidaGraph, StatView and Origin) and follow the criteria described by Sachs (1978). Correlation and linear regressions were performed at a significance level of $P < 0.05$, with r indicating the linear coefficient of regression. The statistical significance of non-linear regressions of data is given by the coefficient of determination, r^2 , at a significance level of $P < 0.05$. Unless stated otherwise, results are presented as means \pm S.D.

Results

Body mass and flight speed of the maturing adult flight system

Ten male and ten female locusts from a colony cage with approximately 150 individuals of both sexes were individually labelled and kept isolated by a mesh inset cage. The body mass of each labelled individual was determined daily starting with the first day after the final ecdysis. Maturation was determined by the observation of copulating couples. In the adult females investigated, relative body mass increased on average by $208 \pm 11\%$ during maturation ($N=10$). For adult males, an average increase of $149 \pm 8\%$ was observed before maturity. In the animals tested, maturation occurred, on average, 18 ± 1 days postmoult ($N=10$). In a different group of 25 males and 25 females, postmoult wing area did not change significantly in either sex ($P > 0.05$, data not shown), indicating that there is a significant increase in wing loading L_w during the adult life span: for males, L_w increased from 5.1 ± 1 to $7.4 \pm 0.6 \text{ N m}^{-2}$ ($N=10$); wing loading increased from 4.9 ± 0.8 to $11.3 \pm 0.7 \text{ N m}^{-2}$ ($P < 0.05$, $N=10$) in females. In general, L_w increased by $0.01 \text{ N m}^{-2} \text{ day}^{-1}$ in males and by $0.24 \text{ N m}^{-2} \text{ day}^{-1}$ in females (data not shown).

In a further set of experiments, 10 adult females and 10 adult males were separated from the colony on the first day after final ecdysis and kept isolated by a mesh cage inset. Starting 5 days postmoult, free-flight experiments were carried out at 5-day intervals, and the mean flight speed was determined. Before the experiments began, the body mass of each individual tested was measured, and the animals were returned to the cage after flight. The results are shown in Fig. 1A. In both sexes, flight speed was significantly correlated with body mass ($P < 0.05$), both increasing over the adult life span. The mean flight speeds of males and females were not significantly different for the first 15 days postmoult ($P > 0.05$); however, the mean flight speed of females was significantly higher after maturation than that of the males ($P < 0.05$). The slopes of the regression lines in Fig. 1A indicate the mean increase in flight speed per gram body mass accumulated. There was no significant difference

between the slopes ($P > 0.05$): the increase in flight speed was $2.04 \text{ m s}^{-1} \text{ g}^{-1}$ body mass in males and $2.06 \text{ m s}^{-1} \text{ g}^{-1}$ in females.

Is an increase in flight speed functionally required by an increase in body mass? To answer this question, we set up a different experiment, in which 15 adult females (16–18 days postmoult, mean body mass $2.8 \pm 0.6 \text{ g}$) were additionally loaded with flattened lead attached to the pronotum. For each animal, 5–7 flight sequences from two experimental flights were evaluated. In the first flight, seven animals started flying with the additional mass attached, and this was then removed for the second flight. The remaining eight animals underwent the same procedure in reverse. The results are shown in Fig. 1B. In 11 of the 15 (i.e. in 73%) locusts tested, flight speed was significantly increased when flying under loaded conditions. The average increase in flight speed as a function of body mass was $0.0236 \text{ m s}^{-1} \%^{-1}$ mass increase ($r=0.57$, $N=31$, $P < 0.05$), indicating that loading the females by 1 g would result in an increase in flight speed of 0.83 m s^{-1} .

Body mass and wingbeat frequency of the maturing adult flight system

In these experiments, 40 females and 40 males were separated from the colony immediately after the final ecdysis. At intervals of 5 days and starting on the fifth day after final ecdysis, the average wingbeat frequency f_{WB} was measured in eight males and eight females by radiotelemetric EMG recordings at 34°C . For a representative 5-day-old and 20-day-old animal of either sex, the activity of the subalar depressor M129 during free flight is shown in Fig. 1C; the increase in wingbeat frequency observed over maturation is highlighted by a grey shaded area. The body mass m^* (including the transmitter mass, which averaged 0.3 g) of each individual tested was determined before the experiment.

In both sexes, f_{WB} was significantly correlated with m^* during maturation ($P < 0.05$, Fig. 1D). f_{WB} in males was significantly higher than in females throughout maturation ($P > 0.05$). The mean increase in f_{WB} was 4 Hz g^{-1} body mass in females and 6 Hz g^{-1} in males; however, the slopes of the regression lines were not significantly different ($P > 0.05$). To investigate whether an increase in f_{WB} is functionally related to an increase in body mass, 12 adult females (16–18 days postmoult, mean body mass $2.9 \pm 0.7 \text{ g}$) were loaded at the pronotum in addition to the transmitter. For each animal, f_{WB} in 15–20 consecutive wingbeat cycles of 5–7 flight sequences from two flight attempts was evaluated. In the first attempt, six animals started flying with the additional mass attached; this was then removed for the second attempt. The remaining six animals were tested without additional load and were then loaded in the second set of experiments. The results are shown in Fig. 1E. In 25%, i.e. in three of the 12 individuals tested, f_{WB} increased significantly ($P < 0.05$); in another 25%, f_{WB} decreased significantly after loading. However, in the remaining six animals, i.e. in 50% of the locusts investigated, there was no significant change in f_{WB} ($P > 0.05$). This indicates that, unlike flight speed, wingbeat frequency does not appear to be strongly affected by acute changes in body mass.

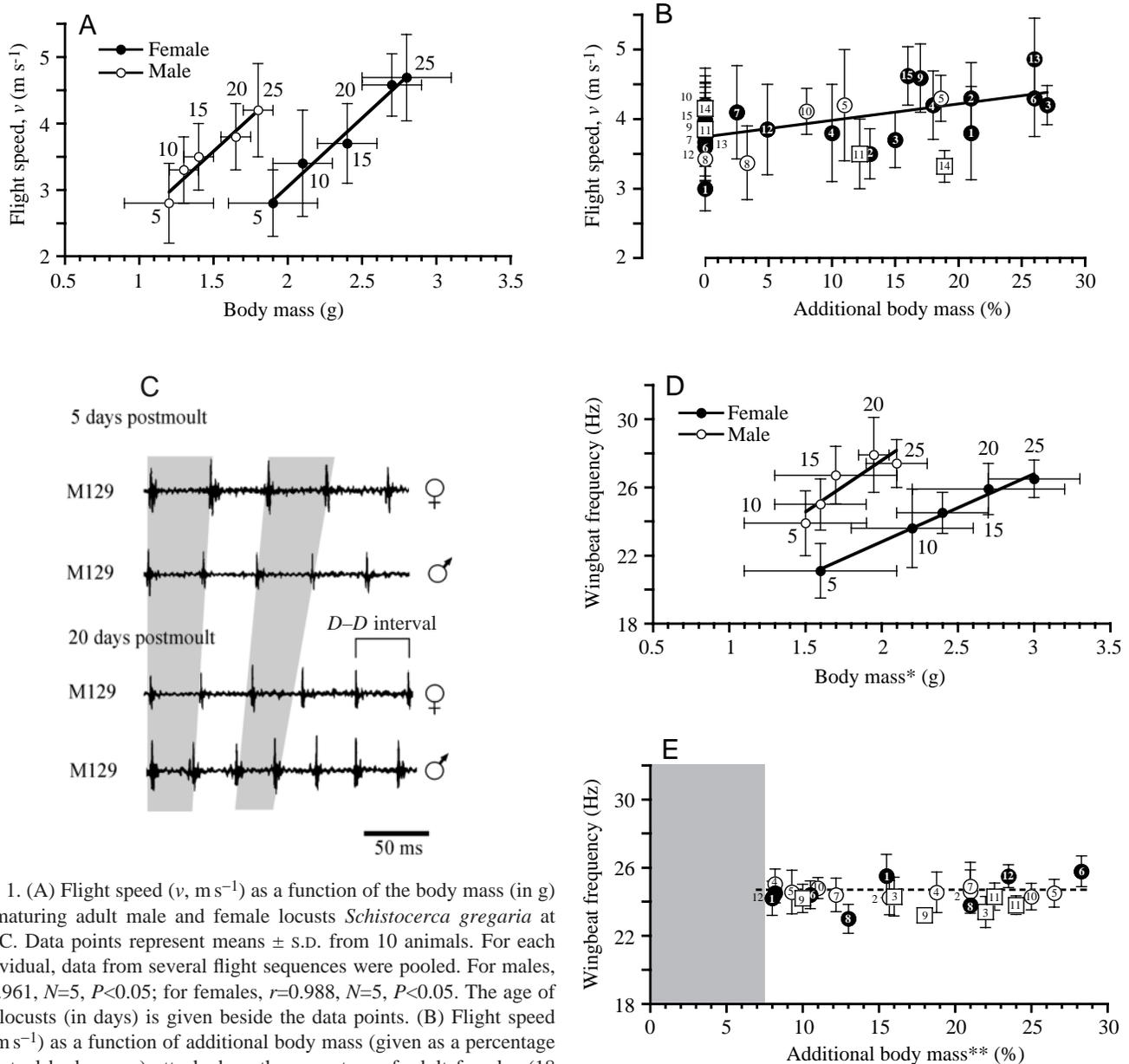


Fig. 1. (A) Flight speed (v , m s^{-1}) as a function of the body mass (in g) of maturing adult male and female locusts *Schistocerca gregaria* at 34°C . Data points represent means \pm s.d. from 10 animals. For each individual, data from several flight sequences were pooled. For males, $r=0.961$, $N=5$, $P<0.05$; for females, $r=0.988$, $N=5$, $P<0.05$. The age of the locusts (in days) is given beside the data points. (B) Flight speed (v , m s^{-1}) as a function of additional body mass (given as a percentage of actual body mass) attached on the pronotum of adult females (18 days postmoult, numbered 1–15, each of which performed flights under loaded and unloaded conditions) flying at 34°C . Data points represent means \pm s.d.; for each individual, the data from several flight sequences were pooled. Filled circles indicate animals with a significantly increased flight speed after loading. Open circles indicate individuals in which no significant change in flight speed was observed, whereas animals in which flight speed decreased significantly after loading are indicated by open squares. Data were pooled to obtain a mean slope and intercept ($r=0.573$, $N=30$, $P<0.05$). (C) Telemetric electromyographic recordings of the hindwing subalar depressor muscle (M129) during free flight of adult males and females 5 days and 20 days postmoult. Shaded areas indicate the general decrease in cycle length, i.e. in the depressor–depressor (D – D) intervals, during adult maturation. (D) Wingbeat frequency (f_{WB} , in Hz) as a function of body mass (g, including the transmitter mass as indicated by *) of adult male and female locusts. For females, $r=0.994$, $N=5$, $P<0.05$; for males, $r=0.892$, $N=5$, $P<0.05$. Data are presented as means \pm s.d. pooled from eight animals. (E) Wingbeat frequency, f_{WB} , as a function of the additional body mass (%) attached on the pronotum (18 days postmoult, locusts numbered 1–12, load including the transmitter, indicated by **). The dashed line indicates no significant correlation between f_{WB} and additional body mass ($N=24$, $P>0.05$). Filled circles indicate animals in which f_{WB} increased significantly after loading. A significant decrease in f_{WB} is indicated by open squares, whereas open circles represent animals in which f_{WB} did not change after loading. The systematic increase of, on average, 8% in locust body mass caused by transmitter attachment is indicated by the shaded area.

The relationships between the free-flight variables investigated are summarised in Table 1. In general, a wide range of ascent angles was observed for the individuals tested

($0^\circ<\chi<60^\circ$). The distribution of χ was not significantly different either between the sexes or between the maturation stages ($P<0.05$). In the majority of animals investigated,

Table 1. Relationships between free-flight variables in maturing adult male and female locusts *Schistocerca gregaria* at 34 °C

Age (days)	Sex	ϕ versus χ	v versus χ	ϕ versus v	fWB versus χ	fWB versus v	fWB versus ϕ
5	F	$r=0.90$	NS ¹	NS	NS ²	NS ³	NS ³
	M	$r=0.97$	$r=-0.20$	NS ⁴	NS ⁵	NS	NS
10	F	$r=0.91$	$r=0.18$	NS	NS ⁶	NS ⁷	NS
	M	$r=0.92$	NS ⁸	NS	NS ⁹	$r=0.23$	NS
15	F	$r=0.95$	NS ¹⁰	NS	NS ¹¹	NS ¹²	NS
	M	$r=0.96$	NS ¹³	NS	$r=0.26$	NS ¹⁴	$r=0.23$
20	F	$r=0.97$	$r=0.29$	$r=0.32$	NS ¹⁵	NS ¹⁶	NS
	M	$r=0.93$	$r=-0.31$	$r=-0.28$	NS ¹⁷	NS ¹⁸	NS
25	F	$r=0.96$	NS ¹⁹	NS	NS	NS ²⁰	NS
	M	$r=0.98$	NS ²¹	NS	$r=0.28$	$r=0.19$	$r=0.22$

¹2 ♀(+); ²2 ♀(+), ♂(-); ³3 ♀(+); ⁴4 ♂(-); ⁵3 ♂(-), ♂(+); ⁶3 ♀(+), ♀(-); ⁷4 ♀(+); ⁸2 ♂(+), 2 ♂(-); ⁹3 ♂(-); ¹⁰4 ♀(+), 2 ♀(-); ¹¹3 ♀(+), 4 ♀(-); ¹²4 ♂(-); ¹³3 ♂(+), 3 ♂(-); ¹⁴3 ♂(+); ¹⁵3 ♀(+); ¹⁶2 ♀(+); ¹⁷3 ♂(+); ¹⁸2 ♂(+); ¹⁹3 ♀(+), 2 ♀(-); ²⁰3 ♀(+); ²¹4 ♂(+), 3 ♂(-).

Relationships between flight speed (v), ascent angle (χ) and body angle (ϕ) were investigated in 10 animals per sex and stage; for wingbeat frequency (fWB), v and ϕ , eight locusts were tested.

r , mean linear correlation coefficient ($P<0.05$): $r>0$, indicates a positive correlation and $r<0$ a negative correlation between the variables tested.

NS, no significant correlation.

Individual relationships are given the footnote; numbers preceding the sex indicate the number of individuals, (+) indicates a positive and (-) a negative correlation ($P<0.05$).

wingbeat frequency and flight speed did not change significantly as a function of ascent angle (Table 1).

Aerodynamic output of the maturing adult flight system

The non-linear characteristics of the maximum effective lifting power, $P_{EL,max}$, measured during adult maturation as a function of the ascent angle χ in 10 males and 10 females are shown in Fig. 2A,B. The maximum effective lifting power, $P_{EL,max}$, is the effective additional lifting power generated during the transition from horizontal ($\chi=0^\circ$) to climbing ($\chi>0^\circ$) flight. The increase in $P_{EL,max}$ that occurs during maturation is not only a result of the increase in body mass but is also achieved by the maturational increases in flight speed.

The proportion of the flight muscle mass as a function of body mass during adult maturation is shown in Fig. 2C. For males, flight muscle proportion was maximal 5 days postmoult, while in females it was maximal at 10 days postmoult. During the first 15 days postmoult, flight muscle mass proportion did not differ significantly between males and females ($P>0.05$); however, after maturation the proportion of the flight muscle mass was significantly higher in males than in females ($P<0.05$, $N=10$).

Body angle during free flight of maturing adult locusts

The body angle ϕ as a function of the ascent angle χ was investigated in 10 males and 10 females during adult maturation. In both sexes, sampling was first carried out 5 days postmoult, and measurements were then performed at 5 day intervals at 34 °C to provide the results shown in Fig. 3. Fig. 3A illustrates locust body silhouettes at three different body angles to the horizontal (the drawing was reconstructed from video recordings). In general, body angle was correlated with ascent angle during climbing flight in each of the

individuals investigated, irrespective of sex and stage of maturation ($P<0.05$; for mean relationships for the gender-specific groups see Table 1). However, in both males and females, mean ϕ decreased significantly with an increase in body mass during adult maturation ($P<0.05$, Fig. 3B), and the slopes of the regression lines obtained for the two sexes were not significantly different ($P>0.05$). A comparison between the body angles of 5-day and 20-day postmoult females as a function of ascent angle is given in Fig. 3C, which shows that mature females exhibit significantly lower body angles during flight than do immature females ($P<0.05$). A similar result was found for males ($P<0.05$, data not shown). This result led us to consider whether a decrease in body angle is functionally related to an increase in body mass.

To investigate this, the instantaneous body angle ϕ was determined as a function of the ascent angle in 10 female locusts (15 days postmoult). In five animals, loads that averaged 10% of body mass (and represented the average increase in body mass occurring between 15 and 20 days postmoult) were attached on the pronotum after control flights. For the remaining five animals, the control flights were performed after flights under loaded conditions. The results showed that, in loaded animals, ϕ decreased significantly compared with that observed in control flights (Fig. 3D, systematic difference: $\Delta\phi=11.8\pm 8^\circ$, $N=10$, $P<0.05$) and that the decrease in ϕ was comparable with that observed in relation to the natural increase in body mass in females (see Fig. 3C).

Body angle and ascent angle with respect to wing area

Preliminary experiments revealed that, 18 days postmoult, females lost their free-flight capability (i.e. the ability to support their body weight during flight, as indicated by ascent angles below 0°) after a reduction (i) of the forewing area by

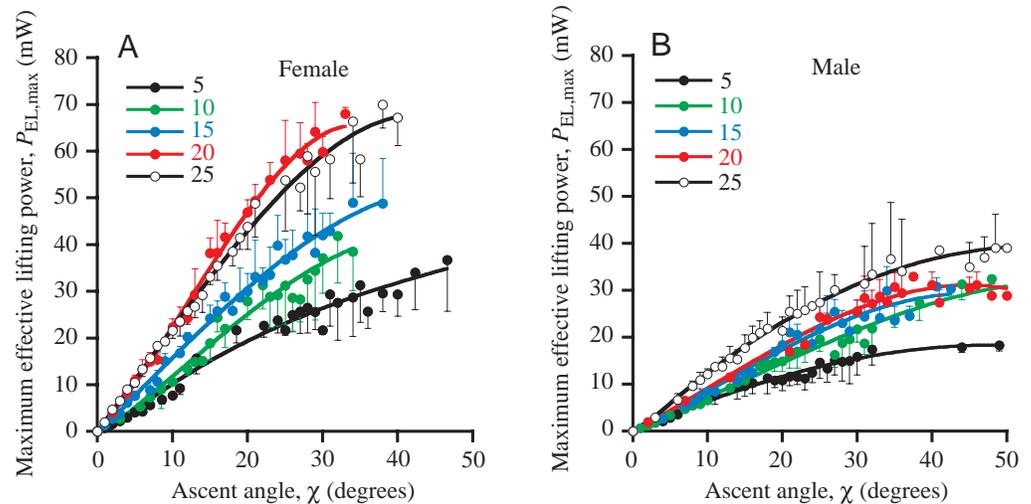


Fig. 2. (A,B) Maximum effective lifting power $P_{EL,max}$ as a function of ascent angle χ in maturing female (A) and male (B) locusts flying at 34 °C. Data points at each stage of maturation (age is given in days in the insets) represent means \pm s.d. obtained for a given χ and pooled from 10 animals that each performed 3–5 flight sequences. All curve fits are significant ($P < 0.01$), values of r^2 in A and B ranging from 0.958 (males 15 days postmoult, $N=28$) to 0.993 (females 20 days postmoult, $N=23$). (C) Mass proportion of the pterothoracic flight muscles as a function of body mass during maturation of adult male and female *Schistocerca gregaria*. Day 0 indicates the day of final ecdysis; maturation occurred between days 16 and 18 postmoult. Data represent means \pm s.d. pooled from 10 animals. Asterisks indicate mean values that are significantly different between males and females.

more than 20% ($N=15$), (ii) of the hindwing area by more than 25% ($N=12$), or (iii) of both forewing and hindwing area by more than 27% of the gross area ($N=10$, data not shown). After control flights, in three groups each containing 10 female locusts (18 days postmoult), the gross area of the wing pairs was reduced by 13% by reduction of (i) the forewing pair, (ii) the hindwing pair and (iii) both wing pairs in equal proportion (Fig. 4).

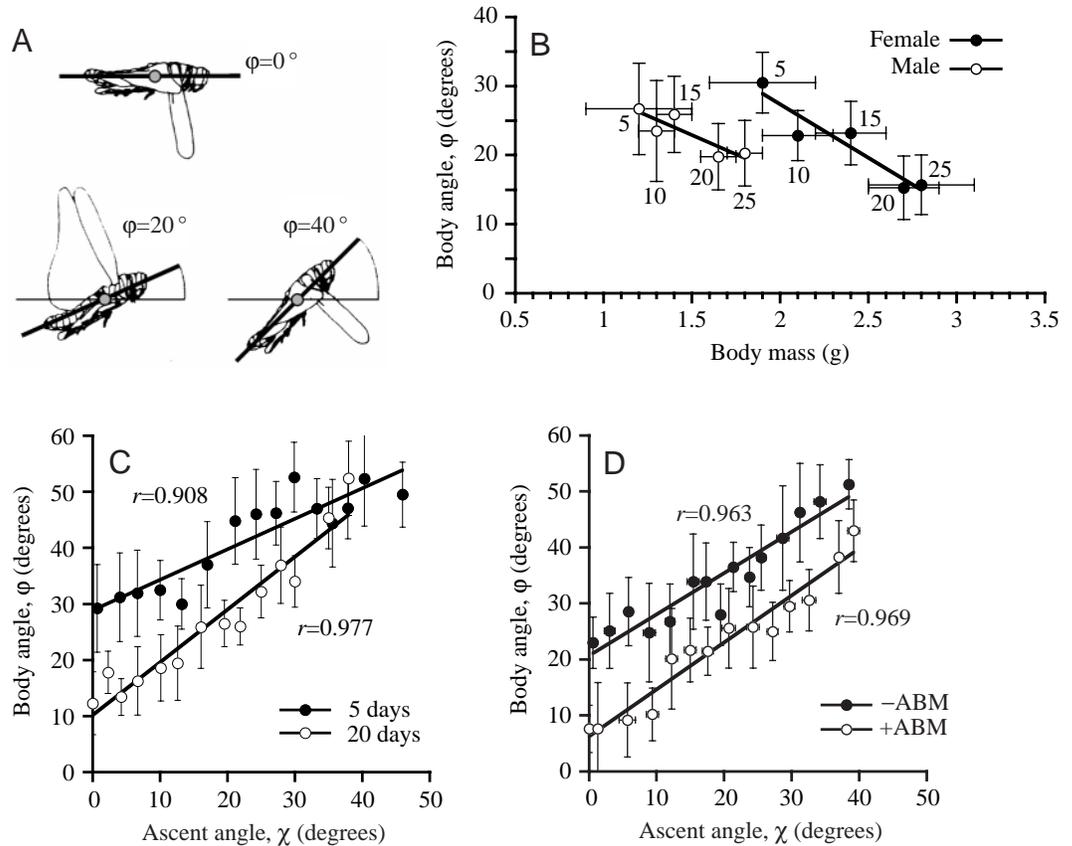
The body angle ϕ decreased slightly after forewing reduction (the intercepts of the regression lines were significantly different, $P < 0.05$; Fig. 4A), but increased strongly after hindwing reduction ($P < 0.05$; Fig. 4B). Compared with intact flights, ϕ increased during shallow ascending flight ($0^\circ \leq \chi \leq 10^\circ$) but decreased during steep ascending flight ($\chi > 10^\circ$) following a 13% reduction of both wing pairs in equal proportions (Fig. 4C). Trimming of the wing pairs also influenced the maximum ascent angles observed: during intact flight, ascent angles of 30–40° were observed in all three groups; however, these did not occur after reduction of the forewings or both wings (as indicated by the grey areas in Fig. 4A,C). Under both experimental conditions, the distribution of the observed ascent angle was shifted

significantly towards lower values compared with the intact condition ($P < 0.05$, $N=10$). A reduction of the hindwing area, however, had no significant effect on the maximum ascent angle achieved (Fig. 4B, observed distributions of χ are not significantly different, $P > 0.05$, $N=10$).

Motor output with respect to wing area

The effects of wing reduction on the motor output of the adult locust flight system was investigated in three groups of animals each containing 12 adult females (18 days postmoult) flying at 34 °C. Any reduction in the wing area increases the wing loading L_w . Since the animals investigated in this particular set of experiments performed flight sequences with the additional mass of the transmitter for telemetric acquisition of f_{WB} , reductions in the gross wing area were limited to, on average, 10% (L_w was increased on average by 8% after transmitter attachment). All animals tested maintained the capability for free flight. As shown in Fig. 5Ai, f_{WB} was not significantly changed in the majority of animals following a reduction in forewing area (for intact locusts, mean f_{WB} was 24.8 ± 0.8 Hz, $N=12$). In the remaining locusts, mean f_{WB} was either significantly increased or decreased (in general, these

Fig. 3. (A) Body silhouettes of locusts exhibiting three different body angles $\phi=0^\circ$, 20° and 40° to the horizontal. The reference point (indicated by a grey circle) was located at 50% of the silhouette length. (B) Mean body angle (\pm s.d., pooled from 10 animals) as a function of body mass during the adult maturation of males ($r=0.881$, $N=5$, $P<0.05$) and females ($r=0.943$, $N=5$, $P<0.05$). Age is given in days beside the data points. (C) A comparison of the relationships between body angle and ascent angle for 5- and 20-day postmolt females during flight. The slopes and intercepts of the regression lines are significantly different ($P<0.05$). Data points represent means \pm s.d. pooled from 10 animals that each performed 4–6 flight sequences. (D) Relationship between body angle and ascent angle in 15-day postmolt females ($N=10$ for each condition) flying either unloaded or after the relative body mass had been increased by 10% by attaching an additional load on the pronotum (ABM, additional body mass). The intercepts of the regression lines are significantly different ($P<0.05$). r , linear correlation coefficient ($P<0.01$).



changes were 5–12% of the intact value) compared with the intact situation ($P<0.05$). The effects of forewing reduction on f_{WB} resembled those observed after additional loading of the animals at the pronotum (see Fig. 1D). Hindwing trimming (Fig. 5Aii) did not affect f_{WB} in 40% of the animals tested (mean f_{WB} was 25.2 ± 1.0 Hz, $N=12$ in intact females). However, f_{WB} was significantly changed in 60% of the locusts investigated (relative changes of 6–11% of the intact value). Wing area reduction spread over both wings changed the mean f_{WB} in 75% of the animals (Fig. 5Aiii, intact situation, mean $f_{WB}=24.2\pm 0.88$ Hz, $N=12$; changes observed in the range 5–14%).

In a different set of experiments, the effects of wing reduction on flight speed were investigated. The wing area was reduced in three groups of 10 adult females (18 days postmolt, without transmitters) to the limits required for support of body weight during free flight (for details, see above). All females tested maintained their free-flight capability throughout the experiments. As shown in Fig. 5B, a reduction in wing area decreases the flight speed in all groups on average from 4.34 ± 0.38 m s $^{-1}$ ($N=30$) to 3.09 ± 0.47 m s $^{-1}$ ($N=30$), representing 71.2% of the intact value, irrespective of which wing pair was trimmed (values from the three groups were not significantly different from one another, $P<0.05$).

Body angle, stroke plane and wing angle of attack

Free-flight sequences of juvenile adult females (12 days postmolt) were recorded using high-speed video. The stroke plane inclination (shown schematically in Fig. 6A,B) as a function of longitudinal body axis (Θ_{BL}) did not significantly change ($P>0.05$, data not shown) when the animals performed climbing flight, i.e. increased χ ($P>0.05$; forewing, $\Theta_{BL}=21\pm 9^\circ$, $N=27$; hindwing, $\Theta_{BL}=12\pm 11^\circ$, $N=23$; data pooled from six animals). However, stroke plane inclination to the vertical (Θ_v) changed because the body angle increased during ascending flight (Fig. 6C).

For the forewing, the angle of attack of the wing profile (α , with the longitudinal body axis used as reference) during the wingbeat cycle was determined in four animals performing horizontal flight sequences (i.e. $\chi\approx 0^\circ$) and in one particular flight with a strong ascending flight path ($39^\circ\geq\chi\geq 48^\circ$; shown schematically in Fig. 7A,B). A value of $\alpha<0^\circ$ indicates wing pronation (i.e. depression of the wind leading edge), whereas $\alpha>0^\circ$ indicates supination of the wing. Determination of a 'common' angle of attack in the hindwing was not possible since the hindwing plane, in particular the anal part, undergoes considerable deformation during the wing stroke. The results from a representative animal are shown in Fig. 7C. During the last two-thirds of the downstroke, values of α were almost

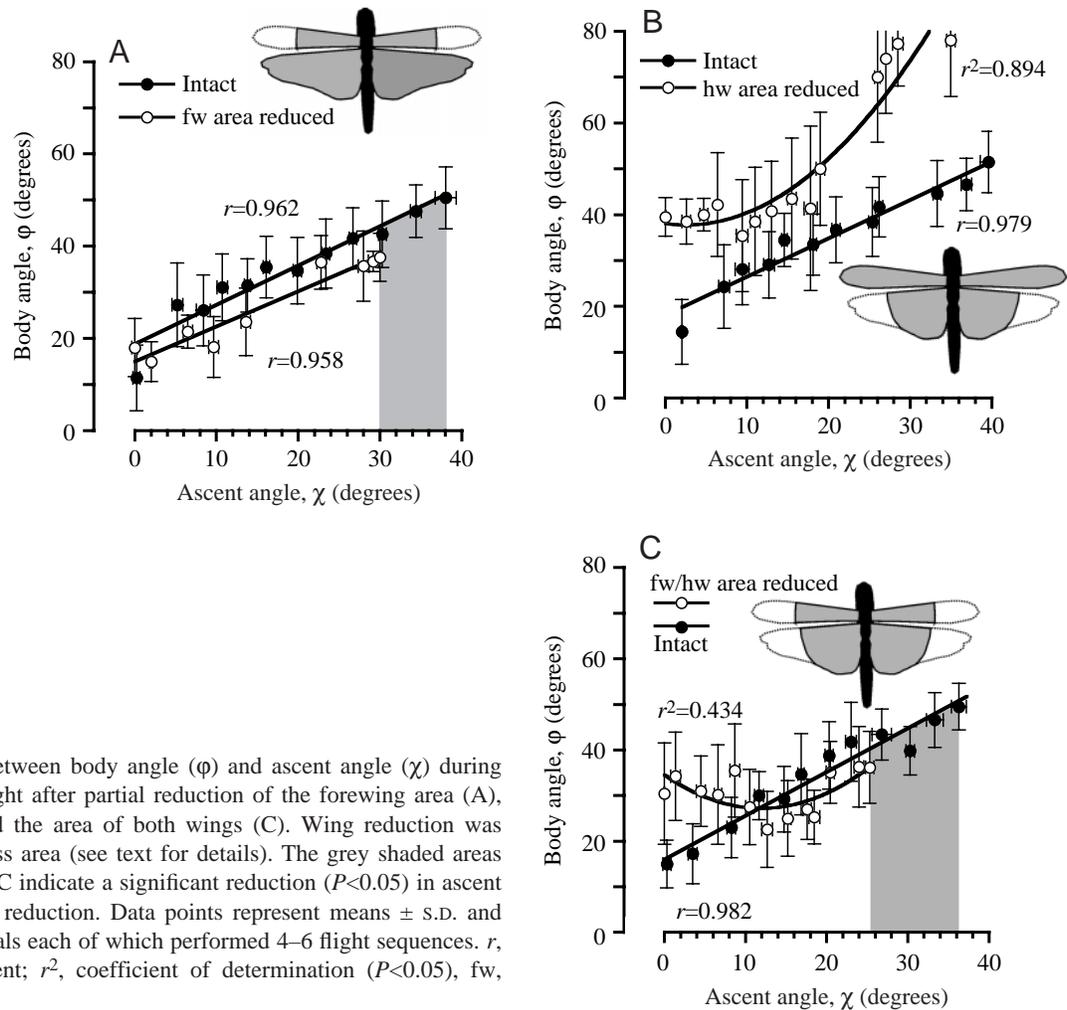


Fig. 4. (A) Relationship between body angle (ϕ) and ascent angle (χ) during intact flight and during flight after partial reduction of the forewing area (A), the hindwing area (B) and the area of both wings (C). Wing reduction was limited to 13% of the gross area (see text for details). The grey shaded areas under the curves in A and C indicate a significant reduction ($P < 0.05$) in ascent angle observed after wing reduction. Data points represent means \pm S.D. and were pooled from 10 animals each of which performed 4–6 flight sequences. r , linear correlation coefficient; r^2 , coefficient of determination ($P < 0.05$), fw, forewing; hw, hindwing.

steady for both horizontal and climbing flight. However, values of α during the last two-thirds of the downstroke during climbing were significantly lower ($P < 0.05$; mean $\alpha = -54 \pm 12^\circ$, $N = 8$) than during horizontal flight (mean $\alpha = -32 \pm 14^\circ$, $N = 5$, data pooled from one of the animals tested), indicating a higher degree of pronation during climbing (these results were confirmed in three of four animals).

Discussion

Aerodynamic output during adult maturation

An understanding of the relationships between wing kinematic variables and the aerodynamic forces produced by wing movements has been provided by the application of unsteady aerodynamic calculations to locust flight (Send, 1992, 1994; Zarnack and Send, 1994; for an overview, see Zarnack, 1997). Investigations using locusts flying on flight balances revealed (i) that the functional task of the complex three-dimensional wing movement, i.e. alternating up and down movement, the time course of the wing angle of attack during the cycle and the pro- and remotion of the wing along the longitudinal body axis, is the generation of thrust not lift, (ii) that the generation of lift during the wing beat relies mainly on

the steady angle of attack and on the speed of the air stream faced by the wings, and (iii) that stroke amplitude and wingbeat frequency have only a weak, if any, influence on the basic lift production required for stable level flight.

Emerging from these results, the locust flight system might theoretically control lift generation during flight in two main ways: (i) by changing the flight speed, and (ii) by changing the wing angle of attack during the wingbeat cycle.

In both sexes of locust, we observed that the increase in body mass during postmoult maturation was correlated with an increase in free-flight speed (Fig. 1A). In addition, mean flight speed of mature females increased after an acute addition of body mass (Fig. 1B). Even though we cannot provide evidence that this addition of small mass units adequately addresses the gradual increase in mass associated with maturation, our data support the hypothesis that the increased lift production required by maturational increases in body mass is achieved functionally by the observed increase in mean flight speed. Since both the accumulation of body mass in both sexes during maturation and the acute addition of mass led to an increase in wing loading, flight speed also increased in proportion to relative wing loading (data not shown). This matches the finding that wing loading is

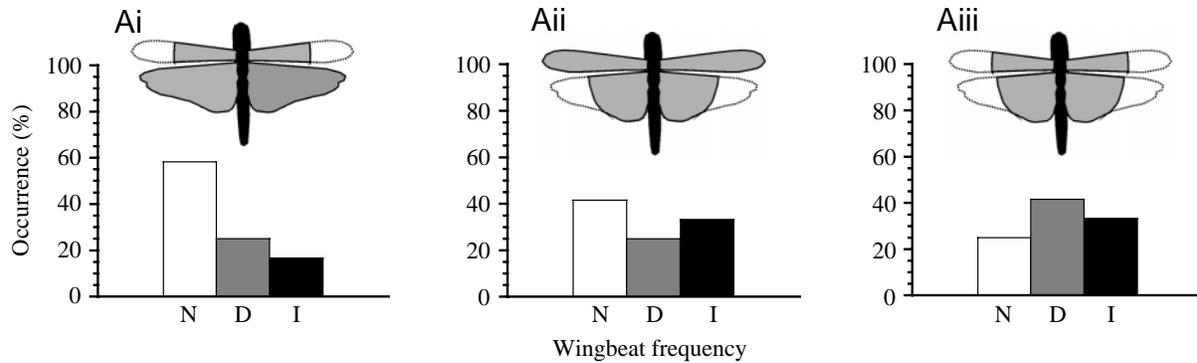
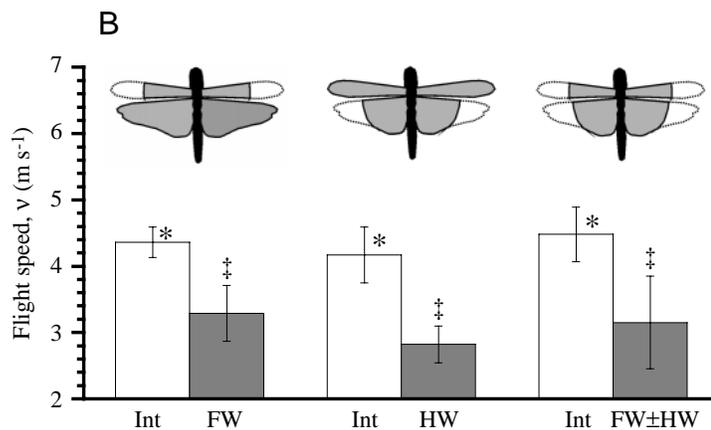


Fig. 5. (A) Changes in wingbeat frequency f_{WB} after partial reduction the area of the forewings (i), the hindwings (ii) and both pairs of wings (iii). Individual data were obtained from 3–5 flight sequences; data were pooled for each animal and were compared at a significance level of $P < 0.05$ ($N = 12$). For details, see text. D, f_{WB} decreased; I, f_{WB} increased; N, no change in f_{WB} . (B) Effects of wing area reduction on the flight speed. The wings were reduced to the limit required while maintaining the ability for free flight. Values represent means \pm s.d. and were pooled from 10 animals each of which performed 4–6 flight sequences. Values labelled with the same symbol do not differ significantly ($P < 0.05$, $N = 10$). All reductions in wing area decreased flight speed significantly ($P < 0.05$). FW, forewing reduction; HW, hindwing reduction; Int, intact wings.



positively correlated with flight speed in various other species (e.g. Dudley and Srygley, 1994).

As reported from tethered flight studies in mature locusts, the minimum flight speed required for continuous support of the body weight was approximately 3 m s^{-1} (Weis-Fogh, 1956; Zarnack and Wortmann, 1989). In accordance with this result, freely flying mature locusts that were artificially 'braked' by clipping their wings to reduce thrust production lost their capability for flight when flight speed was less than 3 m s^{-1} irrespective of which wing pair was clipped (Fig. 5).

In addition to supporting the increasing body mass during maturation, additional lift (i.e. additional effective lifting

power, Fig. 2; see also Fischer and Ebert, 1999) is generated when the locust changes from horizontal to climbing flight. Consistently, 37% of the animals tested in this study increased their instantaneous flight speed when changing to climbing flight. In 47% of the animals investigated, however, instantaneous flight speed did not change during climbing (data from Table 1). This indicates that the control of the instantaneous flight speed might be only one mechanism used by the locust flight system to regulate additional lift production during climbing, since stroke amplitude and/or downstroke duration in particular wings were also observed to change during ascending flight (Fischer and Kutsch, 1999).

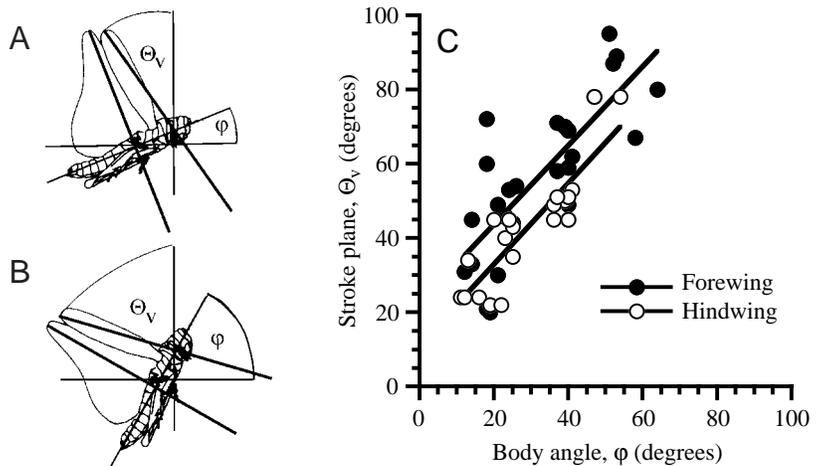


Fig. 6. Schematic drawing of the stroke plane inclination to the vertical (Θ_v) during horizontal (A) and climbing (B) flight. ϕ , body angle to the horizontal. (C) Relationship between stroke plane inclination and body angle in the forewing ($r = 0.753$, $N = 22$, $P < 0.05$) and hindwing ($r = 0.852$, $N = 20$, $P < 0.05$) during free flight of 12-day postmoult adult females. Data represent mean values (s.d. not shown) pooled from 3–5 wingbeat cycles from six animals.

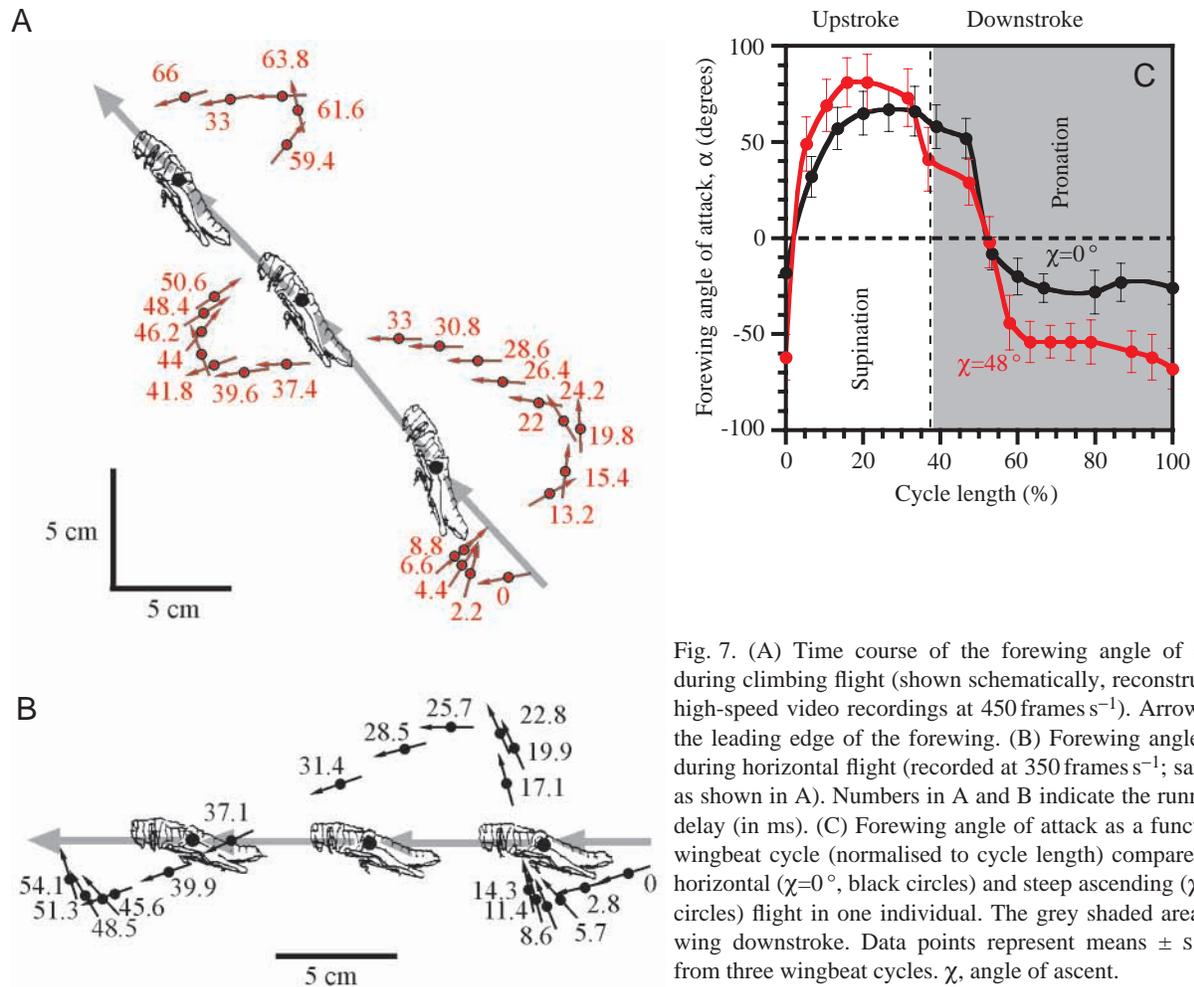


Fig. 7. (A) Time course of the forewing angle of attack (α) during climbing flight (shown schematically, reconstructed from high-speed video recordings at 450 frames s^{-1}). Arrows indicate the leading edge of the forewing. (B) Forewing angle of attack during horizontal flight (recorded at 350 frames s^{-1} ; same animal as shown in A). Numbers in A and B indicate the running frame delay (in ms). (C) Forewing angle of attack as a function of the wingbeat cycle (normalised to cycle length) compared between horizontal ($\chi=0^\circ$, black circles) and steep ascending ($\chi=48^\circ$, red circles) flight in one individual. The grey shaded area indicates wing downstroke. Data points represent means \pm s.d. pooled from three wingbeat cycles. χ , angle of ascent.

In the field, flight activity changes throughout postmolt maturation (Kennedy, 1952): while freshly moulted animals did not fly, flight activity starts 2–3 days postmolt and is maximal between 5 and 12 days postmolt when the animals become ‘fully migrant’ (Weis-Fogh, 1956). This is coincident with the maximal postmolt mass proportion of flight muscles in both sexes (Fig. 2). Flight speed did not differ between the sexes in the fully migrant phase, i.e. when the animals were between 5 days and 15 days postmolt (Fig. 1).

Wingbeat frequency during adult maturation

During free flight in maturing adult locusts, the mean wingbeat frequency f_{WB} increased as a function of adult age and, thus, coincided with the observed increase in average flight speed and body mass (Fig. 1). However, unlike flight speed, instantaneous f_{WB} did not change significantly as a function of an acute application of mass (Fig. 1E) or as a function of climbing (in 60% of the locusts tested, f_{WB} was not significantly correlated with the ascent angle, irrespective of sex and maturation stage; data from Table 1). This indicates that additional lift generation either in response to an acute addition of mass or for climbing flight is, apparently, not achieved by an increase in instantaneous f_{WB} . Furthermore, in

59% of the locusts investigated, irrespective of sex and maturational stage, instantaneous free-flight speed was not correlated with instantaneous f_{WB} (data from Table 1). This constant f_{WB} , which has been observed during a wide range of flight speeds in insects as well as in birds, was previously explained as the characteristic f_{WB} of particular flight systems, which were assumed to be driven damped oscillators in which the characteristic f_{WB} (or ‘resonance frequency’) depended both on the driving frequency and on the mechanical damping properties of the system (Soltavolta, 1952; Greenwald, 1960). Recently, it has been shown that detached wings of the tobacco hawkmoth *Manduca sexta* caused to ‘beat’ by a piezoelectric device produced maximal aerodynamic output when driven in resonance (Scharstein, 1998a,b). In the mechanical, highly condensed thoraces of more recent ‘myogenic’ flyers (e.g. dipterans), which exhibit much higher values of f_{WB} than locusts, wing clipping increased f_{WB} (Soltavolta, 1952). This indicates that, in a myogenic flight oscillator, the characteristic f_{WB} may depend mainly on the damping properties of the system, i.e. on the wing mass and thoracic internal and external frictional forces that determine the ‘resonance conditions’ and, thus, f_{WB} .

In evolutionarily earlier ‘neurogenic’ flyers, however, wing

clipping had little effect on the characteristic f_{WB} (e.g. in cockroaches, Roeder, 1951; Soltavolta, 1952) or led to increased variability (for locusts, see Fig. 5). These effects of wing reduction experiments may indicate that the characteristic f_{WB} in neurogenic flyers such as locusts depends mainly on the driving frequency of the flight oscillator, i.e. on the instantaneous frequency output generated by the neuronal flight network (see Robertson and Pearson, 1985). During postmoult maturation of locusts, specific sensorimotor pathways that participate in the generation of a functional flight motor pattern are reorganised following the first 2 weeks of imaginal ecdysis (Altman et al., 1978; Gray and Robertson, 1996) with respect to the flight interneurons that grow during maturation (Gee and Robertson, 1994). These network-related changes, together with apparent changes in the driving capacity of the flight muscles during maturation (Brösemer et al., 1963), support the hypothesis that the 'proximate' reason for the increase in characteristic f_{WB} during maturation in locusts is a change in driving frequency, i.e. in the resonance conditions of the maturing flight system.

Although f_{WB} seems not to be directly involved in the instantaneous control of the flight speed responsible for additional lift production (e.g. for climbing or in response to acute addition of mass), we cannot conclude from our experiments that f_{WB} , in general, plays no part in the propulsive mechanism of the flight system that provides basic aerodynamic output enabling flight capability throughout maturation. Temperature experiments in mature locusts have shown that, in general, a minimum wingbeat frequency is required for the support of the body mass during free flight (Fischer and Ebert, 1999).

Functional implications of body angle adjustment during locust flight

The fact that body angle and ascent angle are strongly correlated suggests a significant role for the body angle during lift production (see also Baker et al., 1981). Studies in locusts flying in a flight balance revealed that changes in body angle reproducibly manipulate lift production and that, during 'steady' flight, maximum lift is obtained at a mean body angle of 20° (Zarnack and Wortmann, 1989), which matches body angles observed during horizontal free flight (Fig. 3). In the majority of locusts investigated, the body angle was correlated neither with flight speed nor with wingbeat frequency (Table 1).

The mean body angle changes in relation to the increase in body mass that occurs during adult maturation in both sexes (Fig. 3). These changes are more obvious in females, in which a greater postmoult increase in body mass was observed than in males; the relative change in the average body angle was comparable in both sexes. A preliminary study has shown that the location of the centre of gravity of female locusts changed in relation to the longitudinal body axis during the adult life span (probably as the ovaries, which are located in the abdomen, matured). A slight caudal shift in the centre of gravity by, on average, 4% of relative body length was found

when comparing 5-day and 20-day postmoult females (Fischer, 1994). It is not clear whether this slight shift in the centre of gravity could be co-responsible for the considerable decrease in body angle during maturation.

A large decrease in body angle was also observed after acute addition of mass at the pronotum (Fig. 3D). We do not believe that this decrease in body angle is simply the result of placing the mass anterior to the centre of gravity and causing the locust to pitch forward. In these particular experiments, the total mass applied was limited to 10% of the body mass, an amount that did not significantly influence the location of the centre of gravity (Fischer, 1994).

Our experiments suggest that the instantaneous body angle during flight is largely controlled by the aerodynamic force production of the wings rather than by changes in leg position or in abdominal posture. Partial clipping of the forewings decreased the body angle slightly during free flight, while the instantaneous body angle was strongly increased after hindwing reduction (Fig. 4). This also indicates that both wing pairs may contribute to the regulation of body angle during the adult life span in an antagonistic manner. Forewing clipping not only decreased the instantaneous body angle but also limited the range of ascent angles to lower values. This effect was not, however, observed after hindwing reduction. This further supports the idea that increases in body angle play a significant role during climbing flight. When wing area was reduced in both wing pairs, body angle adjustment seemed to be impaired; and this had a general effect on the ability of the insect to perform climbing flight.

Changes in body angle during flight strongly influenced the stroke plane inclination of both wings (Fig. 6); however, in general, stroke plane inclination did not change in relation to longitudinal body axis (see also Gewecke and Kutsch, 1979). The main difference between the time course of the wing angle of attack during horizontal and steep ascending flight was an increase in wing pronation during the downstroke in climbing flight (Fig. 7). It is not clear whether these changes in the angle of attack result in increased thrust production (i.e. flight speed) and, thus, in increased lift production during flight.

The relationship between stroke plane and body axis and, to some extent, the basic time course of the wing angle of attack during the wingbeat cycle are mainly determined (and limited) by wing joint mechanics (Pfau, 1977, 1978, 1982). This suggests that body angle adjustment during locust flight plays an important part in the directional control of the resultant flight force vector, which is directed towards the vertical during climbing. Whether the steeper body angle exhibited by very young adults during flight enables the juvenile immature flight system to provide a resultant flight force vector that is directed more vertically (e.g. for additional support of body mass) is a question that needs to be addressed by further experimentation.

We are grateful to Drs H. Scharstein, A. Büschges and G. Wendler (Universität zu Köln, Germany) and Mr S. Merrywest (University of St Andrews, Scotland) for their

valuable comments, helpful advice and discussion. We wish to thank two anonymous referees for their constructive criticism and valuable suggestions. Thanks are especially due to Ms B. Janisch and Mr E. Ebert (Universität Konstanz, Germany) for their assistance. This project was supported by a DFG grant to W.K. (Ku 240/17-1, 2). H.F. is currently supported by The Wellcome Trust.

References

- Altman, J. S., Anselment, E. and Kutsch, W.** (1978). Postembryonic development of an insect sensory system: ingrowth of axons from hindwing sense organs in *Locusta migratoria*. *Proc. R. Soc. Lond. B* **202**, 497–516.
- Baker, P. S. and Cooter, R. J.** (1979). The natural flight of the migratory locust, *Locusta migratoria*. I. Wing movements. *J. Comp. Physiol. A* **131**, 79–87.
- Baker, P. S., Gewecke, M. and Cooter, R. J.** (1981). The natural flight of the migratory locust, *Locusta migratoria*. III. Wing-beat frequency, flight speed and attitude. *J. Comp. Physiol. A* **141**, 233–237.
- Brösemer, R. W., Vogel, W. and Bucher, T.** (1963). Morphologische und enzymatische Muster bei der Entwicklung indirekter Flugmuskeln von *Locusta migratoria*. *Biochem. Z.* **338**, 854–910.
- Cheu, S. P.** (1952). Changes in fat and protein content of the african migratory locust, *Locusta migratoria migratorioides*. *Bull. Ent. Res.* **43**, 101–109.
- Delcomyn, F.** (1980). Natural basis of rhythmic behaviour in animals. *Science* **210**, 492–498.
- Dudley, R. and Srygley, R. B.** (1994). Flight physiology of neotropical butterflies: allometry of airspeeds during natural free flight. *J. Exp. Biol.* **191**, 125–139.
- Fischer, H.** (1994). Analyse des freien Fluges der Heuschrecke *S. gregaria* mit optischen und radiotelemetrischen Methoden. Diploma thesis, University of Konstanz.
- Fischer, H.** (1998). *Untersuchungen zur Verhaltensphysiologie freifliegender Heuschrecken unter Einsatz von Telemetrie*, vol. 347. Allensbach: UFO Atelier und Verlag GmbH.
- Fischer, H. and Ebert, E.** (1999). Tegula function during free locust flight in relation to motor pattern, flight speed and aerodynamic output. *J. Exp. Biol.* **202**, 711–721.
- Fischer, H. and Kutsch, W.** (1999). Timing of elevator muscle activity during climbing in free locust flight. *J. Exp. Biol.* **202**, 3575–3586.
- Gee, C. E. and Robertson, R. M.** (1994). Effects of maturation on synaptic potentials in the locust flight system. *J. Comp. Physiol. A* **175**, 437–447.
- Gewecke, M.** (1975). The influence of air-current sense organs on the flight behaviour of *Locusta migratoria*. *J. Comp. Physiol. A* **103**, 79–95.
- Gewecke, M. and Kutsch, W.** (1979). Development of flight behaviour in maturing adults of *Locusta migratoria*. I. Flight performance and wing-stroke parameters. *J. Insect Physiol.* **25**, 249–253.
- Gray, J. R. and Robertson, R. M.** (1996). Structure of the forewing stretch receptor in immature and mature adult locusts. *J. Comp. Neurol.* **365**, 268–277.
- Greenwald, C. H.** (1960). The wings of insects and birds as mechanical oscillators. *Proc. Am. Phil. Soc.* **104**, 605–611.
- Kennedy, J. S.** (1952). The migration of the desert locusts, *Schistocerca gregaria* Forskål. I. The behaviour of swarms. II. A theory of long range migrations. *Phil. Trans. R. Soc. Lond. B* **235**, 162–290.
- Kutsch, W.** (1971). The development of the flight pattern in the desert locust, *Schistocerca gregaria*. *Z. Vergl. Physiol.* **74**, 156–168.
- Kutsch, W.** (1973). The influence of age and culture-temperature on the wing-beat frequency of the migratory locust, *Locusta migratoria*. *J. Insect Physiol.* **19**, 763–772.
- Kutsch, W. and Gewecke, M.** (1979). Development of flight behaviour in maturing adults of *Locusta migratoria*. II. Aerodynamic parameters. *J. Insect Physiol.* **25**, 299–304.
- Möhl, B.** (1985). The role of proprioception in locust flight control. I. Asymmetry and coupling within the time pattern of motor units. *J. Comp. Physiol. A* **156**, 93–101.
- Pearson, K. G. and Wolf, H.** (1987). Comparison of the motor pattern in the intact and deafferented flight system of the locust. I. Electromyographic analysis. *J. Comp. Physiol. A* **160**, 259–268.
- Pfau, H. K.** (1977). Zur Morphologie und Funktion des Vorderflügels und Vorderflügelgelenks von *Locusta migratoria* L. *Fortschr. Zool.* **24**, 341–345.
- Pfau, H. K.** (1978). Funktionsanatomische Aspekte des Insektenfluges. *Zool. Jb. Anat.* **99**, 99–108.
- Pfau, H. K.** (1982). Mechanik und sensorische Kontrolle der Flügel-Pronation und Supination. In *Biona Report 1* (ed. W. Nachtigall), pp. 61–77. Stuttgart, New York: Gustav Fischer.
- Phipps, J.** (1950). The maturation of the ovaries and the relation of weight and maturity in *Locusta migratoria*. *Bull. Ent. Res.* **40**, 539–557.
- Reye, D. N. and Pearson, K. G.** (1988). Entrainment of the locust central flight oscillator by wing stretch receptor stimulation. *J. Comp. Physiol. A* **162**, 77–89.
- Robertson, R. M. and Pearson, K. G.** (1985). Neural circuits in the flight system of the locust. *J. Neurophysiol.* **53**, 110–128.
- Roeder, K. D.** (1951). Movements of the thorax and potential changes in the thoracic muscles during flight. *Biol. Bull.* **100**, 95–113.
- Sachs, L.** (1978). *Angewandte Statistik*, fifth edition. Berlin: Axel Springer.
- Scharstein, H.** (1998a). Ein Piezo-Flügelantrieb zur Untersuchung der Biophysik und Aerodynamik des Insektenfluges. In *Biona Report 13* (ed. R. Blickhan, A. Wisser and W. Nachtigall), pp. 189–191. Stuttgart, Jena, Lübeck, Ulm: Gustav Fischer.
- Scharstein, H.** (1998b). Kräfte- und Leistungsbilanz bei der künstlichen Schlagbewegung einzelner Insektenflügel. In *Biona Report 12* (ed. W. Nachtigall and A. Wisser), pp. 257–270. Stuttgart, Jena, Lübeck, Ulm: Gustav Fischer.
- Send, W.** (1992). The mean power of forces and moments in unsteady aerodynamics. *Z. Angew. Math. Mech.* **72**, 113–132.
- Send, W.** (1994). Basic description of animal flight. *Proceedings of the 22nd Goettingen Neurobiology Conference*, vol. II (ed. N. Elsner and H. Breer), p. 273. Stuttgart, New York: Georg Thieme.
- Snodgrass, R. E.** (1929). The thoracic mechanisms of a grasshopper and its antecedents. *Smith. Misc. Collns* **82**, 1–111.
- Soltavolta, O.** (1952). The essential factor regulating the wing-stroke frequency of insects in wing mutilation and loading experiments and in experiments at subatmospheric pressure. *Ann. Zool. Soc. Vanamo* **15**, 1–68.
- Stevenson, P. A. and Kutsch, W.** (1987). A reconsideration of the central pattern concept for locust flight. *J. Comp. Physiol. A* **161**, 115–129.
- van der Wall, M.** (1996). Muskelaktivität während des Freifluges von

- Heuschrecken (Ein-Kanal-Telemetrie). Diploma thesis, University of Konstanz.
- Weis-Fogh, T.** (1956). Biology and physics of locust flight. II. Flight performance of the desert locust (*Schistocerca gregaria*). *Phil. Trans R. Soc. Lond. B* **239**, 459–510.
- Weis-Fogh, T.** (1976). Energetics and aerodynamics of flapping flight: a synthesis. In *Insect Flight* (ed. R. C. Rainey). *Symp. R. Ent. Soc. Lond.* **7**, 48–72. Oxford: Blackwell Scientific Publications.
- Wendler, G.** (1974). The influence of proprioceptive feedback on locust flight co-ordination. *J. Comp Physiol. A* **88**, 173–200.
- Wilson, D. M. and Weis-Fogh, T.** (1962). Patterned activity of co-ordinated motor units, studied in flying locusts. *J. Exp. Biol.* **39**, 643–667.
- Wolf, H.** (1990). On the function of a locust flight steering muscle and its inhibitory innervation. *J. Exp. Biol.* **150**, 50–80.
- Wolf, H.** (1993). The locust tegula: significance for flight rhythm generation, wing movement control and aerodynamic force production. *J. Exp. Biol.* **182**, 229–253.
- Wolf, H. and Pearson, K. G.** (1988). Proprioceptive input patterns elevator activity in the locust flight system. *J. Neurophysiol.* **59**, 1831–1853.
- Wortmann, M. and Zarnack, W.** (1993). Wing movements and lift regulation in the flight of desert locusts. *J. Exp. Biol.* **182**, 57–69.
- Zarnack, W.** (1997). Kinematik und Aerodynamik des Heuschreckenfluges. In *Biona Report II* (ed. W. Nachtigall), pp. 173–200. Stuttgart, Jena, Lübeck, Ulm: Gustav Fischer.
- Zarnack, W. and Send, W.** (1994). Applications of unsteady aerodynamics to the locust flight. *Proceedings of the 22nd Goettingen Neurobiology Conference*, vol. II (ed. N. Elsner and H. Breer), p. 274. Stuttgart, New York: Georg Thieme.
- Zarnack, W. and Wortmann, M.** (1989). On the so-called constant lift reaction of migratory locusts. *J. Exp. Biol.* **147**, 111–123.