

RESPIRATION AND TRACHEAL VENTILATION IN LOCUSTS AND OTHER FLYING INSECTS

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In small insects there is no need for respiratory movements because the rate of diffusion of oxygen and carbon dioxide is adequate even during flight, but when the thorax is more than a few millimetres in diameter the primary tracheae or the air sacs which supply the wing muscles must be ventilated (Weis-Fogh, 1964*b*). Apart from various auxiliary mechanisms described by Miller (1960*a*, 1964), the respiratory movements are of two different types: the well-known abdominal movements which result in *abdominal pumping* of air and haemolymph and the little-known movements of the thoracic walls which are caused by the wing movements themselves and which result in *thoracic pumping* at wingstroke frequency (Weis-Fogh, 1956*a*, 1964*a*). The existence of a thoracic mechanism has been suspected for a long time (du Buisson, 1924; Krogh, 1941; Krogh & Zeuthen, 1941) but was denied by Fraenkel (1932*a*) who investigated the abdominal respiratory movements and their control in a variety of large insects during tethered flight. Lack of suitable methods seems to have prevented further studies.

The main object of the present paper is to determine the rate with which the wing system is ventilated in the flying desert locust and to estimate the contribution made by the thoracic mechanism in locusts and in some other insects. The results are discussed in relation to the direct ventilation of the giant tracheal trunks in some beetles caused by the forward movement of the body through the air (Amos & Miller, 1965; Miller 1966*a*) and due to a Bernoulli-effect first suggested by Stride (1958). This type of unidirectional air flow is of course independent of any pumping movements and may be called *draught ventilation* in order to emphasize its passive, dynamic nature. Moreover, the results represent a new set of data which makes it possible to discuss the ecology of locust flight with special emphasis on water economy.

MATERIAL AND METHODS

Material

Adult desert locusts (*Schistocerca gregaria* Forsk&al, *phasis gregaria*) were supplied by the Anti-Locust Research Centre, London, and were used about 2 weeks after the last moult when the cuticle and the muscles are fully developed but before egg material is laid down (full migrants). By means of size indices all results were recalculated to correspond to a locust of standard size (Weis-Fogh, 1952). The wasps (*Vespa crabro* L.) and the dragonflies were caught in the field (*Aeshna mixta* Latreille, *A. cyanea* Müller, *A. grandis* L.).

Flight and metabolic rate

The insects were suspended from an aerodynamic balance in front of a wind tunnel and flew at their preferred lift and speed in a constant-temperature room, in the case of locusts at 28 or 30° C. (Weis-Fogh, 1956*b*). The metabolic rate was estimated from the excess temperature of the thorax, Δt , during steady-state flight, and the relationship between the rate of heat production and Δt was measured in each individual used (Weis-Fogh, 1964*c*). In the case of *Vespa* and *Aeshna* the air temperature was lowered to about 22° C.

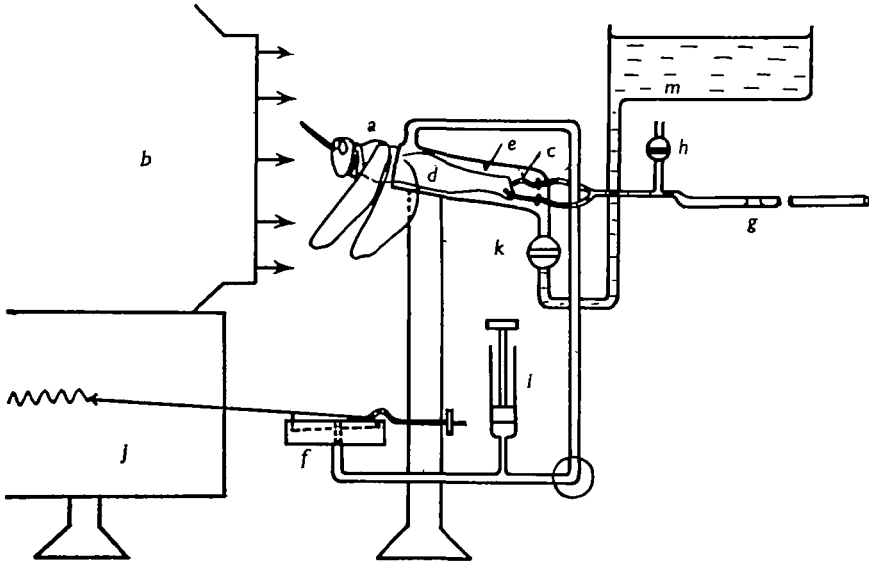


Fig. 1. Apparatus for the simultaneous recording of the total abdominal ventilation in flying locusts and of the component which is unidirectional, i.e. in through the thoracic spiracles and out through the abdominal spiracles (here the large spiracles 10). Further explanation in the text.

Abdominal ventilation

The abdominal movements of flying locusts and the resulting volume changes were recorded in the apparatus shown in Fig. 1. The animal (*a*) was glued to a stand in front of a wind tunnel (*b*) and inclined about 10° relative to the horizontal wind (3.5 m./sec.). The three anterior spiracles 1–3 which supply the head and the thorax were intact while the small spiracles 4–9 on the abdomen were sealed with wax. Each of the large posterior spiracles 10 was provided with a small funnel and a very thin flexible rubber tubing (*c*, made for the purpose). The abdomen (*d*) was placed in a small plethysmograph (*e*) connected to a tiny spirometer of 0.5 ml. capacity (*f*). The plethysmograph was sealed to the animal at the transition between thorax and abdomen by means of a diaphragm of adhesive wax, and the rubber tubes were passed through sealed holes at its rear end and connected to a slightly inclined calibrated glass tube provided with a kerosene droplet (*g*). In this way the wing movements were not interfered with and the abdomen could move freely. Any unidirectional flow of air from the thorax to the last spiracles (Fraenkel, 1932*b*) could be measured independently of the total volume changes which were recorded by the spirometer. Stopcock (*h*) served

to adjust the indicator droplet and the syringe (*i*) was used to calibrate and adjust the spirometer which wrote on a very lightly smoked drum (*j*). At the end of some experiments the plethysmograph and the adjoining glass tubes were suddenly filled with water from the reservoir (*m*) and the system was closed by means of stopcocks (*k*) and (*l*). In this way the abdomen could still change its shape and the normal sequence of muscle contractions continued, but the abdomen was clamped at constant volume so that the respiratory movements did not result in any renewal of the entrapped air.

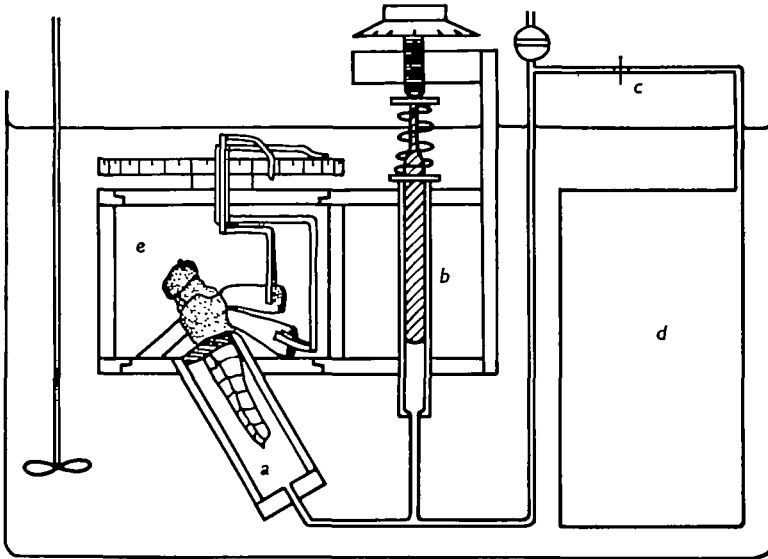


Fig. 2. Apparatus for measuring the change in thoracic volume caused by passive movements of the wings either singly or in a way similar to that observed during flight. Further explanation in the text.

Thoracic volume changes

The alterations of the volume of the pterothorax caused by the wing movements have not been measured before, and it was essential to obtain estimates of the rate of flow in and out of the thoracic spiracles during a typical wingstroke. The insect was suspended in the apparatus shown in Fig. 2. It was starved for 24 hr. previous to the experiment and then exposed to HCN vapour so that the muscles remained completely relaxed and the risk of intestinal fermentation was reduced to a minimum. The wings were spread out and kept unfolded by applying small amounts of wax to the articular sclerites, they were cut down to a length of about 15 mm. and the wounds were sealed with wax. The mouth, the anus and the thoracic spiracles were sealed and most soft membranes in front of the abdomen were stiffened by means of wax (dotted in Fig. 2). The volume changes produced by moving the wings therefore result in air moving in and out of the abdominal spiracles. The abdomen was placed in the lower chamber (*a*) which was connected to a micrometer syringe (*b*) and to the one end of a horizontal glass tube with a kerosene indicator droplet (*c*), the other end being attached to a sealed thermoflask filled with air (*d*), 500 ml.). The anterior part of the animal was placed in the upper chamber (*e*) which was sealed off from the lower compartment. Each wing could be moved independently by means of a bifurcated pointer sealed into the lid of the upper chamber. The apparatus was placed in a water-

bath with a stirrer and left for 2 hr. in order to establish equilibrium of temperature and water vapour pressure (saturated). The long axis of the insect was inclined about 30° to the vertical so that the natural stroke plane was parallel to the upper lid. In locusts the wings were moved in steps corresponding to twelve angular positions of the two pairs of wings, as observed during a *standard stroke*; the duration of a standard stroke is 56–57 msec. (Weis-Fogh, 1956*b*). For dragonflies, a similar set of values was derived from Chadwick's (1940) analysis of a slow-motion film of *Ladona exusta* Say. When the pointers were moved the indicator droplet was pushed away from zero position and the corresponding volume change was measured by bringing it back by means of the micrometer syringe, the accuracy being $0.2 \mu\text{l.}$ in the case of locusts and $0.1 \mu\text{l.}$ in the smaller apparatus used for dragonflies. A small but constant drift towards the animal container was usually observed, probably caused by residual tissue respiration at a low R.Q. All values are corrected for drift.

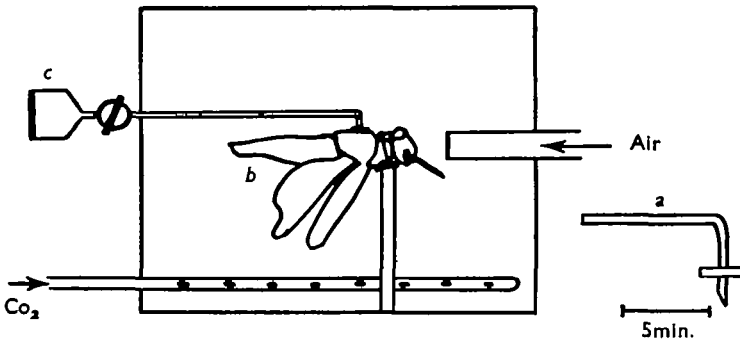


Fig. 3. Arrangement for the recording of the intrathoracic changes in pressure caused by active wing movements of tethered locusts. (a) The tip of the hypodermic saline-filled needle which is connected to the condenser manometer (c). The locust (b) is suspended upside down in a closed box, narcotized by means of CO_2 , and stimulated to 'fly' by means of a jet of air after recovery.

Pressure changes in the air sacs

Both abdominal and thoracic volume changes give rise to pressure changes in the haemocoel. In order to estimate the fluctuating pressure in the thoracic air sacs during tethered flight the tip of a thin hypodermic needle provided with a collar ((a) in Fig. 3, 0.6 mm. external diameter) was inserted through a small hole cauterized in the pterothoracic sternum and was firmly sealed to the thorax. The oblique tip was placed just beneath one of the large air sacs of the sternal system (Weis-Fogh, 1964*a*) so that the fluctuations in blood pressure should correspond almost exactly to the pressure changes inside the thin-walled collapsible air sac. The needle was filled with locust saline and connected to an electronic condenser manometer (Hansen, 1949). The natural frequency of the assembly was 4–5 times higher than the wingstroke frequency and the degree of damping was about 0.7 so that the pressure changes could be resolved in time within about 5 msec. of the true changes, or corresponding to about 10% of a stroke period. The animal (Fig. 3*b*) was suspended upside down in a box, the prothorax being fixed firmly to the pterothorax by means of a mixture of tar and wax. 30% CO_2 in air was used as narcotic during the operation and a jet of air served to stimulate the tethered locust to flap its wings after recovery.

Thoracic ventilation during flight

In order to estimate the true rate of ventilation without being able to measure the volume changes directly when the animal flew in the wind tunnel, a special method had to be designed. Each locust was provided with a small thermistor placed in the pterothorax and the metabolic rate was estimated during steady-state flight at known lift with an accuracy of about 10% (Weis-Fogh, 1964*c*). The locust was provided with a streamlined evacuated glass container of about 50 μ l. capacity (Fig. 4*a*) placed almost horizontally when the animal flew at its normal body angle (10–15°). Its sealed

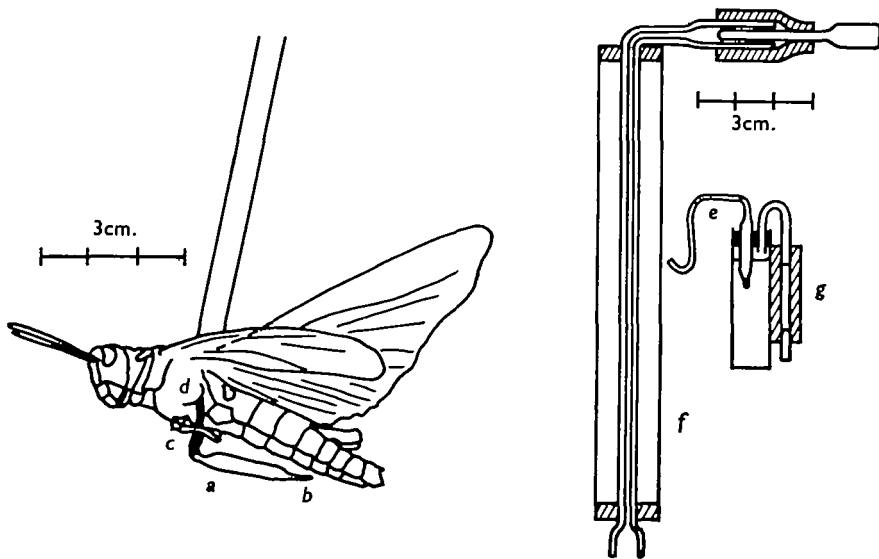


Fig. 4. A suspended, flying locust in which the intrathoracic heat production and the average composition of the tracheal air are estimated simultaneously. (*a*) Evacuated air container with a pointed tip (*b*) and a neck (*c*) which is connected to the second thoracic spiracle of the left-hand side by means of a thin rubber tubing provided with a clamp. (*f*) Simple gas analyser. (*g*, *c*) arrangement for transferring small gas samples to the analyser.

posterior end (*b*) was slightly pointed to facilitate breaking off the tip. A tiny rubber tube (0.4–0.5 mm. internal diameter) with a steel clamp tightened by means of a nylon string connected the anterior end of the container (*c*) to a small glass funnel, the rim of which was glued to the surroundings of the second thoracic spiracle of the left-hand side (*d*); the capacity of the artificial 'atrium' was 2 μ l. Since the spiracle was prevented from closing (and is kept wide open during flight; Miller, 1960*b*), the air present in the 'atrium' should be in equilibrium with the air in the large thoracic air sacs which are supplied by spiracles 1–3 (see Weis-Fogh, 1964*a*). Between the funnel and the clamp the tube was sealed by means of a drop (1 μ l.) of an almost saturated acid solution of sodium citrate which absorbs oxygen and carbon dioxide only to a negligible extent (Scholander, Claff, Teng & Walters, 1951). During a period of steady-state flight a sample of tracheal air was taken by suddenly melting the nylon thread by means of a hot wire. The inflowing air burst the drop which reunited in 1 or 2 sec. to form a new seal at the neck of the container, the tubing was clamped

again and the container was removed for analysis. The rubber tubing was filled with the citrate solution and connected to a U-shaped tube of glass also filled with citrate (Fig. 4e) and the tip of the container was broken off under the solution. In this way the gas sample was sealed by the liquid at both ends and could be transferred to the gas analyser (f) by applying pressure to the pipette (g). The first bubbles were discarded and the concentration of O₂ and CO₂ determined in duplicate samples of 20 μ l. according to Scholander *et al.* (1951) within 0.2–0.3 % of the true percentages. The CO₂ percentage in the pipette arrangement was found to decrease by about 1 % per hour probably due to diffusion through the rubber tubing. Furthermore, control samples of atmospheric air 'contained' only 20.5 % O₂ so that the absorption did not go to completion. The values are corrected accordingly. A duplicate analysis was usually completed about 30 min after sampling.

Knowing the metabolic rate, the thoracic temperature and the average composition of the air in the tracheal system, the rate of ventilation can be calculated as in the following example. Strictly speaking it is the average rate of transport due to ventilation plus diffusion, but diffusion between the ambient air and the thoracic air sacs only accounts for an insignificant share in flying insects as large as the desert locust (Weis-Fogh, 1964b). The locust in question flew at constant lift and with constant wing movements for several minutes and the steady-state thoracic temperature was 35.4° C. or 308.6° K. In this particular animal the rise in temperature above that of the ambient air was found to correspond to an oxygen uptake of 18.1 l. O₂ per kg. locust and per hour, when referred to 0° C. and 760 mm. Hg, but at 35.4° C. and at the actual atmospheric pressure of 745 mm. Hg, the oxygen uptake was

$$18.1 \times (760/745) (308.6/273.2) = 20.8 \text{ l. O}_2/\text{kg./hr.}$$

Since the inspired air becomes saturated with water vapour at 35.4° C. (H₂O vapour, pressure 43 mm. Hg) and since the dry atmospheric air contains 20.5 % O₂ (incomplete absorption), the inspired volume of air contains

$$20.5 \times 702/745 \% \text{ O}_2 = 19.3 \% \text{ O}_2$$

in the animal. The air sample from the working thorax contained 13.2 % O₂ in the dry state which corresponds to 12.4 % in the air sacs, i.e. the average difference between ingoing and outgoing air was 6.9 %. Consequently, the average rate of ventilation was $20.8 \times 100/6.9 = 302$ l. air/kg./hr.

Tracheal pressure and rate of flow

The relationship between the pressure inside the large thoracic air sacs and the rate of flow through the spiracles was measured in the apparatus explained in Fig. 5 and its legend. A thick, short tube of steel was sealed into the two large thoracic air sacs through a hole cauterized in the dorsal cuticle of the pronotum. The spiracles were kept wide open by means of minute pieces of wire and 'closed' by placing small caps over them when need be. In most experiments a constant pressure was applied to the air sacs and the outgoing air flow estimated, but in some experiments the flow was reversed.

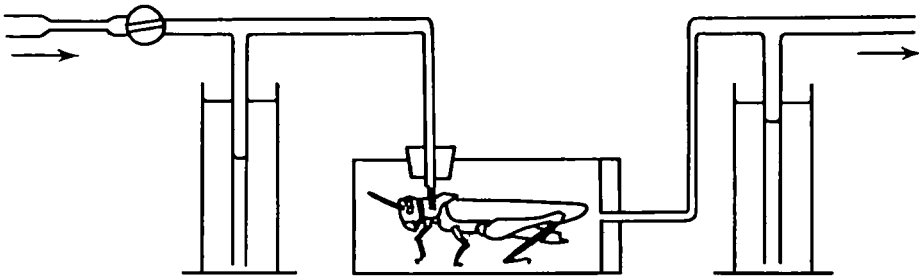


Fig. 5. Simple apparatus for measuring the relationship between the driving pressure and the rate of flow of air between the large thoracic air sacs and the ambient air via the spiracles. The pressure of the inflowing air was stabilized and the rate controlled by means of a constricted capillary tube and a stopcock (left). The right-hand side leads to a small gasometer.

FLYING LOCUSTS

During sustained horizontal flight of full migrants fat is the main fuel and the metabolic rate is 65 kcal./kg./hr. which corresponds to an oxygen uptake of 13.7 l. O₂/kg./hr. (O° C, 760 mm. Hg; Weis-Fogh, 1952, 1964c). The demand depends on the lift produced and the respiratory system must therefore be designed so that it can deliver about 30 l. O₂/kg./hr. when the animal is unusually heavy. If about one-quarter of the inspired oxygen is actually absorbed, as is indicated by the following results, the normal rate of ventilation must be about 330 l. air/kg./hr. but in gravid females it should approach twice as much. These are the requirements which the respiratory system must meet.

Table 1. Average rate of abdominal pumping in the desert locust before, during and after tethered flight (extreme values in brackets)

	Before flight	During flight		After flight
		First 5 min.	Next 10-40 min.	
Number of experiments	19	13	26	7
Pumping frequency (per min.)	33 (20-62)	75 (26-102)	53 (18-80)	(29-58)
Rate of abdominal pumping (l. air/kg./hr.)	42 (11-72)	186 (104-264)	144 (39-245)	(21-138)
Unidirectional rate of flow (l. air/kg./hr.)	33 (10-62)	33 (12-87)	27 (6-45)	(19-66)

(a) Abdominal pumping

In the resting locust the abdominal pumping varies much with the state of excitement and bears no simple relation to the call for oxygen but it is usually much lower than during flight (Fraenkel, 1932a). If, however, the resting locust was exposed to 5% CO₂ the frequency of movement as well as the depth reached a maximum and the pumping amounted to 240-280 l. air/kg./hr., a figure which is higher than observed during flight. From Table 1 it is seen that the average rate of ventilation due to the abdomen was 40 l. air/kg./hr. in resting, suspended animals and 190 during sustained flight. This means that if the abdominal pumping is the only significant mechanism present it can only provide the wing muscles with sufficient air provided that practic-

ally all the inspired oxygen is absorbed. This is very unlikely in any tidal system and particularly here where the tidal volume is small compared with the total (Weis-Fogh, 1964*a*). The only other possibility is that the entire flow is unidirectional during flight and is distributed so that the inflowing air passes the absorbing tissue in a refined and very effective way. But this is not the case, as is seen from Table 1. On the contrary, the unidirectional rate of flow remains at the same constant level of about 30 l./kg./hr. before, during, and after flight activity. The air passes in through the thoracic spiracles (here 1-3) and out through the abdominal spiracles (here no. 10). Reversal of the unidirectional part of the flow was only observed in a single animal which was clearly anomalous. The unidirectional flow is therefore of no quantitative importance for the wing muscles. Since it enters the dorsal orifice of spiracle 1 and passes directly to the cephalic system and back through the ventral paraganglionic tracheae and escapes through spiracles 5-10 (Miller, 1960*b*), it looks as if the abdominal pumping during flight is adjusted not to the needs of the thorax but to needs of the central nervous system. When the flow resistance in the thorax decreases during flight due to the full opening of the thoracic spiracles (Miller, 1960*b*), the abdomen must of course increase its pumping in order to maintain the *same* rate of ventilation in the tracheae supplying the head and the ganglionic chain. As far as respiration is concerned this is considered to be the main function of abdominal pumping in flying locusts, but it must also facilitate the circulation of the haemolymph and function in a way analogous to the venous pump in the working muscles of mammals. However, no specific information is available at present.

The unidirectional part of the flow is therefore of no direct importance for the wing muscles so that the maximum possible ventilation available for the thorax is 150 l./kg./hr., i.e. much less than compatible with normal flight.

(b) *Indirect proof of thoracic pumping mechanism*

It has often been reported that some insects can continue to 'fly' for some time after the abdomen has been cut off, but this cannot be accepted as a proof for an independent thoracic pumping because of the vastly improved conditions for diffusion (see Miller, 1966*b*).

The existence of an effective and sufficient thoracic mechanism for the exchange of air during flight is demonstrated in principle by the following two experiments. In the first case, several locusts had the supraoesophageal ganglion cauterized and this reduced abdominal pumping very considerably. Such animals are able to fly in the flight balance for extended periods of time (Weis-Fogh, 1956*c*) and their metabolic rate was estimated. Before flight it was about 0.7 l. O₂/kg./hr. and the abdomen performed 13 shallow strokes per minute on the average, corresponding to about 10 l. air/kg./hr. During flight the metabolic rate increased to an average of 10 l. O₂/kg./hr., but the abdominal frequency only increased to 19 strokes per minute and, being of medium depth, this would correspond to only 20 l. air/kg./hr. In other words, the working thorax does not need the contribution of air due to abdominal pumping but must have a system of its own. Thus, the most intensely flying decerebrate locusts absorbed 16 l. O₂/kg./hr. with an abdominal frequency of only 21 small strokes per minute.

In another type of experiment with intact locusts the plethysmograph in Fig. 1 was suddenly filled with water and the stopcocks (*k*) and (*l*) closed. The abdominal move-

ments continued and became grossly increased in amplitude, but the movements could not result in any volume changes and the unidirectional flow ceased immediately. Nevertheless, the wing movements went on at normal frequency and stroke angles as long as the wind from the tunnel remained on, i.e. for more than 10 min. after the abdominal ventilation had been completely blocked.

The respiratory movements of the abdomen are therefore neither sufficient nor essential for the supply of oxygen to the working wing system of locusts.

(c) Thoracic volume changes

The wings are suspended from the dorsal edge of the pterothoracic box and when they move up the sclerotized nota move down and vice versa, causing a change in thoracic volume of about 20 μ l. per wing stroke of a standard *Schistocerca* (Weis-Fogh, 1964a). This rough figure corresponds to a rate of thoracic pumping of maximally

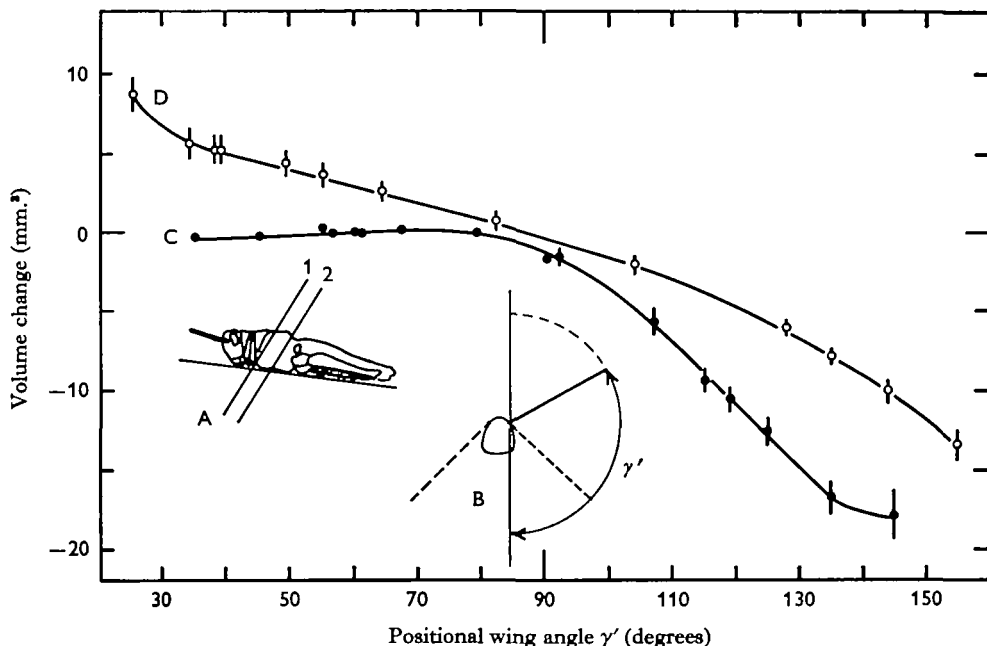


Fig. 6. Changes in thoracic volume of a desert locust of standard size (standard *Schistocerca*) when one pair of wings is kept fixed and near to the horizontal (γ' near to 90°) and the other pair is moved in the natural stroke plane. (A) indicates the stroke planes of forewings (1) and hindwings (2) and (B) shows the positional angle of a wing γ' as measured in the stroke plane. In curve (C) the hindwings are fixed at $\gamma'_2 = 89^\circ$ while the forewings are moved from the extreme lower position (35°) to the extreme upper position (145°). In curve (D) the forewings are kept fixed at $\gamma'_1 = 70^\circ$ while the hind wings are moved. Average results from eight locusts which varied in volume from small males of volume index $v = 40.0 \text{ cm}^3$ to large females where $v = 67.0 \text{ cm}^3$, all figures being recalculated to a locust of standard volume $v = 54.1 \text{ cm}^3$ (Weis-Fogh, 1952). The vertical bars show the standard error and indicate a remarkable geometrical similarity between the locusts used in this and in the succeeding figures.

640 l. air/kg./hr. but the movements of the side-walls (the pleura) have not been taken into account, and moreover, the pumping represents the *potential* ventilation and need not result in an actual ventilation of this magnitude. It was therefore necessary first

to measure the volume changes and then to find out to which extent they result in transport of air.

The two pairs of wings are moved independently of each other but they are coupled both by nervous mechanisms (Wilson, 1961) and also to a certain extent mechanically since they share the fused meso- and metapleura and since the anterior part of the metanotum is firmly hinged to the rear margin of the mesonotum. When one pair of wings was kept fixed and the other pair was moved, the volume of the thorax changed with the positional angle γ' as seen in Fig. 6. Both pairs contribute to the volume

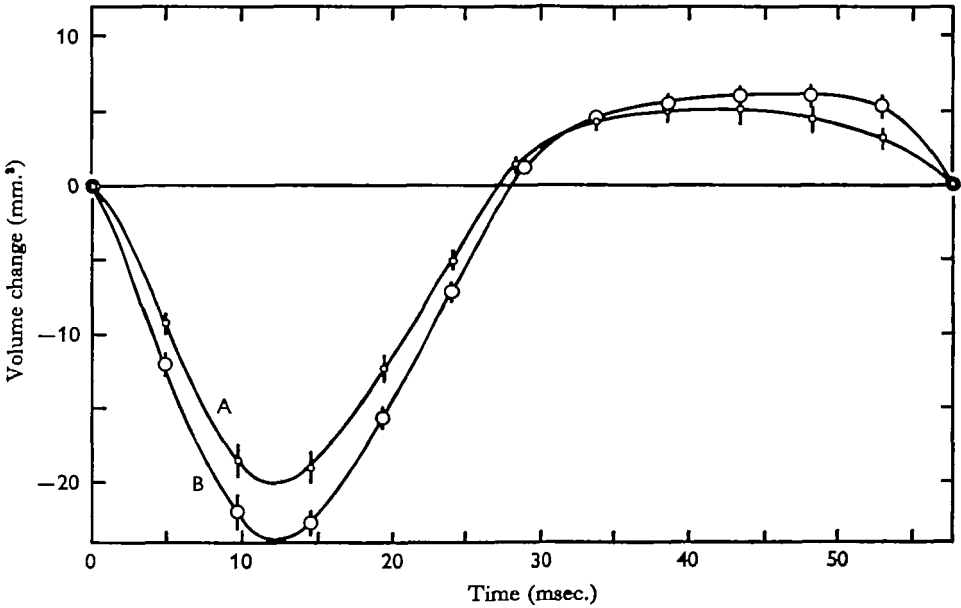


Fig. 7. The change in thoracic volume caused by the wing movements of a standard *Schistocerca* during a wingstroke lasting 56–57 msec. In curve (A) the wings are moved as during a standard stroke (Weis-Fogh, 1956*b*) where the top positions of forewings and hindwings are 125° and 144° respectively and the corresponding bottom positions 57° and 34° . In curve (B) both pairs of wings retain almost the same stroke angles as in (A) but the average position is increased so that the top positions of forewings and hindwings are 131° and 153° respectively and the bottom positions are 63° and 43° . The standard errors from the eight locusts are shown by vertical lines. An increase in volume is plotted as positive values and a decrease as negative (ordinate).

changes, but below 80° the forewings have almost no effect. In order to estimate the true changes during flight the wing angles were therefore changed in a succession of steps which correspond to twelve angular combinations of a standard wing stroke lasting 56–57 msec., as already explained. The changes were plotted against time and Fig. 7A shows that during a standard stroke the volume of the thoracic box alters by $25 \mu\text{l}$. so that the potential rate of ventilation due to the wing movements amounts to not less than $760 \text{ l. air/kg./hr}$.

During continuous steady-state flight both pairs of wings oscillate about the horizontal position, but at the start of flight and during vigorous activity of other kinds the mean angle often increases by a few degrees, particularly in the forewings, while the frequency and amplitude only change slightly (Weis-Fogh, 1956*b*). In Fig. 7B the mean angles were therefore increased by $6\text{--}9^\circ$ while the other parameters remained

as in 7A. This resulted in a potential ventilation of 950 l. air/kg./hr., or in a 25% increase which is due mainly to the forewings (cf. Fig. 6). It also turned out that the two curves in Fig. 7 could be accurately reproduced by the summation of results obtained when the one pair of wings was fixed and the other pair moved. In other words, the notal and pleural couplings play an insignificant role in locusts. The same does not apply to dragonflies.

(d) *Thoracic pressure changes*

In order to estimate how much of the potential ventilation results in a true flow of air through the thoracic spiracles one must know the pressure changes and the flow characteristics of the tracheal system.

During recovery from CO₂ narcosis the abdominal pumping is intense and the pressure in the haemocoel sometimes exceeded the atmospheric pressure by 200 mm. H₂O

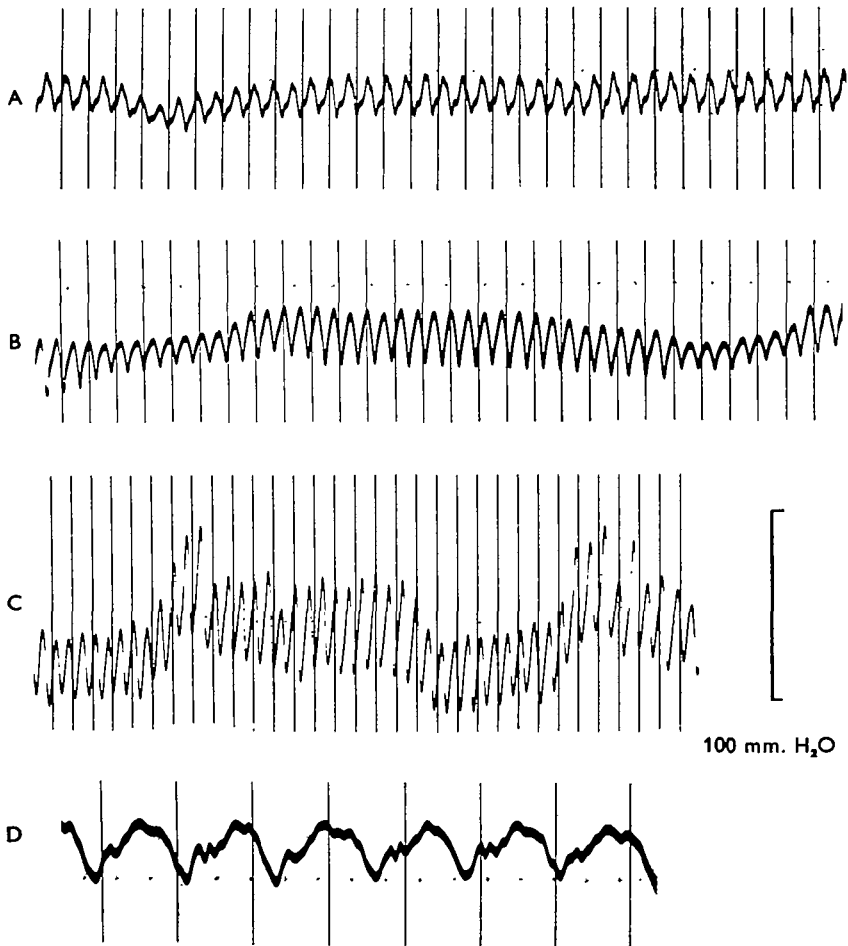


Fig. 8. Recorded changes in intrathoracic pressure of a tethered 'flying' desert locust. The three upper curves have been reproduced so that the ordinates are identical (scale against curve C), the vertical lines being spaced by periods of 10 msec. (A) All spiracles intact as during normal flight. (B) Spiracles 2 closed on both sides. (C) Spiracles 2 and 3 closed on both sides. (D) similar to (A) but recorded at high speed and in another individual. Note also the slow change in average pressure caused by the respiratory movements of the abdomen.

during expiration and falls below it by 50 mm. H₂O during inspiration. This is in accordance with the presence of both expiratory and inspiratory muscles in locusts and with the presence of an effective co-ordination of the spiracular valves. After some time of hyperventilation the figures decreased to a third or less. At the onset of flight, the abdomen was suddenly extended (Fraenkel, 1932*a*), the *mean* pressure also decreased and, in spite of strong abdominal pumping movements, the peak-to-peak amplitude decreased to only 30–50 mm. H₂O or less (Fig. 8). Superimposed upon the slow waves are the rapid oscillations at wingstroke frequency caused by the thoracic volume changes. It was characteristic that in an intact animal the rapid pressure changes amounted to only 10–15 mm. H₂O during abdominal inspiration and to 20–25 mm. during abdominal expiration (Fig. 8A). This demonstrates that the thoracic spiracles must remain open during flight, as has been observed directly (Fraenkel, 1932*a*; Miller, 1960*b*), because the isolated tracheal system of the pterothorax has a capacity of only 100–150 μ l. in a standard *Schistocerca*. If the system were closed the volume changes of 15–30 μ l. per wingstroke would result in changes of the pressure amounting up to 2000–4000 mm. H₂O. There is therefore no doubt that the wing movements actually result in some ventilation of the thorax. When both spiracles were blocked by means of wax, the pressure changes increased to about 15 mm. during inspiration and 30 mm. H₂O during abdominal expiration (Fig. 8B), and when both spiracles 2 and 3 were blocked on both sides the figures rose to 30 and 45 mm. H₂O respectively (Fig. 8C). The locust refused to start if the first three pairs were blocked and it is clear that they all make substantial contributions to the exchange. Fig. 8D illustrates that the shape of the normal pressure curve is far from being simple, but it should be remembered both that the strong vibrations of the flying animal introduce a 'noise' corresponding to 2–3 mm. H₂O and that the nota move in a slightly different way during actual flight compared with the changes induced by the artificial wingstroke (see the discussion). The results were consistent in about twenty experiments performed on five animals.

(e) *Pressure and rate of flow*

The relationship between the air pressure inside the large thoracic air sacs and the rate of flow through the spiracles of a standard *Schistocerca* is illustrated in Fig. 9. The curves are identical for both directions of flow so that no direction-sensitive valves are involved. The relationship between driving pressure P and rate of flow Q can be approximated by a simple power function, but the power of Q varies from 1.1 to 1.9 according to which pair of spiracles is studied. It is seen that the resistance to flow is many times larger through the abdominal than through the open thoracic system. It was also found that the resistance of the system altered very little with the degree of opening of the spiracles until the closed position was approached.

The small scatter of the results in Fig. 7 shows that the locusts are remarkably similar in geometry. It makes it possible to differentiate the curve rather accurately with respect to time and so to calculate the rate of change in thoracic volume, i.e. the *potential* rate of flow in and out of the thoracic spiracles caused by the wing movements (Fig. 10). By combining the results of Figs. 9 and 10 one can now estimate the expected variation in intrathoracic pressure during an average wingstroke. If the entire volume change results in actual ventilation, the pressure should vary with time

as in Fig. 11A so that the peak-to-peak amplitude should amount to 58 mm. H₂O. This is about three times more than actually measured. If the ventilation is reduced by a factor 2 relative to the volume change the difference is 23 mm. H₂O (curve B), and if the reduction factor is 3 it is only 13 mm. H₂O, or very close to the measured values (C).

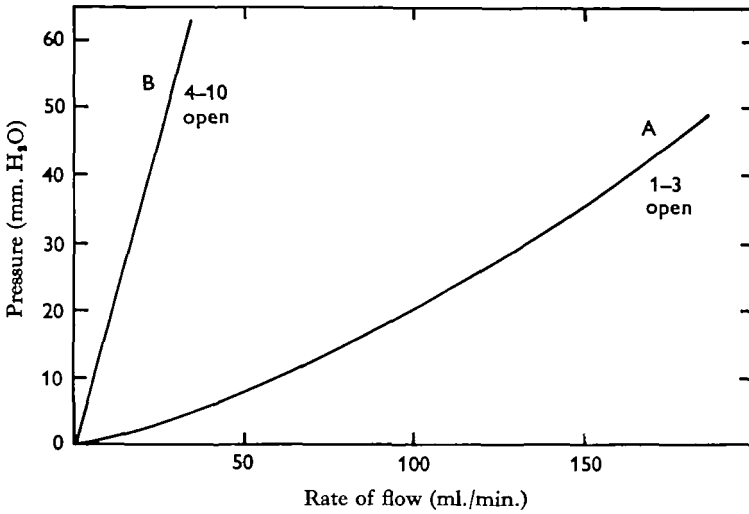


Fig. 9. Relationship between the pressure inside the large thoracic air sacs and the rate of flow out or in through the spiracles of a standard *Schistocerca*. (A) Only the thoracic spiracles open. (B) Only the abdominal spiracles open.

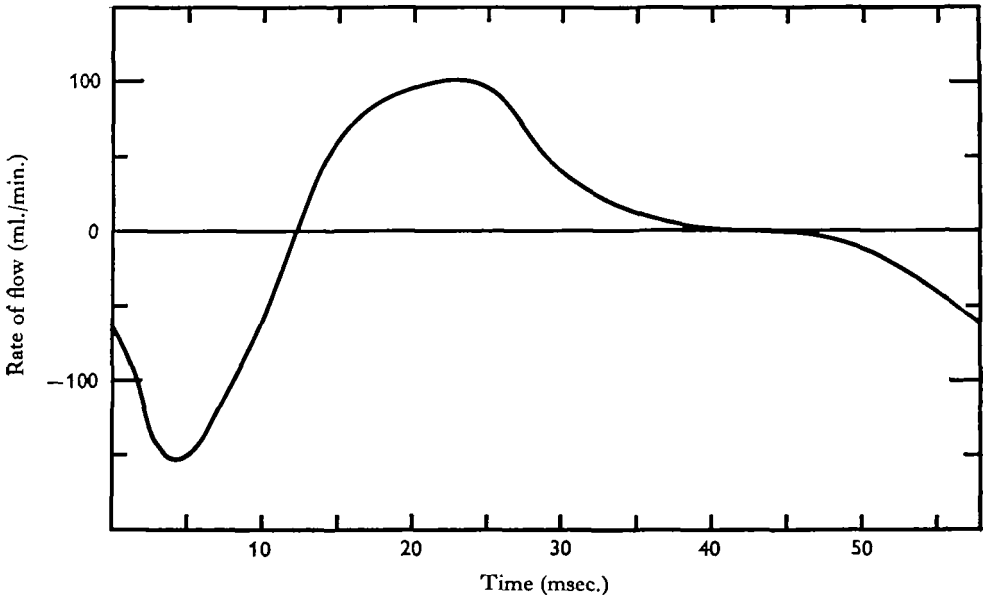


Fig. 10. The potential rate of flow caused by the wing movements in and out through the thoracic spiracles during a standard stroke of a locust of standard size, as deduced by differentiating curve (A) in Fig. 7 with respect to time. When the ordinate values are negative air is being expelled from and when they are positive air is being sucked into the thoracic air sacs.

The pressure measurements therefore show that, during standard flight, the actual exchange of air due to thoracic pumping alone is smaller than the expected value of 760 l./kg./hr. by a factor of about three, i.e. it amounts to about 250 l./kg./hr. A comparison between the inserted diagram in Fig. 11 and Fig. 8D shows that there is a reasonable agreement in shape.

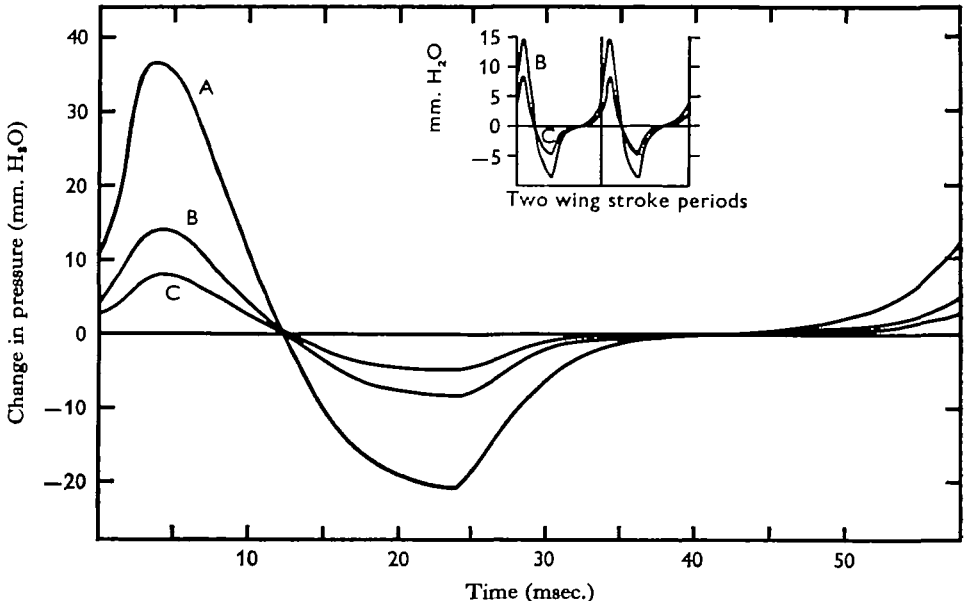


Fig. 11. The expected variations in intrathoracic pressure in a standard locust caused by the wing movements during a standard wingstroke, (A) if the potential rate of flow in Fig. 10 corresponds to the actual flow, (B) if the actual flow is smaller than the potential flow by a factor of 2, and (C) if it is smaller by a factor of 3. Deduced from the curves in Figs. 9A and 10. Insert: the deduced pressure variations in (B) and (C) on a contracted time scale, to be compared with the measured changes in Fig. 8A, D.

(f) *Independent estimate of thoracic ventilation*

The preceding experiments do not offer a direct estimate of the combined effect of thoracic and abdominal pumping in flying locusts. This was provided in two ways, partly by means of simultaneous determinations of the metabolic rate and the average composition of the air in the thoracic air sacs, and partly by calculating the amount of air which corresponds to the known rate of evaporation of water.

The thoracic heat production of large immature females was measured during periods of steady-state flight and the content of O_2 and CO_2 in the air sacs was measured at the end of each period. The results from ten experiments with four animals are seen in Table 2. In these operated locusts the intensity of flight was below normal so that the average lift amounted to only 83% of the basic weight, but the metabolic rate did not differ significantly from the rate which one should expect at this lift (12.7 l. O_2 /kg./hr. against 13.8 here; Weis-Fogh, 1964c). The average thoracic ventilation was 240 l. air/kg./hr. at the pressure and temperature of the working thorax, but it should be remembered that the container for sampling the gas effectively blocked spiracle 2 of the one side. We have seen that if both spiracles 2 were blocked the thoracic pressure changes caused by the wing movements increased by about one-

third (Fig. 7). The two sides of the tracheal system have no direct connexions in the adult thorax, but are separated by the flexible walls of the large air sacs (Miller, 1960*b*; Weis-Fogh, 1964*a*). If one of the six spiracles is blocked the driving pressure will therefore increase by approximately one-sixth and the conductivity of the blocked side will decrease by about one-third. The flow rate of the operated side will therefore become reduced by $7/6 \times 2/3 = 7/9$ compared with unimpeded ventilation. In other words, the normal free ventilation would amount to about $9/7 \times 240 = 310$ l. air/kg./hr. It is difficult to estimate the accuracy of this figure but a rough calculation indicates a standard deviation of about 20%.

Table 2. *The metabolic rate, the content of O₂ and CO₂ in the thoracic air sacs, and the rate of ventilation of the thorax in steadily flying desert locusts*

Animal no.	Relative lift (% of basic weight)	Metabolic rate (l. O ₂ /kg./hr., at 0° C. and 760 mm. Hg)	O ₂ % (dry air)	CO ₂ % (dry air)	Rate of ventilation (l. air/kg./hr., at thoracic pressure and temperature)
2	71	12.7	14.9	4.3	274
	91	10.6	13.8	6.2	192
3	53	9.8	15.3	4.8	225
	104	18.1	13.2	5.4	302
5	93	16.9	10.3	7.0	207
	113	17.9	12.3	6.2	269
	62	14.0	13.5	5.5	246
	62	11.5	15.7	4.4	295
6	79	11.0	14.3	5.3	215
	100	15.0	10.8	7.9	190
Average	83	13.8	13.4	5.7	242

A similar rate is found if we calculate the amount of air necessary for the evaporation of water. In a series of specially designed experiments, where the locusts flew for several hours without interruption, the rate of evaporation amounted to 0.3 ± 0.1 g./kg./hr. per mm. Hg difference in water vapour pressure inside and outside the working thorax (Weis-Fogh, 1964*c*). During standard flight at 30° C ambient temperature and 60% relative humidity the thoracic temperature is 36–37° C and the rate of evaporation is 8 g./kg./hr. Since each litre of expired air contains up to 24 mg. water in excess of the amount in the inspired air, the total minimum ventilation of the thorax is 330 ± 110 l. air/kg./hr.

It is of course true that the water escapes both via the spiracles and through the body cuticle, and Loveridge (1967) has recently found that the ratio between the two rates is about 4:1 in relatively short experiments (less than 1 hr.) with flying *Locusta migratoria*. Since his figures for the rate of evaporation are slightly higher than mine and since I found that the rate decreased with time after handling (hence the long flights), a correction for evaporation through the cuticle would not substantially alter the result.

The two estimates of thoracic ventilation are therefore in reasonable agreement. Taken together, they indicate that the combined movements of the abdomen and of the thoracic box ventilate the wing system at a rate of 320 l. air/kg./hr. of which 250 l. is caused by thoracic pumping and the remaining 70 l. by the abdominal movements.

A more precise determination is hardly justified at present, partly because the abdomen can be left out altogether and partly because a slight increase in mean positional angle of the wings may increase the thoracic contribution by significant amounts. Even with fully opened spiracles the locust therefore has a chance to alter the thoracic pumping, but control reactions of this kind are not apparent from Table 2.

The table also shows that the average decrease in concentration of O_2 in the air sacs was 7.1% but in an intact locust this would correspond to about 5.5%. The concentration of O_2 plus CO_2 averaged 19.1% which is 1.4% less than in atmospheric air (corrected for incomplete absorption). In these and other experiments this discrepancy was always greatest during the first minutes of flight and could then amount to 3%, but it decreased to 0.5–1% as flight progressed which is compatible with fat combustion. Due to the thoracic pumping the oxygen supply should be adequate from the first wingstroke and until flight is discontinued. The high initial difference of 3% therefore indicates that the CO_2 tension of blood and wing muscles was low before start and increased during the first couple of minutes until a steady state was reached.

(g) Conclusions

In flying locusts the abdominal respiratory movements are unable to supply the working thorax with sufficient air and seem to be adjusted to the needs of the head and the central nervous system rather than to the needs of the wing muscles. During flight of average intensity the thoracic ventilation amounts to about 320 l. air/kg./hr. of which about 250 l. is caused by the deformations of the pterothorax which accompany each wing stroke, i.e. it is due to thoracic pumping.

The abdominal pumping amounts to 180 l. air/kg./hr. of which about 30 l. is directed towards the head and down through the ventral tracheae (unidirectional), about 70 l. is pumped in and out of the working pterothorax, and the remaining 80 l. is used for ventilating other parts of the animal.

DRAGONFLY AND WASP

We shall now examine representatives of two other insect orders, Odonata and Hymenoptera, although in a much less detailed way. Their metabolic rate has not been measured before during flight of known intensity.

(a) Metabolic rate

Aeshna and *Vespa* are both excellent and enduring flyers, but it is not easy to make them perform at constant lift and stroke parameters for periods long enough to ensure that the excess temperature, Δt , is measured under steady-state conditions. The few successful experiments are listed in Table 3. It is seen that the net rate of heat production, P_n , is 80–90 kcal./kg./hr. in both insect types when they lift their own body weight. This is 40–50% higher than in locusts flying under similar conditions (see Weis-Fogh, 1964c, for details) and it is therefore reasonable to assume that the net aerodynamic power, P_a , is increased by a similar amount from 4.4 to about 6 kcal./kg./hr. The other unknown quantity is the rate of heat dissipation, P_w , due to the evaporation of water in the working thorax. In locusts it amounts to 0.17 kcal./kg./hr./mm Hg \pm 30% and if this figure is adopted, P_w would amount to 3–4 kcal./kg./hr.

in the present experiments. The rate of evaporation may of course be larger in dragonflies and wasps than in locusts, but since both *Libellula* and *Aeshna* take part in long-range migrations without feeding (see review by Fraenkel, 1932c), it is reasonable to assume that they do not lose significantly more water by evaporation than their metabolism produces, as is often the case in locusts and in aphids (Weis-Fogh, 1952; Cockbain, 1961). If this is so, Pw could not exceed 6 kcal./kg./hr. and when we take all uncertainties into account, $Pw + Pa$ amounts to 11 ± 4 kcal./kg./hr.

During level sustained flight *Aeshna* and *Vespa* therefore require about 100 ± 15 kcal./kg./hr. which corresponds to an oxygen uptake of 17–24 l. O₂/kg./hr.

Table 3. Flight performance and metabolic rate P during steady-state flight at normal lift in *Aeshna grandis* and *Vespa crabro*

(Lr is relative lift, v is air speed, ϕ_1 and ϕ_2 are the stroke angles of forewings and hindwings, N is stroke frequency, Pn is rate of net heat production, P is metabolic rate, Pw rate of heat dissipation due to evaporation of water, and Pa aerodynamic power (see Weis-Fogh 1956b, c).)

	Lr (%)	v (m./sec.)	ϕ_1', ϕ_2 (°)	N (min. ⁻¹)	Δt (°C)	Pn (kcal./ kg./hr.)	$P = Pn + Pw + Pa$ (kcal./ kg./hr.)
<i>Aeshna grandis</i> ♂ (0.83 g.)	100	3.0	c. 60	c. 1800	7.9	87	
	100	2.8	—	c. 1800	8.0	89	
				Av. 1800		Av. 88	c. 100
<i>Aeshna grandis</i> ♀ (0.95 g.)	100	2.3	50, 47	1650	7.5	90	
	100	2.3	—	1540	6.3	75	
	100	2.3	59, 56	1430	5.9	71	
	100	2.3	62, 64	1800	7.9	95	
			Av. 57, 56	Av. 1600		Av. 83	c. 95
<i>Vespa crabro</i> worker (0.46 g.)	85	3.1	—	6000	6.7	115	c. 125
	70	2.9	—	5400	5.3	90	c. 100
	100	0	—	6000	9.3	88	c. 100

('hovering')

(b) Ventilation in *Aeshna*

The true rate of ventilation is not known, but it is clear that abdominal movement cannot be responsible for more than an insignificant part because the frequency and the depth of pumping remain small and do not change significantly from rest to flight (78/min. in *A. mixta*) and show a small increase only after flight had stopped (95/min.). The same applies to *Libellula* (Fraenkel, 1932a). The thoracic mechanism, on the other hand, should offer ample opportunities for an adequate exchange, as is seen from Fig. 12 in which the four wings were moved as one pair and the resulting volume changes are plotted against the angular position γ' (measured in the stroke plane). The volume is maximum about the resting angle of 85–90° and decreases at either side mainly due to the inward movement of the pleura (Weis-Fogh, 1964a). In *A. mixta* (0.49 g., 2000 strokes/min.) the potential ventilation of the thorax as estimated from the graph was 950 l. air/kg./hr. at a stroke angle of 50°, 1200 at 57° (normal for flight, Table 3), and 2400 at 90° which is about the maximum stroke angle in this genus. However, the two pairs of wings are mechanically coupled by means of the common pterothoracic pleura and it is therefore necessary to move them in a way similar to normal flight. The result for *A. cyanea* is seen in Fig. 13A in which the average stroke angle from the slow-motion film (Chadwick, 1940) was 92°. With a wingstroke frequency of 1600/min.

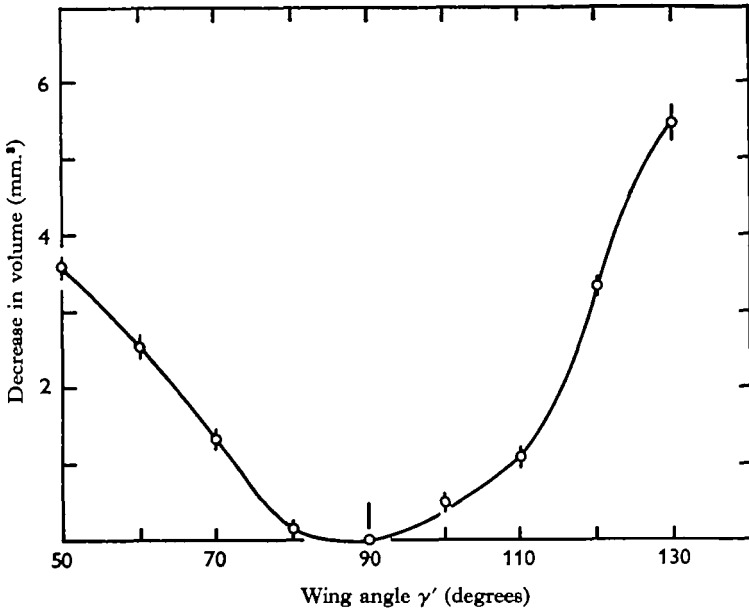


Fig. 12. Decrease in thoracic volume (ordinate) with wing position (abscissa) in the dragonfly *Aeshna mixta*. The four wings were moved as one pair and not with a phase difference as in flight.

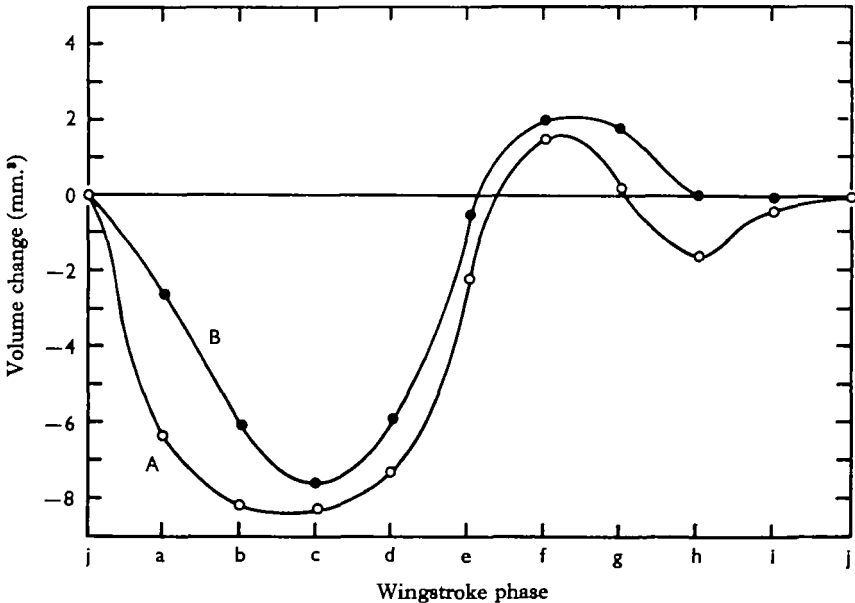


Fig. 13. The change in thoracic volume caused by the wing movements in a large dragonfly *Aeshna cyanea* during one wing stroke with fairly large stroke angles (92°) but with correct phasing between fore- and hindwings (curve A). In curve (B) each pair was moved while the other pair was kept horizontal and the results from the two sets of measurements were summated: the summated curve (B) does not correspond to the directly measured curve (A), as was the case in locusts, because in dragonflies there is a strong pleural coupling which is almost absent in locusts. The abscissa represents ten combinations of wing positions during a normal wing stroke.

the potential rate of ventilation in *Aeshna cyanea* would amount to 1600 l. air/kg./hr. By comparison with Fig. 12 this figure should be reduced to about 800 l./kg./hr. when the stroke angle is only 57° (Table 3) instead of 92° .

The curve in Fig. 13 B is the sum of the two curves obtained when one wing pair is moved while the other is kept horizontal. Due to pleural coupling it differs from the curve measured when both pairs are moved simultaneously in the normal way, but this has very little effect upon the estimate of the *rate* of ventilation.

The potential rates are therefore of the same order of magnitude in locusts and in dragonflies, but the anatomy of the tracheal systems strongly indicates that the true thoracic ventilation is significantly larger in Odonata than in Orthoptera. The reason is that by far the largest air volume in the dragonfly pterothorax is confined to the thick peripheral layer of functionally *closed* air sacs which are firmly suspended between the thoracic cuticle and the dense core of wing muscles (Weis-Fogh, 1964*a*).

The air sacs which supply the muscles themselves, however, are directly connected to the spiracles, they are relatively small, and since their walls are not supported they collapse under a small pressure. Moreover, the tracheal system of the wing muscles is placed in the pterothoracic capsule which has only narrow connexions with the rest of the body in front and behind, and it communicates with the anterior and posterior systems through narrow tracheae (see Miller, 1962). In locusts the pterothorax is in wide open connexion with the prothorax and the abdomen so that thoracic volume and pressure changes must affect air sacs and blood pools which are not directly concerned with the flight system. It is therefore reasonable to assume that the major part of the potential ventilation of 800 l. air/kg./hr. in dragonflies will result in a real renewal of the air in the central trachea of the muscles. If this is so, the average decrease in oxygen percentage is about 2.5 %. If, on the other hand, the rate is only 400 l. air/kg./hr. the oxygen deficit will increase to 5 % which is near to the critical limit for diffusion from the central tracheae to the muscle fibres, at least in the largest muscles (Weis-Fogh, 1964*b*). However, a moderate increase in stroke angle could increase the ventilation by significant amounts.

(c) *Notes on Vespa*

The pterothorax of most wasps and bees is a hard round capsule in which the visible changes in volume are very small when the animal flies. It is easy to show that the abdominal pumping is very effective in this group. Thus, when a suspended *Vespa crabro* was excited either during feeding or when stimulated in other ways, the wing muscles were sometimes active and produced heat at rates exceeding 60 kcal./kg. body weight/hr. without the slightest trace of vibration of the wings of the thoracic box. At the same time the abdominal respiratory movements were greatly increased in amplitude and frequency (180/min.) as is always the case during flight. This heating and pumping has also been observed in bees (Sotavalta, 1954) and it is the normal state for wasps feeding under exposed conditions, for instance, in the baker's shop. It resembles the flight preparation of large beetles and moths (Dotterweich, 1928; Krogh & Zeuthen, 1941), but should be considered rather as a sign of alertness since non-prepared wasps can take to the wing without any pre-heating.

Since the wing muscles can be supplied adequately by means of abdominal pumping during periods of alertness, and since the volume changes of the pterothorax are very

small, we must conclude that the exchange of air in *Vespa* is caused by the abdominal respiratory movements combined with diffusion. As to diffusion, it is most probable that the reciprocal activity of the wing muscles in truly flying wasps will result in a considerable mixing of the air inside the pterothorax so that transport in the thorax is facilitated, but this cannot be the case in the alert panting insect. The overall picture is in accordance with the anatomy, as discussed elsewhere (Weis-Fogh, 1964*b*), and also with the observation that in the honeybee the air stream has a strong unidirectional component during flight, in through the first—and out through the third spiracles, (Bailey, 1954).

(d) Conclusion

During sustained horizontal flight, the metabolic rate of large dragonflies and wasps is 40–50% higher per unit weight than in locusts, namely about 100 kcal./kg./hr. or 20 l. O₂/kg./hr. In dragonflies the entire increase in ventilation during flight is caused by thoracic pumping which has a sufficient capacity to secure an adequate supply. In the large wasp abdominal pumping appears to be the dominating mechanism.

DISCUSSION

(a) Thoracic pumping and ventilation

In his famous monograph Chabrier (1822) described the volume changes which accompany each wingstroke in dragonflies, and on this basis he formulated the idea that the entrapped air is being elastically compressed and expanded so that it assists the movements of the oscillating wings. The theory did not receive much support by later authors, but it is interesting to note that an isolated, closed system of air sacs in the locust thorax would represent a major factor in the energetics of flight. The thoracic deformations would then increase the pressure by 100–200 mm. Hg, corresponding to a load of 80–180 g. on the two nota. However, the system is open through the spiracles and is separated from the rest of the animal only by the flexible walls of air sacs and the common pool of haemolymph. The volume changes do not serve flight directly but provide for the respiration of the wing muscles.

In many large insects the thoracic volume changes were conspicuous when I viewed them in stroboscopic light (many Orthoptera, all Odonata, large Coleoptera like *Oryctes* and *Rhinoceros*, large Lepidoptera like *Sphinx*), and Miller (1966*a, b*) has recently discussed several observations relating mainly to beetles. In Cerambycidae and Scarabaeidae he estimated that the pumping often exceeds 1000 l./kg./hr. and many approach 2000, i.e. figures of the same order of magnitude as found in Odonata. It is not known to what extent the pumping results in an actual ventilation since neither the flow characteristics nor the changes in pressure are known for the time being. However, in the case of the large Cerambycidae (Miller, 1966*a*), it seems most likely that the thoracic pump provides almost the maximum possible amount of air, or about 1950 l./kg./hr. in *Petrognatha gigas*, because the volume changes are confined to the secondary tracheae while the giant primary trunks exert so little resistance to flow that they can be effectively ventilated by the draught mechanism (see next section).

In dragonflies the major factor in the thoracic mechanism is the bending of the

pleura because the nota are so small that their vertical extensions are of little quantitative significance (Weis-Fogh, 1964*a*). In locusts, on the other hand, it is the latter movements which dominate, and this introduces a complication. If one measures the extreme excursions of the nota in relation to the wing movements, there is no significant difference between direct observations on flying animals (Weis-Fogh, 1964*a*) and measurements made when the wings are moved passively as in the present experiments. But there is a difference during part of the stroke due to the rubber-like nature of the wing hinges (Weis-Fogh, 1960; and unpublished). During the first half of the upstroke when the nota begin to move downwards, the resulting force on the hinges is directed towards the ventral side and the hinge material is compressed. When the wings have passed the middle position and are being decelerated, the direction of force is reversed, the hinges become extended and the nota move up to a higher position than before. This notal ascent is therefore a dynamic phenomenon and it could introduce a relatively rapid reduction in tracheal pressure during the compression phase and may explain the brief oscillation seen in Fig. 8D. However, this complication does not significantly alter the total amount of ventilation.

It is characteristic of the flying locust, at least during sustained flight, that the animal may change the lift without altering the stroke frequency or the stroke angles to any appreciable extent, the main variable being the twisting of the wings (Weis-Fogh, 1956*b*). This means that the thoracic pumping remains the same and independent of the work produced, as is indeed indicated in Table 2. However, for locusts flying under natural conditions, this does not imply that the actual renewal of air, the ventilation, remains at a fixed value. If a locust has eaten much, is very fat or is full of eggs it has to lift this extra load and the volume of the load is accommodated by the deflation mainly of the large thoracic and abdominal air sacs. These compliant structures therefore become less compliant and a larger proportion of the pumping will result in a ventilation of the thorax than before, i.e. the efficiency of the pump increases. In the experiments only full migrants were used so that this automatic control was not observed.

We can conclude that thoracic pumping contributes to the ventilation of the working thorax by very significant amounts in most large insects. In Odonata it seems to be the only essential mechanism at work and in effect the Cerambycidae belong to the same functional group; in other groups it is combined with effective abdominal pumping (Orthoptera, most beetles belonging to the Scarabaeidae); and in some insects abdominal pumping, intrathoracic mixing and diffusion are sufficient (e.g. Hymenoptera).

(b) *Draught ventilation*

Bernoulli's theorem relates to the energy content of a fluid which streams in a tube. The tube could be surrounded by solid walls or be a conceptual streamline tube. In both cases we have for any part of the tube

$$p + h\rho g + \frac{1}{2}\rho v^2 = \text{a constant,}$$

where p is the pressure, ρ the mass density of the fluid, g the acceleration of gravity and v the velocity of flow. Since the elevation h can be considered constant here, the second term is constant. The theorem then says that the pressure p is maximum where the velocity is zero and that it decreases by an amount equal to the velocity head $\frac{1}{2}\rho v^2$

which represents the maximum driving force in draught ventilation in the absence of turbulence. The maximum force can only be obtained if a spiracle is placed directly against the relative wind at a point of virtual stagnation, but a reduced driving force is possible if there is a difference in flow velocity over the surface of the body due to its shape and if the spiracles are strategically placed in relation to the flow pattern. Higher pressure differences are of course possible if the body is aerodynamically irregular.

It is obvious that the Bernoulli effect is absent during tethered flight and hovering, and since the three insects examined here can 'fly' under such conditions, draught ventilation cannot be of major importance. In the case of the desert locust the normal flying speed is 3.5 m./sec., which corresponds to a velocity head of 0.76 mm. H₂O, but 5 m./sec. has often been observed, corresponding to 1.56 mm. H₂O. If a wide cannula is inserted into the big thoracic air sacs and its free end is bent against the wind, these figures represent the maximum driving pressure available. Fig. 9 shows that the flow out of the six thoracic spiracles could not possibly exceed 5 ml./min. or 100 l. air/kg./hr. In fact, the spiracles are all situated on the sides of the cylindrical thorax so that the actual draught ventilation is likely to be smaller by one or two orders of magnitude, if it occurs at all in these insects. It has therefore been disregarded in this study, but the mechanism could be of particular importance in insects with a high flying speed, a tracheal system with a low resistance, and a body shape which favours large differences in flow velocity.

These requirements are met by the large cerambycid beetles, the Elateridae and the Anthribidae, as recently shown by Miller (1966*a*). Even in very large species the abdominal movements are absent in flight, there are no air sacs, and one or two pairs of giant air trunks connect spiracles 2 and 3. These spiracles are also of giant size and are kept open during flight. In *Petrognatha gigas* spiracle 2 is placed on the pronounced 'shoulders' of the metanotum and spiracle 3 further back on the lateral wall. The secondary tracheae which supply the muscles are collapsible and emerge from the non-collapsible giant trunks (Amos & Miller, 1965). The mechanism seems to be that the thoracic pumping (1950 l./kg./hr.) ventilates the secondary tracheae, and the primary trunks are subject to draught ventilation which may amount to 3800 l./kg./hr. at a flying speed of 5 m./sec. and a driving pressure between spiracle 2 and 3 of only 0.4 mm. H₂O (Miller, 1966*a*). In flight the giant trunks can be considered almost part of the external surface and the thoracic pump works against the free atmosphere, but the system is closed and protected during rest. There is therefore no doubt about the importance of draught ventilation in some insects but it is hardly present in locusts (cf. Stride, 1958).

(c) Ecology of locust flight

In the absence of radiant heat, the desert locust can fly uninterruptedly for hours at air temperatures between 25 and 35° C., it can start at 22° C. but does not continue for more than about $\frac{1}{2}$ hr., and if the air temperature is 37° C. the insect is prone to stop at short intervals and 'pant' (Weis-Fogh, 1956*b*). During level flight at 3.5 m./sec. the metabolic rate is 65 kcal./kg./hr. and the temperature of the thorax is 6.5° C. above that of the ambient air, but in sunshine the net heat radiation can increase the temperature of the working thorax by about 2° C. at medium radiation load in the tropics

(0.55 cal./cm²/min.) and by 4° C. during periods of high load (1.25 cal./cm.²/min.; Weis-Fogh 1964*c*; Muus & Weis-Fogh, unpublished). Since, the rate of ventilation of the pterothorax is about 320 l./kg./hr. in full migrants it is now possible to estimate the water economy and the possibility of sustained flight at high altitudes.

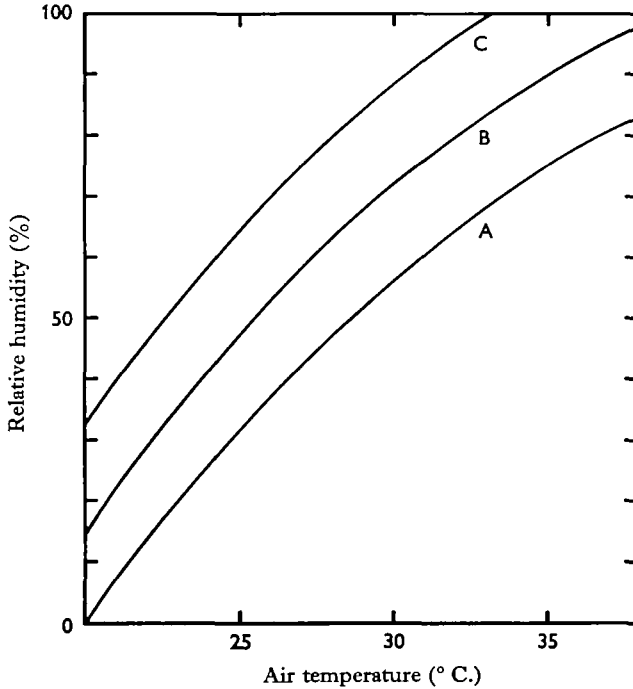


Fig. 14. The relationship between the relative humidity (ordinate) and the air temperature (abscissa) at which flying desert locusts lose water by evaporation through the spiracles at the same rate as water is produced by the combustion of fat. (A) no net radiation heating, (B) thoracic temperature increased relative to (A) by 2° C. due to a net absorption of radiation heating of 0.55 cal./cm.²/min., and (C) by 4° C. caused by a radiation load of 1.25 cal./cm.²/min. For points above the curves the locusts gain water while they lose water when the points fall below the curves.

The rate of metabolism corresponds to the combustion of 7.0 g. of fat (Weis-Fogh 1952) and therefore to the production of 8.1 g. H₂O/kg./hr. The curves in Fig. 14 show the combinations of temperature and relative humidity of the ambient air at which there is balance between water production and water evaporation from the thorax, in curve (A) with no radiation heating and in (B) and (C) when the radiation increases the thoracic temperature by 2 and 4° C. respectively. For points falling below the curves, the locusts gain water and above the curves they lose water. It is seen that a combination of high air temperature and radiation requires an almost saturated atmosphere (75–100 % R.H.) for sustained flight without feeding or drinking, while 35 % R.H. at 25° C. is sufficient in the absence of heating radiation. The respiratory system of desert locusts is obviously well adapted to dry conditions, but long uninterrupted migrations at 30° C. require 55–75 % R.H. Under true desert conditions it would therefore be an advantage to ascend to higher altitudes.

In Table 4, I have listed the average decrease in temperature, pressure and density of the air with altitudes as averaged over the year, but specific situations may of course deviate appreciably from these values. On a warm day with sun and air temperatures at ground level near 35° C., a swarm of locusts should be able to continue to fly at an elevation of 3 km., but the temperature will become too low if they climb to higher altitudes. The pressure will be 30–32% less than normal but the ventilation can be increased by a similar amount by adjusting the average angle of the stroke by about 10° (cf. Fig. 7B). As to air density, a full migrant flying at sea level is able to lift 50–75% more than its body weight without altering frequency or amplitude much, so that a reduction in air density by 27–29% could be compensated by a change in the angle of attack and should not be a serious handicap. This deduction is confirmed by an observation made on 9 July 1953, when Mr J. B. Tyson saw a number of

Table 4. *Variation in temperature, pressure and density of the atmosphere with altitude, expressed in per cent of the values at sea level and averaged for summer and winter (according to Handbook of Chemistry and Physics, 27th ed., 1944)*

Altitude		Reduction in temperature (° C.)	Relative pressure (%)	Relative density (%)
(km.)	(ft.)			
0	0	0	100	100
1	3,048	2–4	88–89	89
2	6,096	5–8	78–79	79–81
3	9,144	10–12	68–70	71–73
4	12,192	16–19	60–61	64–66

actively flying *Schistocerca gregaria* at the top of the Urai Lagna Pass in Nepal (Tyson, personal communication; travel described in Tyson, 1954). Although cloudy, the air temperature was unusually high for an altitude of 5200 m., so that short flights were possible in spite of the fact that the barometric pressure on that day was only 535 millibar or reduced to almost half the pressure at sea level (Rainey, personal communication). There is therefore good reason to believe that the flight of locusts is governed by temperature and perhaps humidity rather than directly by altitude. However, sexually mature swarms with many gravid females could hardly cope at high altitude, and in the laboratory egg-laying females are disinclined to perform long flights anyway. The main advantage of a climb therefore appears to be that a positive water balance can be obtained. A decrease in air temperature from 35° C. at ground level to 23° C. at 3 km. altitude should permit sustained flight at 35% R.H. even in sunshine. At ground level this amount of water corresponds to only 18% R.H. as in a true desert. Provided that a swarm of locusts is lifted to a height of 2–3 km. by means of thermal upcurrents it should be able to cross a large desert without suffering from water shortage when on the wing.

In evaluating the radiation experiments it should be borne in mind that the radiation load in the laboratory refers to net load in the infrared which is almost totally absorbed by an insect of the size of a locust. Rainey, Waloff & Burnett (1957) have treated the thermal balance of *Nomadacris septemfasciata* flying in nature in considerable detail and their main results are essentially in agreement with the conclusion reported here. They also point out that both the latent heat of evaporation of water and the cooling

effect of the ventilated air play an insignificant role relative to the heat gained by metabolism and radiation.

Finally, it remains to be discussed how important water economy is for actual migration in nature. While *Schistocerca gregaria* is disinclined to fly at low relative humidity in the laboratory (Weis-Fogh, 1956*b*), the same does not apply to *Locusta migratoria*, a species which is very similar to the desert locust in all respects considered here (Loveridge, 1967). It should be stressed that a negative water balance in flight is no serious problem for short flights or rolling swarms provided there is a possibility of eating green food or drinking dew, etc. Due to the design and function of the tracheal system of these insects the problem mainly arises during sustained flight over barren, hot and dry country. Under such conditions a high degree of atmospheric turbulence is likely and locust swarms can be seen to be lifted to considerable heights (2000–3000 m) but apparently so that the swarm retains contact with the ground (Rainey, 1958). It seems likely that the locusts often glide rather than flap their wings under such conditions (cf. Roffey, 1963) since the air temperature was only 7° C. at the highest recorded altitude for flight in mid air (3000 m., Rainey, 1958). It therefore appears that air temperature and radiation heating are the dominant factors for active flight of locusts and that neither respiration, mass density of the air or water economy are of much importance, except under special circumstances.

SUMMARY

1. New methods were designed for the simultaneous determination of the unidirectional flow of air and the total abdominal pumping in flying locusts, for measurements of the potential and the actual rate of flow caused by thoracic pumping, and for an independent estimate of the total ventilation of the flight system.

2. During rest, flight and recovery in the desert locust, the unidirectional flow caused by abdominal pumping remains small and almost constant at 30 l. air/kg./hr., in through the thoracic spiracles and out through the abdominal ones. The total pumping amounts to about 180 l./kg./hr. in flight of which 70 l. ventilate the thorax and 80 l. the other parts of the body.

3. Abdominal pumping can be blocked reversibly or reduced to insignificance without impairing the wing movements of the desert locust.

4. During average horizontal flight of the desert locust, the thoracic ventilation is about 320 l. air/kg./hr. of which 250 l. are moved by the thoracic pump, but the capacity of this pump is 760 l./kg./hr. and can be increased to at least 950 l./kg./hr. The relatively low efficiency is likely to increase when the abdominal air sacs are deflated due to ingested food, fat or eggs, i.e. when the animal has to lift more.

5. The pressure changes caused by the thoracic pumping only amount to 10–25 mm. H₂O and are of no mechanical significance for the moving wings.

6. Draught ventilation due to a Bernoulli effect is of no significance in locusts and probably not in dragonflies and wasps.

7. The oxygen in the thorax of flying locusts is reduced by about 5.5% relative to the atmosphere at sea level.

8. At small to medium relative humidities, and at temperatures between 25 and 30° C. at sea level, the rate of ventilation permits sustained flight of the desert locust

without risk of desiccation (Fig. 14). In order to retain a positive water balance at higher air temperatures the locusts must fly at high altitude, and 3 km. is estimated as a maximum for sustained, active flight.

9. Large dragonflies (*Aeshna* spp.) depend almost exclusively on thoracic pumping during flight, while large wasps (*Vespa crabro*) depend on abdominal pumping. For both types the metabolic rate is about 100 kcal./kg./hr. during level flight.

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