

BIOLOGY AND PHYSICS OF LOCUST FLIGHT
VIII. LIFT AND METABOLIC RATE OF FLYING LOCUSTS

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(Received 6 September 1963)

INTRODUCTION

The external work performed by an animal during *natural* locomotion is known only very approximately in dogs and man working a treadmill, a rolling carpet or an ergometer. At normal rates of movement it is clear that the total power expenditure, the metabolic rate, is closely related to the work done, but at high frequencies of movement the internal loss due to limb inertia and damping tend to dominate. The latter is held to be true particularly in flying insects because of the relatively large moment of inertia of the wing mass and the high stroke frequencies observed within this group of animals (Sotavalta, 1947, 1952). However, calculations have shown that the aerodynamic work claims a very significant fraction of the metabolic rate (Weis-Fogh & Jensen, 1956), and both observations (Weis-Fogh, 1959, and unpublished) and calculations (Weis-Fogh, 1961) demonstrate that locusts and other insects must be provided with an elastic system which counteracts the losses due to wing inertia.

Any further analysis of this problem is hampered by lack of knowledge concerning the metabolic rate during natural flight. How big is the total expenditure and how big a share does the aerodynamic work claim? This can be studied if a method is devised by means of which the metabolic rate (given in kcal. kg.⁻¹ hr.⁻¹) can be measured under steady-state flight at known intensity, as has been done here. Furthermore, the real aerodynamic work should be known. So far, this has only been estimated experimentally in one type of flying animal, the locust (Jensen, 1956). From his figures of aerodynamic torque (figs. III, 22 and 23), I have calculated (a) the work which the four wings do on the air, mainly during the downstroke, and which we shall refer to as positive aerodynamic work, and also (b) the negative aerodynamic work, i.e. the work which the wind forces do on the wings, mainly during the upstroke. During almost level steady flight of a female locust the positive work corresponded to an aerodynamic power expenditure of 8.9 kcal. kg.⁻¹ hr.⁻¹ and the negative work to -4.5 kcal. kg.⁻¹ hr.⁻¹. It is clear that, during steady-state level flight, the energy for negative work must in some way derive from the positive aerodynamic work done. Its immediate source must be either the kinetic energy of the flying animal relative to the stationary air or air currents produced by the wings during some previous phase of positive aerodynamic work. Consequently, the *net amount of aerodynamic power*, P_a , which is transferred from the animal to the air in other forms than as heat is the sum of the two, i.e. $8.9 + (-4.5) = 4.4$ kcal. kg.⁻¹ hr.⁻¹. This figure relates to horizontal flight of average intensity and normal stroke parameters.

It must be strongly emphasized that Pa in no way represents the mechanical power for flight but only the amount of power which is not eventually dissipated as heat in the thorax but as heat in the slip-stream. If, then, we can measure the rate of heat production in a flying locust, its metabolic rate can be estimated. Let the net rate of heat production in the working thorax be Pn and the heat dissipated by evaporation of water in the respiring thorax be Pw . The gross heat production is $Pn + Pw$ and the metabolic rate is

$$P = Pn + Pw + Pa. \quad (1)$$

From this should be subtracted the rates due to the metabolism outside the wing muscles, but, since this amounts to only 1–2% of P , the correction is not essential.

It will be shown that, when the main average force component, the lift, is changed by the animal from 50% of the body weight to 170%, the metabolic rate increases almost linearly by 2.7 times, and this was found to be in reasonable agreement with theoretical deductions. Moreover, the extra expenditure due to the simultaneous increase in wingstroke frequency is small in comparison. From the point of view of energetics the locust thorax is therefore designed for its main task, to fly, and the expenditure due to wing inertia is counteracted mainly by an elastic system (Weis-Fogh, 1959, 1961).

METHODS

(a) *Insects and flight*

Full-grown, sexually immature desert locusts (*Schistocerca gregaria* Forskål, *phasis gregaria*) were flown in an aerodynamic balance at their preferred flying speed v and lift L ; the wingstroke frequency N and the other main stroke parameters were measured in stroboscopic light (Weis-Fogh, 1956a). For each individual the size-dependent quantities were corrected to those for a locust of average size by means of size indices (Weis-Fogh, 1952).

(b) *Net rate of heat production, Pn*

The method of estimating the metabolic rate by indirect calorimetry is based on a technique designed by Krogh (1948) for non-flying insects. Pn was estimated indirectly from the *excess temperature* Δt of the working thorax above that of the ambient, streaming air. All experiments took place in subdued light in a constant-temperature room and usually at about 30° C. and 50–60% relative humidity.

Excess temperature. The suspension was of the sternal type (3). A Standard Electric thermistor, type U, was inserted through a small hole cauterized in the metabasisternum at the medio-posterior border of the origin of the dorso-ventral elevators in the metathorax. The dry wound (light CO₂ narcosis) was immediately sealed with a small amount of adhesive wax. The thermistor bead was placed between the muscles and the gut almost at the transition between meso- and metathorax, 3–4 mm. above the sternum. Here the temperature of the working thorax is maximum, according to simultaneous measurement of the temperature distribution by means of five such thermistors (Weis-Fogh & Muus, unpublished). The sensitive bead and the leads were covered with a thin layer of celluloid and, being flexible, they did not seem to hamper movement. The accuracy was $\pm 0.2^\circ$ C.

The animal was freely exposed to the wind except for (a) three pointed plastic pegs,

5 mm. long and 2 mm. in diameter, to which the sternum was glued by means of minute amounts of wax, and (b) the thermistor shaft consisting of Marco resin of similar dimensions. Together, the four projecting rods covered about 15 mm.² of the pterothoracic surface area of 500 mm.², i.e. about 3%. The rods may increase heat loss by convection from this area by maximally 50–100% compared with the free surfaces, and thereby alter Δt by about 2% relative to a freely flying locust. Since the relationship between Δt and P_n was estimated with similarly suspended animals, the error is of no consequence here, and the results may also be applied to freely flying locusts.

Heat production. The supraoesophageal ganglion of a locust was cauterized (decerebration) to prevent flight and other spontaneous activity. The first five pairs of spiracles were closed by means of wax to prevent evaporative loss from the pterothorax while permitting ordinary respiratory movements and blood circulation. The insect was suspended as before, but with the wings spread out horizontally and, in addition, four heating electrodes of platinum, each 5 mm. long and 0.5 mm. in diameter, were inserted through the ventral cuticle and pushed up into the interior of each group of dorso-ventral wing muscles. The electrodes were connected to the exterior via short lengths of 0.05 mm. platinum-iridium wire. The high frequency a.c. generator (3.3 kcyc./sec.) was adjusted continuously to give a fixed rate of heat production (Krogh, 1948). The heat loss through the sealed-in platinum-iridium wires would correspond to less than 1% of the production. It was also found that the distribution of temperature within the pterothorax was similar during artificial heating and natural flight. This is in accordance with Church (1960b), who found that circulation of the haemolymph during flight contributes little to the heat flow and that only 5–15% of the heat generated is conducted towards other parts of the locust, about 80% being lost by convection from the pterothorax itself. In both sets of experiments the exchange by long-wave radiation was negligible. In all essentials the heat situation of the artificially heated locust therefore resembled that of a flying animal and, since the evaporation through the closed spiracles is insignificant, a sufficiently accurate relationship between P_n and Δt could be established for any wind speed and size.

(c) *Heat of evaporation*

The rate of heat loss by evaporation of water from the pterothorax, P_w , was estimated in experiments in which a roundabout was used. Studies of the ventilatory mechanism have shown that the pterothorax is ventilated locally by the thoracic pumping of air (Weis-Fogh, 1964) mainly in and out through the wide-open second and third spiracles (Miller, 1960). The cooling can therefore be localized to the pterothorax, more precisely to the air tubes inside the wing muscles. In the first series of experiments small groups of locusts were flown in a roundabout for several hours and the metabolic rate was estimated from the average flying speed (Weis-Fogh, 1952). The animals were weighed before and after flight and the decrease in weight was corrected for the faeces passed. Only flights lasting several hours at constant speed and with an insignificant amount of truancy were used, partly because one must be sure that the locusts mainly used fat for combustion and partly because they tend to spit and pass many faecal pellets during the first hour. This would increase the apparent rate of evaporation. The rate of evaporation of water was calculated from the metabolic

rate and the water produced by combustion, the true weight loss, the thoracic temperature and the humidity. It is expressed in g. lost per kg. body weight per mm. Hg difference in water vapour pressure of the air saturated at thoracic temperature and that of the ambient air ($\text{g. kg.}^{-1} \text{ hr.}^{-1} \text{ mm. Hg.}^{-1}$). In two experiments lasting 4.5 hr. (15 females) and 9 hr. (12 males) the loss was 0.36 and 0.27 $\text{g. kg.}^{-1} \text{ hr.}^{-1} \text{ mm. Hg.}^{-1}$, respectively, the error being $\pm 30\%$. Church (1960a) used single individuals having mouth and anus sealed with wax. He found values corresponding to 0.34 and 0.41 in short experiments ($\Delta t = 6^\circ \text{C.}$). He also found that about one-third of the loss was due to transpiration through the cuticle and the remainder through the tracheal system. We may therefore adopt 0.3 $\text{g. kg.}^{-1} \text{ hr.}^{-1} \text{ mm. Hg.}^{-1}$ as a reasonable value, corresponding to Pw of approximately $0.17 \pm 0.05 \text{ kcal. kg.}^{-1} \text{ hr.}^{-1} \text{ mm. Hg.}^{-1}$. The saturation deficit was known from the temperature measurements in each case. The large inaccuracy is of little consequence because Pw is small relative to Pn under all conditions of steady flight.

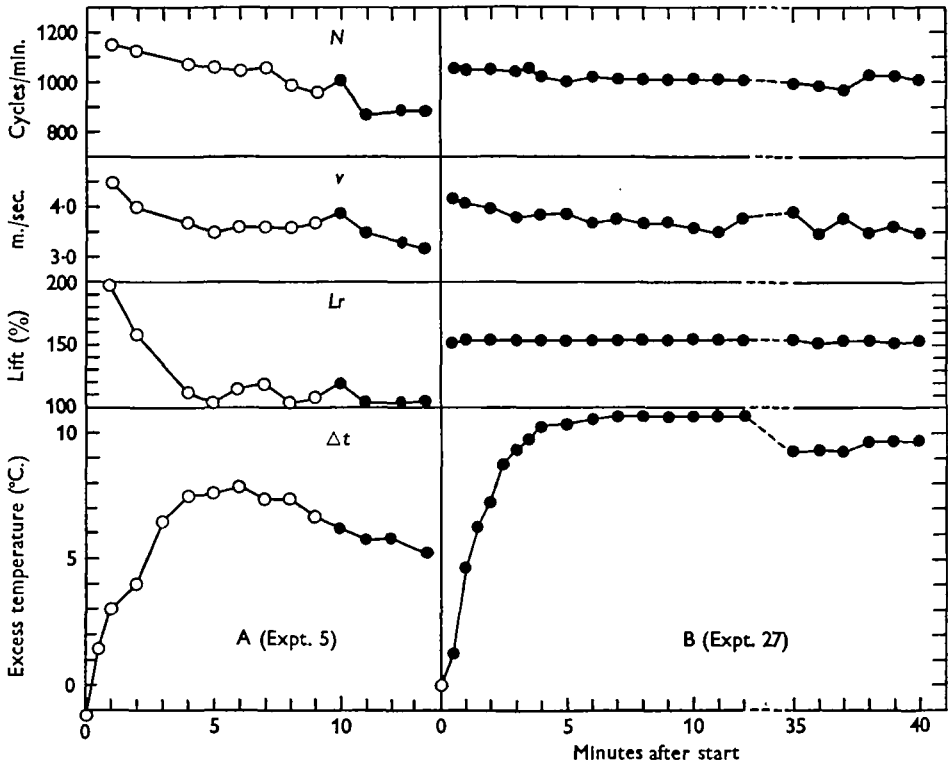


Fig. 1. The relationship between the excess temperature Δt of the pterothorax of a desert locust and the time after the beginning of flight, together with the simultaneous variations in relative lift Lr , flying speed v and wingstroke frequency N . (A) is the typical case and (B) is exceptional because the lift remained constant from the start and until flight was stopped after 40 min.

RESULTS

In all experiments the suspended locust flew at its preferred flying speed against wind from a wind tunnel. The average vertical force which the wind imparts to the body is called the lift; it is expressed as the relative lift Lr , i.e. in per cent of the basic

weight of the individual in question, so that all the results are comparable (Weis-Fogh, 1956*a*).

(*a*) Excess temperature Δt

Fig. 1 shows how rapidly Δt increases when flight starts; it may exceed 10°C . in less than 4 min. (A) is the more typical case since the locust starts with maximum lift (Lr), speed (v) and wingstroke frequency (N), all of which decline towards the normal values for level sustained flight during the first few minutes. It is obvious that steady-state flight was not reached after 10 min. when the animal took up complete flight posture with folded-up hind tibiae (filled circles). In most cases 30–150 min. of flight were required, before it became possible to obtain some periods during which Δt , Lr , v and N remained steady, the other stroke parameters were normal and symmetrical, and the animal maintained flight posture for several minutes in succession (5–40 min.). All subsequent results refer to such steady-state situations. Fig. 1 B is an exception since the locust took up a steady performance at once and continued until stopped after

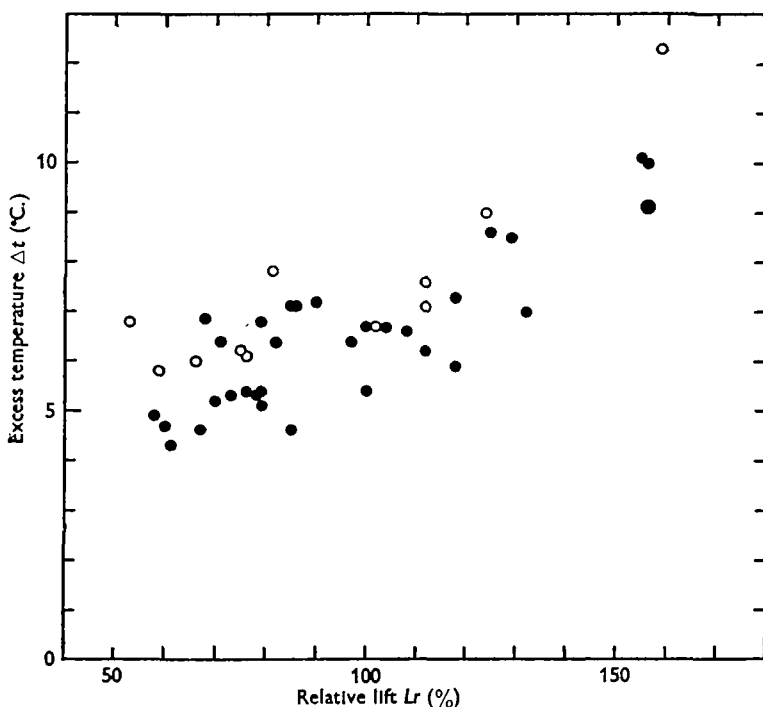


Fig. 2. The excess temperature of the pterothorax of desert locusts in steady-state flight as a function of the lift produced. Open circles mean that the flight posture was not complete, filled circles that it was complete.

40 min. It illustrates the rate of heating at a constant, high-lift output and, also, that flight may become less expensive in energy with time since Δt decreased slowly from 10.7° to about 9.6°C . In order to obtain values representative for free flight, readings were therefore not taken earlier than 15 min. after start and usually much later.

It is clear from Fig. 2 that in 44 cases of steady-state flight Δt increased significantly with the lift produced. The open circles refer to experiments in which the hind tibiae were not drawn up (incomplete posture); in the remaining 33 experiments performed

with 14 individuals from three batches of females posture was complete (filled circles). Since Δt depends on size, wind speed and net heat production, it does not follow directly that the animals in the first group flew less economically than those in the second group, but, since estimates of the total power output demonstrated that this was the case, the results from the first group were discarded.

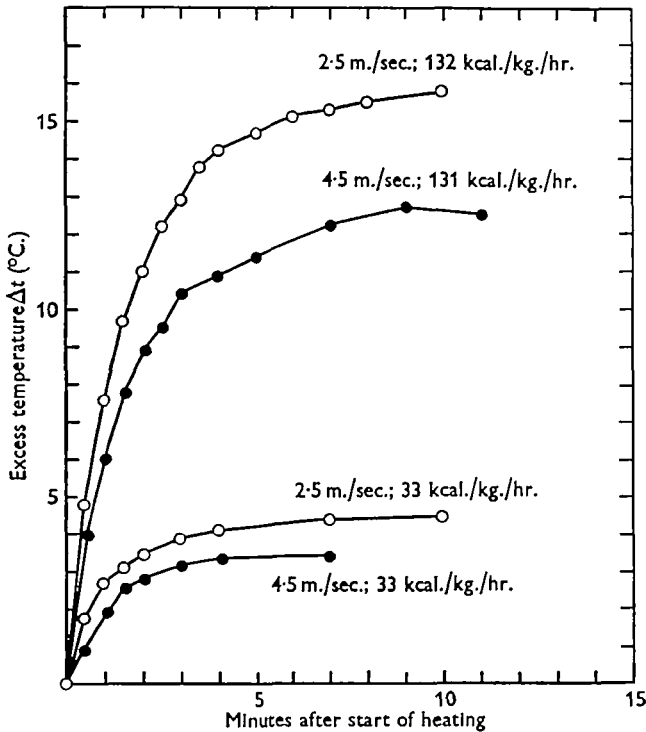


Fig. 3. Excess temperature Δt during the initial period of artificial heating of a resting decerebrate desert locust with unfolded wings. Two different wind speeds and two levels of constant rate of heating.

(b) *Excess temperature and P_n*

In order to estimate P_n , a relationship must be established between Δt , P_n , v and the size of the individual expressed by the surface index s . Fig. 3 is an example of the heating-up of a decerebrate locust at different wind speeds. The curves are similar to that in Fig. 1 B and it is seen that a steady state is reached 5–10 min. after a constant rate of heat production has begun, depending upon rate and speed. Fig. 4 shows how steady-state values of Δt depend on the rate of heat production at different flying speeds. The highest speed was 4.5 m./sec. and the lowest 2.5 m./sec. and it is seen that the effect of changes in speed within this range is sufficiently small to justify a linear interpolation between the slightly curved graphs. The relative amounts of blood, fat and eggs vary much during adult life, and since it was found that the temperature gradient in the longitudinal direction depends markedly on the amount of blood (Weis-Fogh & Muus, unpublished), Ringer solution was injected in a small group of animals in order to see if it had any significant effect upon the heat balance. Fig. 5 shows that the effect of increasing the body weight by 10–15 % of liquid is so small

that the individual variations found in subsequent experiments probably derive from other factors, namely from variations in the degree of insulation of the pterothorax itself offered by the subdermal air sacs (Church, 1960*b*; Weis-Fogh, 1964).

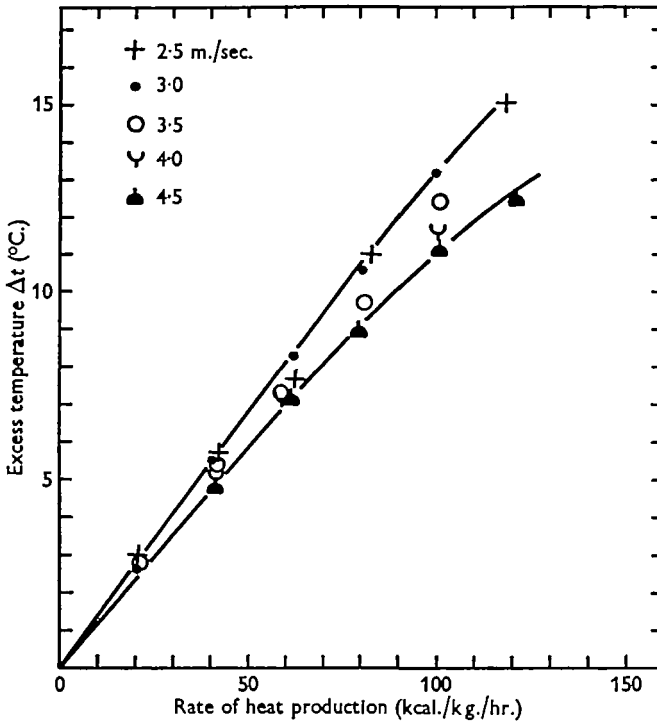


Fig. 4. Steady-state values of excess temperature Δt as a function of constant rates of heating of the pterothorax of a resting decerebrate desert locust placed in a wind tunnel with unfolded wings. The wind speed was altered within the natural range observed during normal flight.

We can now analyse the relationship between Δt and Pn in a more general way. Four males and four females were used, the volume indices of which ranged from 47.5 to 67.5 cm.³ (the average for *Schistocerca* is 54.1 cm.³; Weis-Fogh, 1952). In three cases the gut was full of food while the remainder had been starved for 13–40 hr. previous to the experiments. The results were corrected to an animal of average size (standard *Schistocerca*) by multiplying the heat output by $s/14.3$ where s is the surface index of the individual and amounts to 14.3 cm.² in a standard *Schistocerca*. The eight individual curves for 2.5 and 4.5 m./sec. respectively were averaged and the results are shown in Fig. 6, in which the horizontal bars indicate the standard deviations (9% at low speeds and 11% at high speeds). In any single experiment Pn could then be estimated with an accuracy corresponding to s.d. \approx 10%, and since the curves are almost linear below $\Delta t = 10^\circ$ C. the result can be expressed as

$$Pn = \Delta t(8.5 + a)14.3/s \text{ kcal. kg.}^{-1} \text{ hr.}^{-1}, \quad (2)$$

where a is the speed in m./sec. in excess of 2.5 m./sec.

The rate of increase of Δt during the initial heating up could also be used to estimate

Pn at the start of flight. If the increase during the first minute is $A^\circ\text{C}$., $Pn = 22 \times A \times 14.3/s \text{ kcal. kg.}^{-1} \text{ hr.}^{-1}$, and, if it is B during the second minute, $Pn = 48 \times B \times 14.3/s \text{ kcal. kg.}^{-1} \text{ hr.}^{-1}$. Thus, during eight typical starts, Pn was estimated to about 120 $\text{kcal. kg.}^{-1} \text{ hr.}^{-1}$, s.d. being 20%.

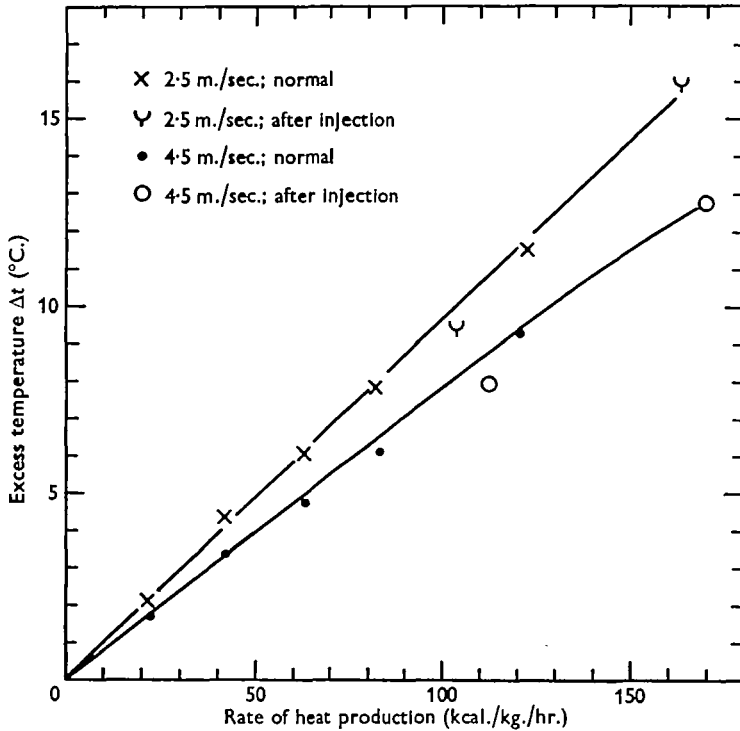


Fig. 5. Same type of experiment as in Fig. 4 with the exception that the animal was heated before (normal) and after injection of 0.4 ml. saline into the haemocoel.

(c) Lift and metabolic rate

The main experimental result is seen from Fig. 7, in which the individual values represent the calculated gross rate of heat production, $Pn + Pw$. Under the experimental conditions Pw was rather small and amounted to only 5–10% of Pn . There is therefore no doubt that the energy output increases significantly and conspicuously with increasing lift. This is seen from the over-all distribution of the results and also from the values obtained with such individuals which, in the course of an experiment, chose to fly at different levels of lift. In these cases the points are connected by thin lines. In addition it is noticeable that an individual may improve its economy to some extent as flight proceeds, a fact already indicated in Fig. 1B. The thick continuous line was calculated according to the method of least squares. In terms of relative lift, Lr , it describes the general result as follows:

$$Pn + Pw = a + bLr = (12.3 + 0.53Lr) \text{ kcal. kg.}^{-1} \text{ hr.}^{-1}. \quad (3)$$

The standard deviation of the sum is 7.3 $\text{kcal. kg.}^{-1} \text{ hr.}^{-1}$, of a it is 4.5 $\text{kcal. kg.}^{-1} \text{ hr.}^{-1}$ and of b it is 0.043. The increase in power output with lift is therefore highly significant. We may describe the relationship between gross rate of heat production and

relative lift as being linear within an accuracy corresponding to a standard deviation of 11 % of the rate for 100 % lift. This is satisfying since it corresponds to the accuracy with which Pn could be estimated in an individual by indirect calorimetry according to equation (2).

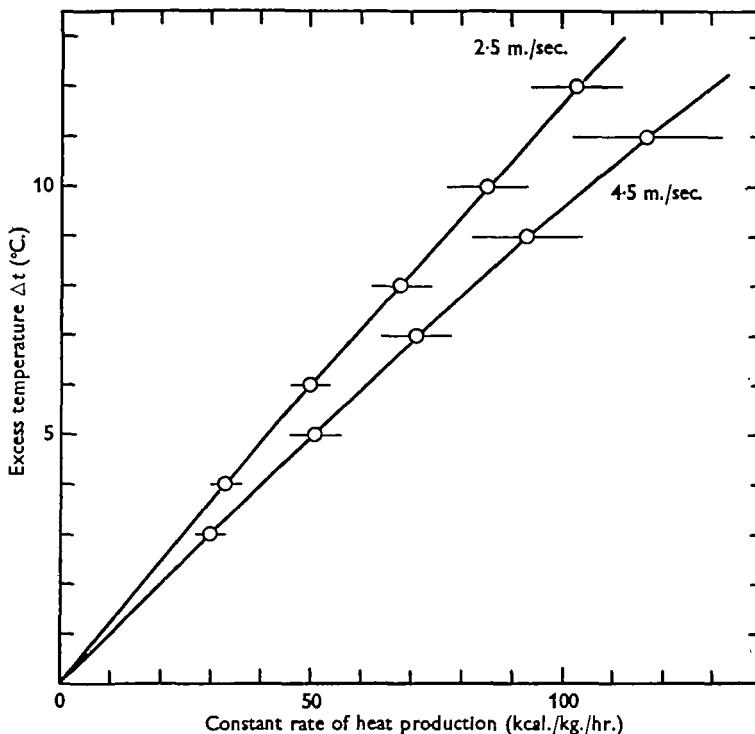


Fig. 6. The relationship between steady-state values of the excess thoracic temperature Δt and constant rates of heat production in eight resting decerebrate desert locusts placed with unfolded wings in a wind tunnel at 2.5 m./sec. and 4.5 m./sec. respectively. The individual results were corrected so as to relate to a *Schistocerca* of standard size. The horizontal bars indicate the standard deviations of the pooled, corrected values.

In order to find the metabolic rate, P , we must now add the net aerodynamic power Pa , amounting to 4.4 kcal. kg.⁻¹ hr.⁻¹ at 97 % lift (Jensen, 1956; and Introduction above). Because of its *relatively* small magnitude and because of the distinct relationship between heat production and the main aerodynamic component of force (the thrust is 20 times smaller than the lift in locusts), Pa has been added by amounts in proportion to the lift, as illustrated by the broken line in Fig. 7. It shows that the metabolic rate increases linearly by 2.7 times when the lift increases from 50 to 170 %, i.e. by 3.4 times.

With respect to magnitude, the metabolic rate was 41 kcal. kg.⁻¹ hr.⁻¹ at 50 % of lift, 65 at 100 %, 98 at 150 %, 110 at 170 %, and (by extrapolation) 127 at 200 %. These figures are in good accordance with earlier experiments in which, however, the rate could not be related to the aerodynamic performance. Thus, the average respiratory exchange of locusts flapping in a container corresponded to an oxygen uptake of 15 l. O₂ kg.⁻¹ hr.⁻¹ or to 70 kcal. kg.⁻¹ hr.⁻¹ (Krogh & Weis-Fogh, 1951). Similarly,

locusts flying at their average speed in a roundabout oxidized fat and glycogen at a rate corresponding to $75 \text{ kcal. kg.}^{-1} \text{ hr.}^{-1}$ (Weis-Fogh, 1952), but in both types of experiment the individual values ranged from 50 to $140 \text{ kcal. kg.}^{-1} \text{ hr.}^{-1}$. There is therefore no doubt that this is the natural variation. We now know that $65 \text{ kcal. kg.}^{-1} \text{ hr.}^{-1}$ is the rate necessary for level continuous flight of a full, sexually immature migrant.

The next problem is to decide, if possible, how much of the power output is accounted for by aerodynamic work and how much can be related to other types of expenditure. We can expect no precise answer with the present procedure but only a semi-quantitative estimate.

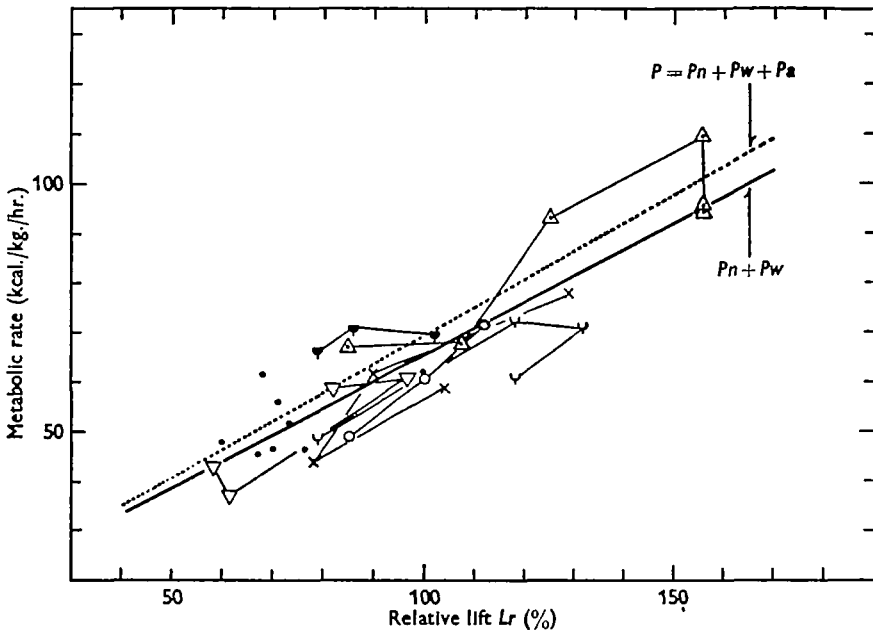


Fig. 7. The relationship between the metabolic rate and the relative lift produced by flying desert locusts. $P_n + P_w$ is the net heat production while $P = P_n + P_w + P_a$ is the total metabolic rate after the net aerodynamic power has been added. 33 experiments with fourteen different animals. The thick full line was constructed according to the method of least squares while the thin lines connect values obtained with the same individuals.

(d) Metabolic rate and frequency

The following three methods all tend to show that the cost of oscillation without doing external, aerodynamic work is relatively small in locusts—about three to four times less expensive than actual flying.

When we extrapolate the line in Fig. 7 to zero lift, i.e. to zero aerodynamic work, the metabolic rate would be about $12 \text{ kcal. kg.}^{-1} \text{ hr.}^{-1}$. If in a similar way we extrapolate the relationship between wingstroke frequency and relative lift, N for a standard *Schistocerca* would amount to 900 min.^{-1} when the lift is zero, 975 for 50% of lift, 1040 for 100%, and 1135 for 170% (Weis-Fogh, 1956a; eq. II, 5). Since the work of oscillation should depend on N^3 (because the other stroke parameters remain almost constant; see Weis-Fogh, 1956a), the cost of wing oscillation should amount to

12 kcal. kg.⁻¹ hr.⁻¹ at 0% lift, 16 at 50% lift (against 41), 19 at 100% lift (against 65), and 25 at 170% lift (against 110). In other words, the oscillation itself should cost three to four times less than the actual expenditure during level flight.

A similar result is obtained if instead of extrapolating we use the measured values only. We have seen that the metabolic rate increased from 1 at 50% lift to 2.7 at 170%, i.e. an addition of 1.7 units. The ratio for N^3 was 1:1.6, so that the corresponding increase was only 0.6.

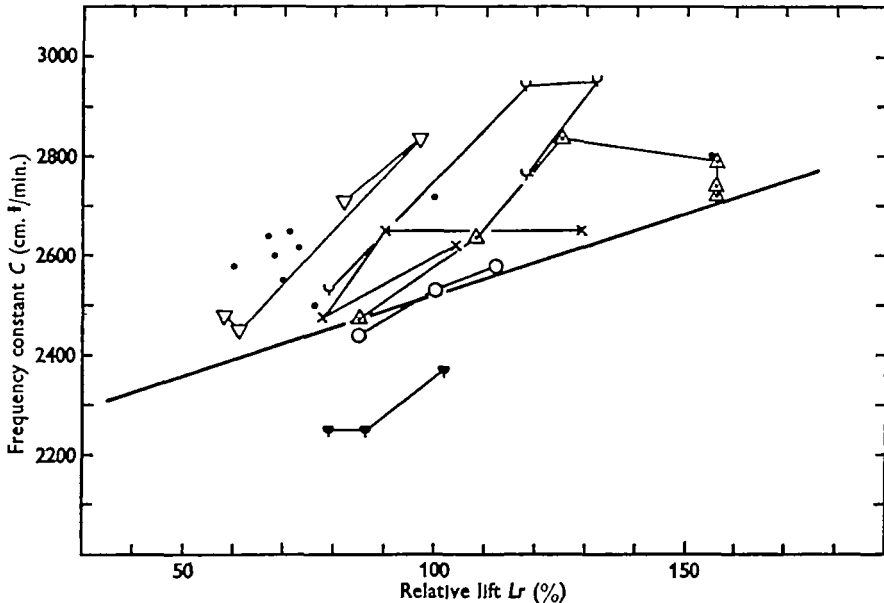


Fig. 8. Relationship between the frequency constant C and the relative lift in the same experiments as in Fig. 7.

The third procedure supports the above results but it also indicates that the effect of frequency is smaller than indicated above. If we calculate the so-called frequency constant C for each individual from the relationship given by Weis-Fogh (1956*a*), we can compare the actual frequency constants (the symbols in Fig. 8) with the expected ones (thick line in Fig. 8). It is then seen that in the present experiments the average wingstroke frequency was about 8% higher than that to be expected from earlier observations based on a much larger material, and we observe the same increase in frequency with lift as before. If the frequency is a dominating factor in the energy account, one would expect that the locusts with the highest frequencies would also have the highest metabolic rates. However, a comparison between Figs. 7 and 8 shows just the opposite tendency (individuals marked ∇ , \times and ψ). Conversely, the only locust which had a frequency lower than normal also had a metabolic rate higher than the average (marked \blacktriangledown).

There is therefore neither qualitative nor quantitative justification for the belief that the increase in power with increasing lift is correlated mainly with frequency. On the contrary, the results tend to show that locust flight becomes more economical if the frequency is increased somewhat above the values given earlier. This is probably

due to the elastic system, which may be designed to operate at somewhat higher frequencies (and mass forces) than hitherto believed. The mere oscillation may then account for about one-quarter of the expended energy while the remaining three-quarters are spent against wind forces. From the point of view of energetics the flight system of locusts is adapted to its function—to make the insect airborne with as little extra cost as possible.

DISCUSSION

We have seen that over a large range of lift the metabolic rate, i.e. the *total power* output, increases linearly with this major *force* component. We have also seen that the work necessary for oscillating the wings in the absence of wind forces constitutes a relatively small fraction of the total expenditure. It is therefore instructive to consider the type of relationship between *aerodynamic power* and lift which one can deduce from theories of flapping flight. If, in the case of locusts, this relationship is also linear there is agreement between theory and observations.

(a) Power and lift

According to the treatment of Holst & Küchemann (1941), the total aerodynamic drag which a wing is working against is

$$D = (\pi/2)\rho v^2 S(dC_L/d\alpha) \sin \Phi n \alpha_a / v.$$

The aerodynamic power Pa is then

$$Pa = (\pi/2)\rho S(dC_L/d\alpha) a \sin \Phi [\alpha_a v^2 n]. \quad (4)$$

The model on which this equation is based, the symbols used, and the validity of the expressions have been discussed previously (Weis-Fogh & Jensen, 1956, pp. 440-4). Here, the main point is that all quantities in front of the brace do not alter with lift when locusts fly in complete posture, while those within the brace depend upon the lift. α_a is the amplitude of the sinusoidally changing angle of attack, v is the flying speed, and n the wingstroke frequency. In the optimum case, which corresponds well to actual flight of locusts (Jensen, 1956), the angle of attack α varies from zero to 5-15%, depending on the lift. Within this range, the coefficient of lift C_L remains almost linearly related to α ($dC_L/d\alpha$ is constant) so that lift is proportional to α_a . Since both v and n increase little with lift (Weis-Fogh, 1956a) there is a tendency towards a linear relationship between Pa and Lr in flying locusts.

Walker's theory (1925, 1927) is based upon a more complete treatment of flapping flight. For each element of wing surface we have for the work W_a^d done during the all-important downstroke (superscript d ; see Weis-Fogh & Jensen, 1956; eq. 1, 23):

$$W_a^d = (\rho/4)v^3 k \sqrt{(1+k^2)} \{C_L^d + kC_D^d\},$$

where ρ = mass density of air, v = flying speed, k = flapping ratio, and C_L^d and C_D^d are the coefficients of lift and drag, respectively, of the element during the downstroke. According to eq. 1, 21, in Weis-Fogh & Jensen (1956), the total lift L is

$$L = (\rho/4)v^2 \sqrt{(1+k^2)} \{(C_L^d + C_L^u) + k(C_D^d - C_D^u)\} \sin(\phi/2)/(\phi/2),$$

where u indicates the upstroke. In the optimum case, C_L^u and C_D^u are both zero so that the ratio $W_a^d/L = (vk\phi)/(2\sin(\phi/2))$, and the power per unit lift becomes $P_a^d/L = (nvk\phi)/(2\sin(\phi/2))$. Since the flapping ratio is $k = 2n\phi r/v$, the ratio between

the aerodynamic power of a wing element and the lift produced by that element becomes

$$P_a^2/L = n^2\phi^2r/\sin(\phi/2). \quad (5)$$

In flying locusts r remains constant while n increases with the lift and, in the forewings, ϕ decreases, so that n^2 increases from 1 to 1.4 and ϕ^2 decreases from 1 to 0.9 when the lift changes from 50 to 170%. The ratio is therefore not constant but the relationship between aerodynamic power and lift does not deviate much from linearity. Neither the theoretical nor the experimental procedures justify more accurate statements for the time being.

(b) Metabolic rate and size

There are only few determinations of the metabolic rate of freely flying animals. Thus Lasiewski (1963) recently measured the oxygen uptake to be 42 l. O₂ kg.⁻¹ hr.⁻¹ in a humming-bird (*Calpyte costae*) hovering for not less than 35 min. in a respiration chamber. This corresponds to about 200 kcal. kg.⁻¹ hr.⁻¹. In various moths flapping freely against the walls of a container, Zebe (1954) found values from 120 to 500 kcal. kg.⁻¹ hr.⁻¹ but the lift of these animals was not known. There are numerous determinations from tethered insects and in the present study we have seen that there are good reasons to believe that the range observed corresponds to that in free flight. On the basis of such data, Sotavalta & Laulajainen (1961) claim that the metabolic rate per unit weight should increase as (body weight)^{0.2}. However, if we insert the values for *Calypte* and *Schistocerca* in their fig. 8 (in which the scatter is very great), it is obvious that the metabolic rate per unit weight lifted is almost independent of the size of the flapping animal, as has been pointed out before (Weis-Fogh, 1961). This result is in agreement with the extensive aerodynamic calculations performed by Osborne (1951, his fig. 10). Moreover, he found that the lowest probable aerodynamic power output of insects is about 8 kcal. kg.⁻¹ hr.⁻¹ and 30 kcal. kg.⁻¹ hr.⁻¹ is about the highest. If these values are compared with the metabolic rates, it is obvious that Pa must claim a very considerable share of the mechanical power of the contracting muscles, as previously discussed (Weis-Fogh & Jensen, 1956, tables 1, 10). In locusts and in *Drosophila* (Chadwick & Williams, 1949; Chadwick, 1951) it is now clear that the aerodynamic load is the essential term in the energy account, a result which seems to apply to most insects but which contrasts with the opinion of Sotavalta (1952).

(c) Control of power

Chadwick (1951, 1953) and Chadwick & Williams (1949) found that the metabolic rate of *Drosophila* often remained constant during short tethered flights in spite of alterations of the mass density of the air. These alterations were accompanied by distinct changes in frequency and stroke angle in a way reminiscent of a homeostatic system which tended to keep the aerodynamic power-output constant. According to the present results the constant-lift reaction exhibited by the desert locust would have the same effect; the locusts tend to move their wings in a rather constant way but, if the orientation of the body axis relative to the wind changes, they tend to keep the lift constant by changing the wing-twisting (Weis-Fogh, 1956*b*). If other insects possess a similar control system with respect to lift, and since the aerodynamic expenditure is the dominating one, the control of power and metabolic rate may then be a consequence of a receptor system specifically sensitive to lift.

Another problem concerns the considerable change in power output of the same individual at different times. In insects with fibrillar wing muscles Pringle (1960) has discussed various possibilities based upon specific level systems which may alter the load on the indirect wing muscles. It is now known that in the locusts, which have ordinary muscles, a continuous change in power output is obtained partly by changing the small number of active motor units and partly by changing the amount of double firing of each unit (Wilson & Weis-Fogh, 1962). The latter procedure may result in two to three times more work than in an ordinary twitch (Neville & Weis-Fogh, 1963). From a neuromuscular point of view, it is therefore not difficult to explain the results in Fig. 7.

SUMMARY

1. A calorimetric method was designed which makes it possible to estimate the metabolic rate of a flying insect with an accuracy of $\pm 10\%$.
2. For the first time, the metabolic rate of a flying animal has been related to the main aerodynamic component of force, the lift.
3. The metabolic rate of locusts increases almost linearly from 41 kcal. $\text{kg}^{-1} \text{hr}^{-1}$ at 50% relative lift to 110 kcal. $\text{kg}^{-1} \text{hr}^{-1}$ at 170%.
4. The results are in accordance with theoretical deductions and they show that the work necessary to accelerate the oscillating wings (inertia terms) is small compared with the aerodynamic work—probably three to five times smaller.
5. In flapping insects and small birds the metabolic rate per unit weight seems to be independent of size. The control of power is discussed.

The locusts were supplied by the Anti-Locust Research Centre, London, and the experimental work was supported by the Carlsberg Foundation, Copenhagen, and the Scandinavian Insulin Foundation, Copenhagen.

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