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The Natural Flight of the Migratory Locust, *Locusta migratoria* L.

III. Wing-Beat Frequency, Flight Speed and Attitude

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Summary. High speed cine film of *Locusta migratoria* swarms was analysed. The following variables were studied and compared where possible with laboratory data: 1. Wing-beat frequencies of locusts of Australian and New Guinea swarms (mean 22.9 Hz) were higher than laboratory figures (19.8 Hz; Fig. 1). 2. Mean flight speed was 4.6 m/s, which was higher than laboratory figures (3.3 m/s; Fig. 2). 3. Mean body angle to horizontal was 7.4°, and to flight path (in the vertical plane) was 5.2°. Flight speed was found to be correlated with wing-beat frequency with a similar regression line to that found in laboratory work (Fig. 4). Ascent angle was positively correlated with the body angle to horizontal, but not correlated with body angle to flight path (Figs. 3, 5, 6).

Introduction

Locust flight has been the subject of many laboratory investigations, and many variables including wing-beat frequency, body angle, flight speed, lift etc. have been studied and relationships between them established (Weis-Fogh 1956; Wilson 1961; Zarnack 1972; Wendler 1974; Gewecke 1975; Baker 1979; Cooter 1979). However, there are few reports of such measurements in natural conditions. Waloff (1972) measured flight speeds directly, and Riley (1974), Schaefer (1976) and Riley and Reynolds (1979) have measured wing-beat frequencies using radar techniques.

Recently, it has been possible to make high speed film of *Locusta* swarms (Baker and Cooter 1979a, b) and in the following paper some aspects of their flight performance will be analysed, and compared with laboratory and field studies. Observations of the locusts in natural flight are necessary before their flight performance really can be assessed. Without a detailed knowledge of the range of flight manoeuvres made by these insects under natural conditions it is not possible to interpret the significance of laboratory experiments with tethered flying locusts satisfactorily. The present analysis attempts to clarify how the migratory locust adjusts such important flight variables as wing-beat frequency, flight speed and body angle under natural conditions during free flight.

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Methods

Locusts (*Locusta migratoria* L.) were filmed (lateral view) with a high-speed camera (Locam; max. 500 frames/s) in Australia and New Guinea (for details of the filming procedure see Baker and Cooter 1979a). Most of the data were taken from film of the Australian swarm (individuals at least 6 days old) recorded at midday in March. Wind speed during the filming period was less than 0.5 m/s (2 m above the ground). Air temperature was 30 °C, relative humidity 78% and light intensity about 10^5 Lux. The swarm was observed for 30 min prior to filming, few insects were seen taking off or landing and although flying continuously the swarm did not displace significantly. The New Guinea swarm of mature individuals was filmed at midday in February. Wind speed was less than 0.5 m/s and light intensity $1.75 \cdot 10^5$ Lux.

For analysis the film was projected onto a drawing table using an LW201A analysis projector. Wing-beat frequency was calculated from wing-tip positions on the drawings of successive images (e.g. Fig. 3) and the number of frames required to complete one whole stroke. The flight speed was calculated by help of average body length and displacement on successive frames (Baker and Cooter 1979a). The ascent angle (α) was constructed by measuring the angle between a line drawn through successive head positions, i.e. flight path within the vertical plane, and the horizontal. Body angle was recorded in two ways, between the long axis of the body and either the horizontal, i.e. body angle to horizontal (χ), or the flight path, i.e. body angle to flight path ($\delta = \chi - \alpha$); the line parallel to the ventral thorax was taken as the longitudinal body axis (Weis-Fogh 1956).

The laboratory measurements referred to in this paper were from tethered flying *Locusta migratoria* (females and males, 10

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or more days old, samples taken 10 min after flight had started; Gewecke and Kutsch 1979; Kutsch and Gewecke 1979).

For statistical evaluation all variables were objectively grouped and tested for normal distribution ($P=0.01$); F-, t- and U-tests were used for the comparison of two samples respectively (Lienert 1973; Zar 1974).

Results

1. Flight Variables

a) Wing-Beat Frequency

Wing-beat frequency was measured from 53 locusts of unknown sex in the Australian swarm. Between three and five wing-beats per individual were measured and averaged. The normal distribution of frequencies ranges between 17.4 and 26 Hz with a mean of 22.4 Hz. Wing-beat frequencies were also measured from 45 locusts from the New Guinea swarm. The distribution of frequencies is normal and ranges from 20.7 to 26.2 Hz with a mean of 23.5 Hz, slightly higher than for the Australian locusts.

When all wing-beat frequencies measured from locusts in free flight are pooled and compared with results from locusts used in a laboratory study (Gewecke and Kutsch 1979), a significant difference in spread of data can be seen (Fig. 1), the mean for

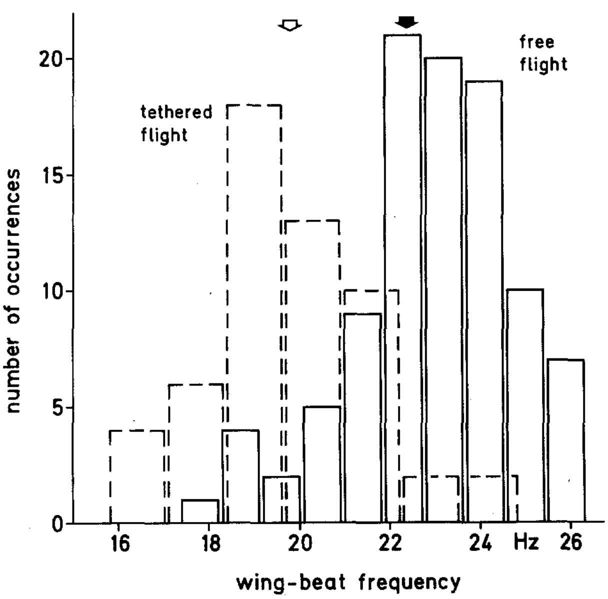

Fig. 1. Comparison of wing-beat frequencies of free flying locusts (solid lines, n=98, normal distribution, min. 17.4 Hz, max. 26.2 Hz, mean 22.9 Hz, SD=1.7) with laboratory figures (from Gewecke and Kutsch 1979) of tethered flying *Locusta migratoria* (females and males, at least 10 days old, 10 min after flight start; broken lines, n=55, normal distr., min. 16 Hz, max. 24.5 Hz, mean 19.8 Hz, SD=1.8). In this and the next fig. the data are objectively grouped (Lienert 1973); arrows denote means

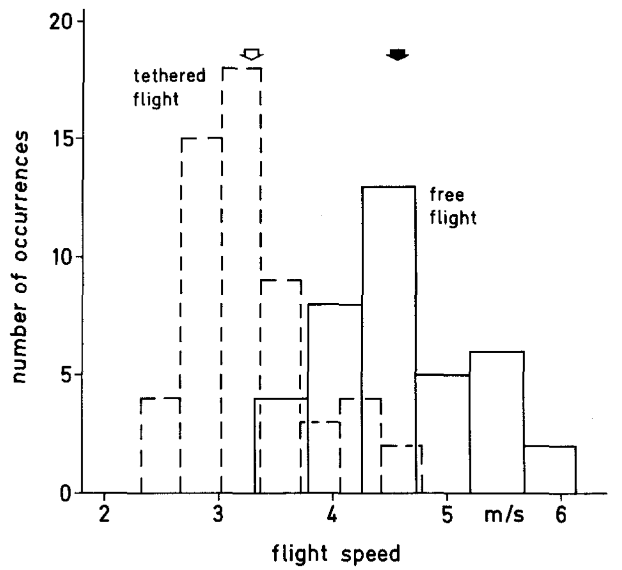

Fig. 2. Comparison of histograms of flight speeds of Australian swarm (solid lines, n=38, normal distr., min. 3.3 m/s, max. 6.1 m/s, mean 4.6 m/s, SD=0.65) and tethered flight (broken lines, n=55, not a normal distr., min. 2.3 m/s, max. 4.7 m/s, mean 3.3 m/s, SD=0.52) (from Kutsch and Gewecke 1979)

the tethered fliers being 19.8 Hz and for the free fliers 22.9 Hz ($P<0.001$). As the frequencies of the laboratory study insects were measured 10 min after the start of flight the initial higher frequency at take-off had time to subside (Gewecke 1975). Both swarms had been flying for at least 15 min, and as few insects were landing and taking off, it can be assumed that most of them were past the initial take-off stage.

The following sections relate only to the Australian swarm.

b) Flight Speed

The flight speed of 38 migratory locusts were measured containing samples of ascending, descending and level fliers (Fig. 3). A histogram of all speeds measured shows a normal distribution from 3.3 to 6.1 m/s with a mean at 4.6 m/s (Fig. 2). This is significantly higher than laboratory measurements from tethered flying locusts ($P<0.001$; Fig. 2).

c) Body Angle

Body angle can be measured either with reference to the horizontal or to the ascent path of the insect (Fig. 3). The field insects exhibit considerable variation in both types of angle. The body angle to horizontal (χ) varies between $-5.1°$ (pitching down) and $20.5°$ (pitching up), the mean being $\chi=7.4°$ (Fig. 5). The body angle to flight path (δ) varies from $-5.3°$ to $18.4°$ with a mean of $\delta=5.2°$ (Fig. 6).

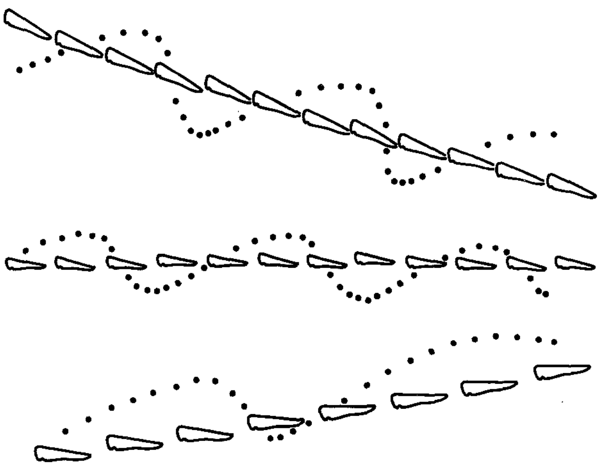

Fig. 3. Three examples recorded simultaneously of locusts (lateral view) in rising, steady and sinking flight, with forewing tip positions drawn in. Body positions are at 0.01 s intervals. Body size differs with distance of insect from the camera

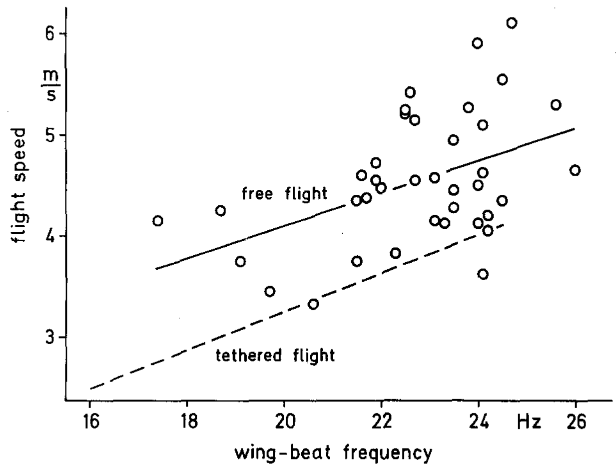

Fig. 4. Relationship between flight speed and wing-beat frequency. Solid line and data points refer to free flight ($r=0.45$), and broken line to tethered flight experiments ($r=0.67$)

d) Ascent Angle

The ascent angle (α) is the angle between the flight path in the vertical plane and the horizontal and in still air is effectively a measure of rate of ascent or descent (Fig. 3). In the present study the angle varied between $-10.3°$ and $16.3°$ (Figs. 5, 6). When taking off, however, the locusts can adopt much steeper angles (up to 90°) although they are not maintained for long (Baker and Cooter in prep.). The mean value of ascent angle in the present study is 2°, so the swarm could be regarded as in nearly horizontal flight; but the sample was taken over only a few seconds of flight and it is probable that this value varied with time and prevailing conditions.

2. Correlation of Flight Variables

a) Wing-Beat Frequency and Flight Speed

If the speed of freely flying locusts is plotted against wing-beat frequency (Fig. 4) a positive correlation ($r=0.45$; $P<0.01$) is seen which is similar to that found in the laboratory studies of Kutsch and Gewecke (1979; $r=0.67$; $P<0.001$; Fig. 4, dashed line). The relation between wing-beat frequency (f, in Hz) and flight speed (v, in m/s) of the free flying locusts is given by $v=0.91+0.16f$, and of the tethered flying insects by $v=-0.56+0.19f$. The regression coefficients do not differ significantly ($P>0.05$) although there is a significant difference between ordinate values ($P<0.001$).

The considerable scatter of points for the free flying locusts (Fig. 4) suggests that other flight variables, such as stroke angle or angle of attack of the wings, in addition to wing-beat frequency may control flight speed. Also as nothing is recorded of the events immediately before the locust appeared in the field of view, for instance a locust may have just finished a glide (Baker and Cooter 1979b) and therefore be flying slower than normal and with a body angle inappropriate for steady level flight, little more can be said about this point.

b) Body Angle and Ascent Angle

The ascent angle (α) shows considerable variation and, when plotted against the body angle to horizontal (χ), a positive correlation (Fig. 5; $r=0.66$; $P<0.001$). It can be seen in general that χ slightly greater than α is preferred. One of the reasons for the scatter of the values may be that the locust has some control over its wing-stroke plane angles so that changes in body angle do not have to be accurately mirrored by changes in ascent angle (Baker and Cooter 1979a).

The relationship between ascent angle (α) and body angle to flight path (δ) on the other hand shows no significant correlation (Fig. 6; $r=-0.34$; $P>0.01$). However, there is a slight tendency for the climbing locust to have a smaller body angle to flight path, or even a negative one, than when descending. This effect is particularly noticeable in gliding locusts where descent is often accompanied by an initial steep body angle (Baker and Cooter 1979b).

c) Other Relationships

The following relationships were also examined: wing-beat frequency was found to be uncorrelated with ascent angle ($r=0.14$; $P>0.05$), with body angle to horizontal ($r=0.22$; $P>0.05$), or with body angle

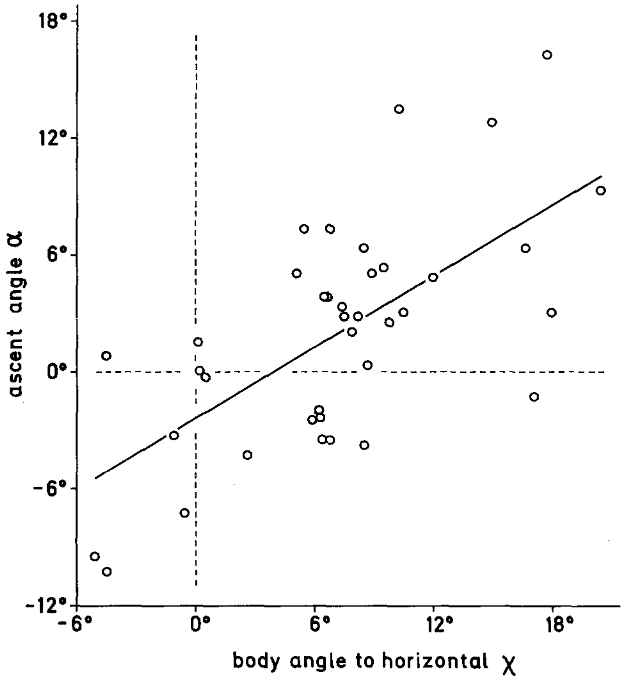

Fig. 5. Relationship between ascent angle (α) and body angle to horizontal (χ). There is a positive correlation ($r=0.66$)

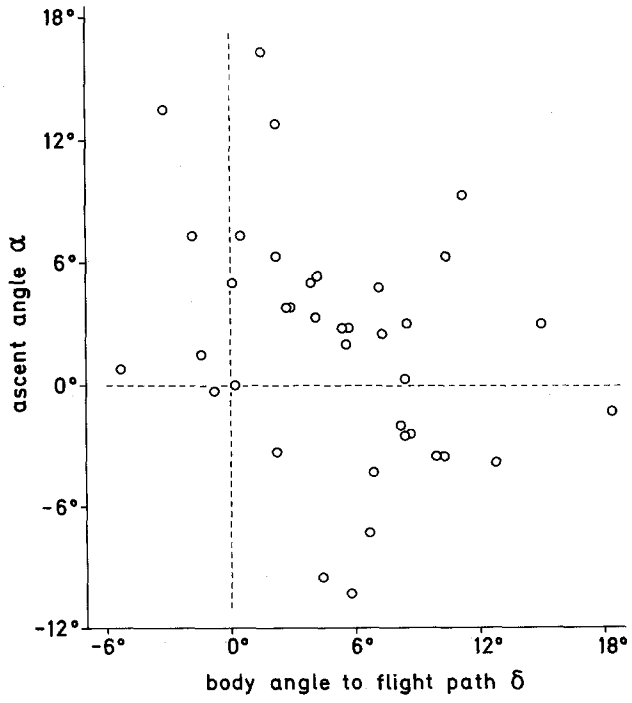

Fig. 6. Relationship between ascent angle (α) and body angle to flight path (δ)

to flight path ($r=0.12$; $P>0.05$). Flight speed was not correlated with ascent angle ($r=-0.14$; $P>0.05$), or with body angle to horizontal ($r=-0.14$; $P>0.05$), or with body angle to flight path ($r=-0.02$; $P>0.05$).

Discussion

Previous accounts of locust flight in the natural state have tended to lack measurements of wing-beat frequency, flight speed, ascent angle etc., so that we have only an inprecise picture of the behaviour of individual locusts within a swarm, and of the range and amount of variability in flight variables that occurs. Such information is important not only for the understanding of flight ability of locusts, but also in relation to how closely tethered flight performance is related to field performance. This information is also necessary to the radar entomologist who requires as much information as possible in order to correctly identify the target insect reflecting the return signals he receives. In practice the wing-beat frequency is the most important diagnostic feature in radar signal analysis because the signal when reflected from the target insect has detectable modulations at its wing-beat frequency. Radar studies with positive visual sightings are rare, e.g. Riley (1974) on single released specimens, and Schaefer (1976) who correlated radar signals with high-speed cine recordings of flying *Schistocerca*. In this latter case the wing-beat frequencies were closely matched, and had a range of only 2.5 Hz (mean 19 Hz) compared with 8.8 Hz in the present study (Fig. 1).

A positive correlation between wing-beat frequency and flight speed was first found in the laboratory for mature females of *Locusta* (Gewecke 1975) and later demonstrated to hold true for adults of all ages (Kutsch and Gewecke 1979). The results of the present study indicate that this relationship holds for free flight conditions (Fig. 4), and thus confirm the validity of an analytical approach to the study of some of the problems associated with insect flight in the laboratory. However, the absolute values of wing-beat frequencies and flight speeds measured in the field and in the laboratory, respectively, are significantly different from each other, the laboratory values being lower (Figs. 1, 2).

In addition, the effect of the tethering is clearly demonstrated by the fact that during tethered flight recorded lift was generally less than that which would support the body weight (Gewecke 1975; Kutsch and Gewecke 1979). In these experiments the locusts controlled their flight speed with respect to the air (from a wind tunnel) but were not able to adjust their lift to their body weight, because there was no feedback from the upward aerodynamic force as there was from the frontal one, the thrust, which generates the flight speed. Since this is positively correlated with the lift (Gewecke 1975) one can assume that tethered locusts with both low wing-beat frequency and low flight speed could not produce enough lift to support their body weight.

Secondly, it follows from our present results that body angle has an important influence on lift production. Whereas in most tethered flight experiments the body angle was fixed, locusts in natural flight show great variation in body angle to the horizontal (Fig. 5). This angle is positively correlated with the ascent angle which must depend upon the generated lift. Only if the body angle to the horizontal is greater than 4° on average can locusts fly forward or upward. With smaller body angles they descend. These findings should be taken into account in future investigations of locust flight in the laboratory.

The control of flight speed by the flying locust has some interesting implications for flight range and behaviour too. Weis-Fogh (1956, 1976) stated that in *Schistocerca* the speed for maximum flight endurance should be about 3.5 m/s, which should therefore be the preferred flight speed for locusts migrating and displacing *with the wind*. They would merely stay aloft at minimum cost and let the wind carry them along. However, Weis-Fogh also calculated that for maximum range *in still air*, the speed for minimum cost of transport is higher (i.e., 4.5 to 5.5 m/s). These theoretical values fall within the range of results (3.3 to 6.1 m/s) from the present study, and the recorded mean flight speed (4.6 m/s) of *Locusta* flying in a swarm tends towards Weis-Fogh's figure for minimum cost of transport.

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References

Baker PS (1979) Flying locust visual responses in a radial wind tunnel. J Comp Physiol 131:39–47

Baker PS, Cooter RJ (1979a) The natural flight of the migratory locust, *Locusta migratoria* L. I. Wing movements. J Comp Physiol 131:79–87

Baker PS, Cooter RJ (1979b) The natural flight of the migratory locust, *Locusta migratoria* L. II. Gliding. J Comp Physiol 131:89–94

Cooter RJ (1979) Visually induced yaw movements in the flying locust, *Schistocerca gregaria* (Forsk.). J Comp Physiol 131:67–78

Gewecke M (1975) The influence of the air-current sense organs on the flight behaviour of *Locusta migratoria*. J Comp Physiol 103:79–95

Gewecke M, 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

Kutsch W, Gewecke M (1979) Development of flight behaviour in maturing adults of *Locusta migratoria*: II. Aerodynamic parameters. J Insect Physiol 25:299–304

Lienert GA (1973) Verteilungsfreie Methoden in der Biostatistik. 2nd edn. Anton Hain, Meisenheim am Glan

Riley JR (1974) Radar observations of individual desert locusts (*Schistocerca gregaria* (Forsk.) (Orthoptera, Locustidae)). Bull Ent Res 64:19–32

Riley JR, Reynolds DR (1979) Radar-based studies of the migratory flight of grasshoppers in the middle Niger area of Mali. Proc R Soc London Ser Biol 204:67–82

Schaefer GW (1976) Radar observations of insect flight. In: Rainey RC (ed) Insect flight. Symp R Ent Soc London, 7. Blackwell Scientific Publications, Oxford, pp 157–197

Waloff Z (1972) Observations on the airspeeds of freely flying locusts. Anim Behav 20:367–372

Weis-Fogh T (1956) Biology and physics of locust flight. II. Flight performance of the desert locust (*Schistocerca gregaria*). Phil Trans R Soc Ser B 239:459–510

Weis-Fogh T (1976) Energetics and aerodynamics of flapping flight: a synthesis. In: Rainey RC (ed) Insect flight. Symp R Ent Soc, London, 7. Blackwell Scientific Publications, Oxford, pp 48–72

Wendler G (1974) The influence of proprioceptive feedback on locust flight co-ordination. J Comp Physiol 88:173–200

Wilson DM (1961) The central nervous control of flight in a locust. J Exp Biol 38:471–490

Zar JH (1974) Biostatistical analysis. Englewood Cliffs, Prentice Hall

Zarnack W (1972) Flugbiophysik der Wanderheuschrecke (*Locusta migratoria* L.). I. Die Bewegungen der Vorderflügel. J Comp Physiol 78:356–395