VOL. 18, NO. 1 MARCH, 1941

THE MECHANISM OF FLIGHT PREPARATION IN SOME INSECTS*

BY AUGUST KROGH AND ERIK ZEUTHEN
From the Laboratory of Zoophysiology, University of Copenhagen

(*Received* 5 *February* 1940)

(With Eight Text-figures)

IN 1928 Dotterweich published under the title "Beiträge zur Nervenphysiologie der Insekten" some very interesting and important observations and measurements mainly on Sphingidae, showing that the rapid vibration of the wings regularly observed in large moths before they take flight produces an increase in temperature of the wing muscles which is necessary to enable them to fly at all. The temperature reached was nearly the same in all cases, 32–34° C., and the time taken to reach it varied with the initial temperature deficit, up to 6 min. with a deficit of 23°. Moths kept at 34° or above would fly off at once, without any preparation, when stimulated. It had been assumed by v. Buddenbrock that this preparation was mainly required to attain the high frequency of the wing movements necessary for actual flight, but a number of observations made by Dotterweich on butterflies (*Vanessa*), in which the normal frequency is much lower, made it very probable that in these also preparatory wing movements were responsible for a rise in temperature necessary for actual flight.

The general interest of these observations became greatly enhanced when it was shown by Marius Nielsen (1938) in this laboratory that, in man, muscular work is closely correlated with a rise in body temperature which is regulated to very sharply defined higher levels corresponding closely to the rate of work.

The present paper contains a confirmation and extension of Dotterweich's results. Temperature measurements have been made throughout by means of thermojunctions made of 0·1 mm. constantan and 0·2 cm. copper wires inserted through the integument of the insect in question. In most cases the wires ending in the thermojunction had a vertical free length of 30–40 cm. allowing the insect a considerable amount of freedom to move, while flight could be induced, in certain conditions, by lifting the insect from the support (Fraenkel, 1932).

THE TEMPERATURE OF INSECTS DURING REST

Bachmetjew (1901), Necheles (1924) and others have shown and we have confirmed that during rest the temperature of insects is not very different from that of the environment, being in moist air slightly higher and in fairly dry air often definitely lower on account of the evaporation of water.

---

* Owing to war conditions, the authors have been unable to submit a corrected proof prior to publication.

We found, for instance, on a bumble bee weighing 200 mg. the results shown in Table I, and in a dor-beetle, *Geotrupes stercorarius*, weighing 900 mg. in dry air the figures given in Table II.

Table I

In saturated air			In dry air		
Temperature of			Temperature of		
Chamber ° C.	Thorax ° C.	Diff. ° C.	Chamber ° C.	Thorax ° C.	Diff. ° C.
			14·4	14·1	−0·3
			20·5	20·0	−0·5
26·8	27·4	+0·6	28·3	27·6	−0·7
			31·8	31·2	−0·6
36·1	37·2	+1·1	35·9	35·1	−0·8
			39·9	38·9	−1·0
			42·2	41·2	−1·0

Table II

Chamber ° C.	Thorax ° C.	Diff. ° C.
12·1	12·2	+0·1
23·1	23·0	−0·1
29·9	28·8	−1·1
37·1	35·1	−2·0
42·6	40·1	−2·5

In order to raise the temperature significantly above that of the environment the metabolism must be considerably increased, and this is done and can apparently only be done by muscular activity.

THE PREPARATION FOR FLIGHT IN BUTTERFLIES (*VANESSA*)

It is a common observation that butterflies, which at a medium or rather low temperature can be quite active so long as they can absorb a great deal of radiant heat from the sunshine, will come to rest almost immediately when a cloud passes. In this state they are not capable of instant flight, but, as Dotterweich has described and figured, flight is preceded by a period of preparation during which the wings move. Dotterweich distinguishes between two main types of such movements. In the "pumping" type the wings are moved at a not very rapid rate (1 per sec.) through an angle of about 40° from the horizontal. In the vibratory movements ("Schwirren") the movements are much more rapid, but the angle quite small. Vibration takes place usually about the resting position with wings almost vertical, but may also occur in wings spread out almost horizontally. We have observed the same types as Dotterweich and find most often the vertical vibration with a frequency of about 15 per sec. as judged from the sound produced.

In the typical experiment recorded in Fig. 1 a thermojunction was inserted into the wing muscles of a *Vanessa atalanta* and the temperature read at frequent intervals. The animal was suspended by the thermojunction wires and, sometimes spontaneously, sometimes after a slight mechanical stimulus, either flew or heated itself by wing vibrations. In the first period wing vibration caused a rapid rise in temperature in the animal which was otherwise quiet and did not attempt to fly. In the second period flight was induced by stimulation and lasted for about 2 min. during which the temperature rose from 22 to 29°.

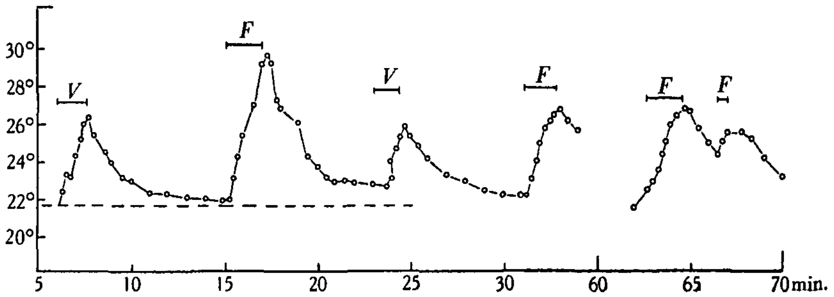

Fig. 1. Temperature record of *Vanessa*. *V*, vibration of wings; *F*, flight; --- air temperature.

In another individual (Fig. 2) flight began spontaneously when a temperature of 35° had been reached by vibration. Generally we find that flight is possible in butterflies at all temperatures above 20°, but usually the animals will raise their temperature by vibration before flight, or alternatively during the first minutes of flight the temperature is seen to increase rapidly. During this same period the flight is intensified, the animal lifting itself and the suspending wires higher and higher and the angle through which each wing is beating increasing from 120° to nearly 180°.

We cannot subscribe to Dotterweich's statement that moths require a definite temperature to be able to fly at all. We made a few observations on *Catocala sponsa*, measuring thoracic temperature and then throwing the moth into the air. These observations indicate that at muscle temperatures above 25° this species is able to fly.

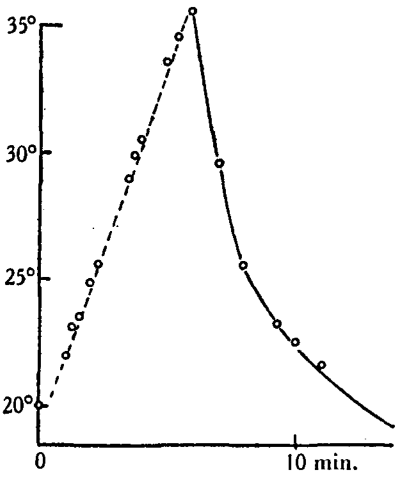

Fig. 2. Heating of *Vanessa* by vibration, with subsequent cooling.

OBSERVATIONS ON BUMBLE BEES, *BOMBUS HORTI*

In several cases the thoracic temperature of a bumble bee was measured, the thermojunction removed and the bee thrown into the air. At measured temperatures below about 30° the insect was unable to sustain itself in the air. Thoracic temperatures in bees caught during flight and rapidly put on to the thermojunction were found to vary between 37 and 42° with air temperatures between 22 and 32°. No clear correlation between thoracic and external temperature was observed, but the abdominal temperature measured in a few cases was clearly influenced by the environmental temperature which it exceeded by 2–5°. The inability to fly at lower temperatures does not mean that no flight movements are performed, but that they are insufficient to support the animal in the air. This is well brought out in the experiment illustrated in Fig. 3, in which the insect "flew" while suspended on the needle. The angular excursions of the wings increased from about 30° at 25° C. to 120° when the temperature had reached 30° C.

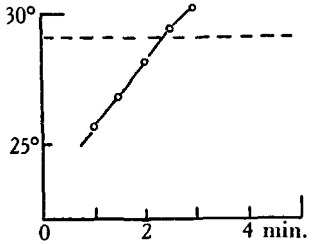

Fig. 3. Heating by flight movements of bumble bee.

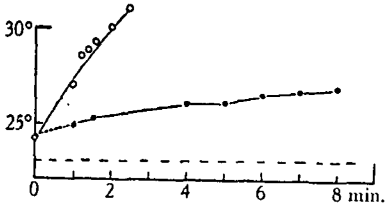

Fig. 4. Thoracic (o) and abdominal (•) temperatures of bumble bee during process of heating.

In a few cases a preparation for flight was observed, consisting in vibratory movements of the wings before they were spread for flight. This produced a loud sound with a frequency above 100 per sec., localized in the muscles, since removal of the wings did not change it. During such vibration the thoracic temperature rose rapidly, the abdominal only slowly (Fig. 4). It is worthy of note that this thermoregulatory mechanism is utilized not only as a preparation for flight, but also in response to stimulation by low temperature when the insects were transferred from 20 to 5° C.

EXPERIMENTS ON THE DOR-BEETLE (*GEOTRUPES STERCORARIUS*)

While the butterflies, moths and bumble bees rank as fairly good fliers, capable of varying the rate of flight within wide limits, the flying power of the lamellicorn beetles is limited and they can vary the speed only within a narrow range. It is well known that they have normally to "pump" for a certain length of time before flight. This "pumping" is a series of deep and frequent abdominal respiratory movements. It was very generally assumed formerly that the pumping served to fill up the tracheal system with air or to raise the concentration of oxygen, but Dotterweich suggested that it was correlated with a process of heating, necessary for flight. There is the difficulty, however, that no wing movements are visible during "pumping", and it is scarcely to be imagined that the respiratory movements themselves could liberate sufficient energy.

A dor-beetle can be induced to prepare for flight when placed on a small platform like a cork from which it is difficult to climb down, provided the conditions of light and temperature are suitable. In the typical experiment recorded in Fig. 5 the thermojunction was introduced through the scutellum into the wing muscles of the mesothorax. From the 2nd to the 5th minute the animal "pumped" but did not attempt to fly and cooled off again. Later, the elytra and wings were spread repeatedly and abortive attempts at flight were made, but were promptly inhibited by the restraining influence of the wires. All the experiments on this specimen agree in indicating a temperature of 35° ± 0·5 in the wing muscles just before flight, but from one animal to another the flight temperature may vary between 32 and 37°. Attempts occasionally made at lower temperatures were unsuccessful. As shown in Fig. 6 the thoracic temperature when flight begins is

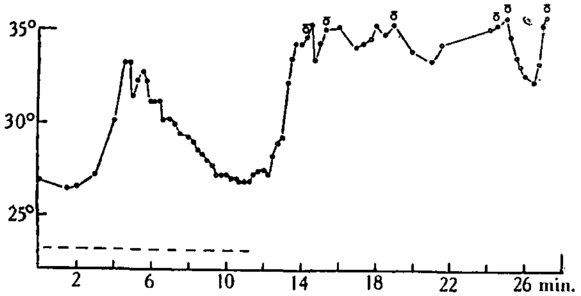

Fig. 5. Temperature record of *Geotrupes*. ō, attempts to fly.

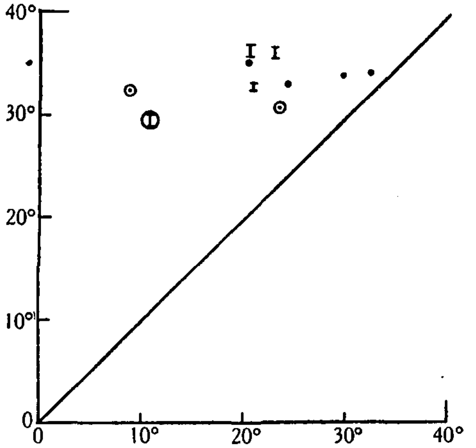

Fig. 6. Relation between thoracic and environmental temperature in *Geotrupes* at beginning of flight. I, repeated attempts. • unsuccessful attempts.

practically independent of the environmental temperature. The animals attempting flight at about 30° thoracic temperature did not succeed. In these cases the frequency of the wing beats appeared normal, but the amplitude was much reduced. Even when not restrained by any instrument certain specimens would attempt flight after insufficient preparation at environmental temperatures of 11, 20–22 and even 32°, and tumble down.

In the following experiments temperatures in the mesothorax containing the principal wing muscles were compared with abdominal and prothoracic. In all cases it was found that the temperature outside the wing muscles is lower by about 5–6°. The difference may be even larger in a first preparation for flight, but is gradually reduced after a series of attempts as shown in Fig. 7. The abdomen contains only small respiratory muscles, but the prothorax contains the powerful muscles supplying the forelegs and used in digging. It is evident therefore that at least the main and probably the total activity responsible for the increase in temperature is confined to the wing muscles.

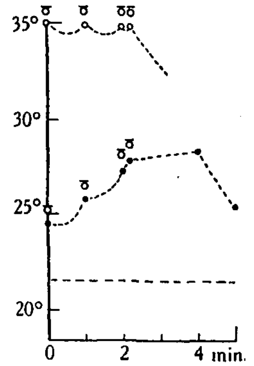

Fig. 7. Prothoracic (•) and mesothoracic (o) temperatures of *Geotrupes* attempting to fly (ŏ). Prothoracic temperatures were actually measured, mesothoracic inferred from a similar experiment on the same specimen.

It is a very curious fact that this activity does not cause any visible movements of the wings as is ascertained by observations with a lens after complete removal of the elytra. That the activity does nevertheless take the form of muscular contractions has been shown by recording the action currents. We are greatly indebted to Dr F. Buchthal for his valuable suggestions and kind assistance in carrying out these experiments. Microelectrodes were introduced into the muscles along with the thermojunction, and the potentials amplified and photographed from an oscillograph. A typical curve is reproduced in Fig. 8.

The frequency of the electrical oscillations is difficult to estimate (about 60 per sec.), but there is no indication of any change with increasing temperature within the interval 24–35°. It is a very characteristic fact, verified repeatedly, that the muscular activity stops completely shortly before the flight begins. Less than a second later the elytra and wings, which up to then were only slightly lifted from the abdomen, are spread and, after another second, flight begins, showing of course renewed electrical oscillations.

THE VENTILATION OF THE TRACHEAL SYSTEM

During rest (at about 22°) the respiratory movements show a frequency of only 20–25 per min. They are confined to the anterior part of the abdomen and can be conveniently observed only after removal of the elytra and wings. In preparation for flight the frequency is at once increased to between 180 and 240 per min., while the depth is increased gradually until involving the whole of the abdomen, and at the same time the elytra are lifted and spread slightly. During the pause in muscular activity intervening between preparation and actual flight there is a definite decrease in respiratory amplitude, and during the initial stages of flight no abdominal respiration can be observed as noted by Fraenkel (1932).

A diagram of this course of events is included in Fig. 8.

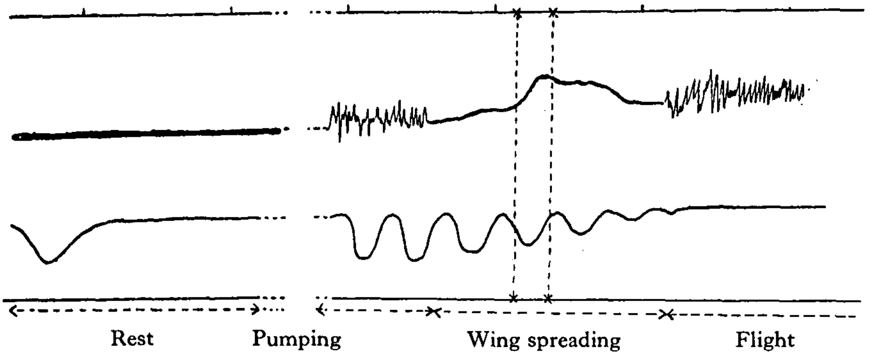

Fig. 8. Oscillogram of wing muscles and rhythm of respiration in *Geotrupes* preparing for flight. Upper line time in seconds. The action potentials cease 1½ sec. before the flight. The spreading of the wings causes a displacement of the electrode. The respirations are reduced during this period and cease when flight begins.

Like the bumble bee the dor-beetle is sometimes seen to react to a cold environment by heat production in the wing muscles. In these cases the oscillogram indicated a lower frequency, e.g. 7–14 per sec. at 11° body temperature.

THE HEAT PRODUCTION INCIDENTAL TO THE PREPARATION FOR FLIGHT

From the curve (Fig. 2) the increase in temperature of the wing muscles of the butterfly can be read off from minute to minute. When after 6 min. the animal took flight this was immediately inhibited, and the animal cooled down to the initial temperature. From the cooling curve approximate rates of heat loss during the heating process can be made out. These figures are put together in Table III, cols. 1 and 2, and col. 3 gives the approximate temperature increment corrected for

Table III. Vanessa atalanta. *Preparation for flight*

Min.	(1) Temperature increment °C.	(2) Estimated loss °C.	(3) (1)+(2) °C.	(4) (3) × 0·8 heat produced cal./g./min.	(5) Whole animal	(6)
					Cal./kg./hr.	l. O_2/kg.h.
1	20 –22	0·5	2·5	2	40	8
2	22 –24·6	1·5	4·1	3·3	66	13
3	24·6–27·5	2·5	5·4	4·3	86	17
4	27·5–30·2	4	6·7	5·35	107	21
5	30·2–33·0	5	7·8	6·25	125	25
6	33·0–33·5	7	9·5	7·6	152	30

heat loss. The wing muscles in which the heat is produced make up a little over one-fifth of the total body and we assume the total mass of substance heated to the temperature measured to make up one-third of the body weight and to have a heat capacity of 0·8 %, the normal value for animal tissues. Making these assumptions we have the total heat production in cal./g./min. of the active tissue (col. 4) and the corresponding heat production for the whole animal given in cal./kg./hr. (col. 5). As the butterfly feeds on sugar we can take this heat to result from carbohydrate combustion, using 1 l. oxygen and eliminating 1 l. CO_2 to produce 5 cal. This gives us the figures in col. 6. In this case direct determinations were made of the CO_2 eliminated during two consecutive periods from 0·5 to 2·3 min. and from 2·3 to 4·7 min. corresponding to the temperatures 20·9–25·6° and 25·6–32·1°. These determinations gave respectively 0·12 and 0·24 ml. CO_2 for the butterfly weighing 320 mg. or, calculated per kg./hr., 12·5 and 18·8 l. CO_2, a satisfactory agreement with the values deduced from the temperature measurements.

Similar calculations of metabolism were made from temperature curves obtained on *Geotrupes* indicating only slightly lower maximum values (26 l. CO_2/kg./hr.), but a more rapid rise with increasing temperature. In actual flight much higher rates of metabolism can be reached.

DISCUSSION

While the possibility that the heating process described is essential for the discharges of nervous impulses from the corresponding ganglion to the muscles cannot be definitely excluded, it appears much more likely that it is required to allow the muscular engine to develop the energy required for flight.

If the mechanism had to do primarily with the nervous discharges one would expect the frequency to be mainly involved, but this is certainly not the case, as shown by the fact that the heating vibrations have a similar frequency as, but a much smaller amplitude than, the regular flight movements, a frequency which is probably less than 20 per sec. in butterflies and more than 100 per sec. in bumble bees.

Accepting the heating as essential for the muscular production of energy we may attempt a rather wide generalization. It is well known that the minimum or "standard" metabolism of animals during rest is governed by body temperature and can be expressed as a definite function of temperature, the same for quite a number of forms, different in others. The present temperature measurements (and a number of observations of animal behaviour) suggest an equally definite relationship between the possible maximum muscular activity and the temperature of the working muscles. It should be emphasized, however, that at present we cannot get beyond the suggestion of a relationship; to prove its existence or to obtain a quantitative formulation will be a very difficult task.

The need for "heating up the engine" before flight is no doubt widespread among insects, but by no means general. We believe it to exist in all "bad" fliers who require a maximal or nearly maximal muscular effort to fly at all, as is the case with many beetles. It is probably significant that several species of *Hydrometra* are wingless near the northern boundaries for their distribution, but farther south are winged and able to fly. The good fliers, especially among the Diptera, are able to fly at rather low temperatures, but attain to high velocities only when the environmental temperature is fairly high, as it can be easily observed on the common housefly. It is scarcely conceivable that small insects like mosquitos are able to raise the temperature of their wing muscles more than a couple of degrees above the environment, but nevertheless *Trichocera hiemalis* can be observed flying in winter at temperatures about the freezing point.

The line of investigation initiated in this paper will be followed up in two distinct directions. One of us (E. Z.), who began these experiments, is mainly interested in the problems of heat regulation. It is evident that, when during flight the metabolism is further greatly increased, mechanisms must come into play which will prevent any increase in temperature beyond a certain point, and it is suggested that a regulation of evaporation is responsible. The senior author has been interested for years in problems concerning economy of locomotion and proposes to study the metabolism of insects during flight at various known velocities, and to discover if possible, the influence of temperature upon the maximal rate of flight.

SUMMARY

Temperatures have been measured by means of thermojunctions at several points in the body of insects preparing for flight.

In butterflies (*Vanessa*), moths and bumble bees (*Bombus*), preparation consists in vibratory movements of the wings raising the temperature of the wing muscles usually above 30° C. In lamellicorn beetles (*Geotrupes*) there are no visible movements of the wings, but the vibrations can be demonstrated by leading off action potentials from the muscles. The heat production takes place always in the wing muscles, but there is a gradual and much slower increase in the temperature of the rest of the body.

The muscle temperature necessary for flight is high (above 32°) and nearly constant in bad fliers (*Geotrupes*), while the good fliers can fly at different temperatures, *Vanessa* from about 20 up to 42°. Even in the latter type a high rate of flight can be attained only when the wing muscles have become heated above 35°.

The heat production in the vibrating muscles can be estimated from the temperature increment during the heating process combined with the decrement during subsequent cooling. It increases rapidly with increasing temperature. The final value found in *Vanessa* just before flight at 34° corresponds to a metabolism of 30 l. O_2/kg./hr. The metabolism in actual flight reaches much higher values.

It is suggested that a definite relationship may exist between temperature and the maximum work of which a muscle is capable.

Our thanks are due to Dr F. Buchthal for his valuable suggestions and kind help to obtain oscillograph records of muscular vibrations.

REFERENCES

BACHMETJEW, P. (1901). *Experimentelle entomologische Studien vom physikalisch-chemischen Standpunkt*, **1**. Leipzig.

DOTTERWEICH, K. (1928). *Zool. Jb., Abt. allg. Zool. Physiol. Tiere*, **44**, 399–425.

FRAENKEL, G. (1932). *Z. vergl. Physiol.* **16**, 394–417.

NECHELES, H. (1924). *Pflüg. Arch. ges. Physiol.* **204**, 72–86.

NIELSEN, M. (1938). *Skand. Arch. Physiol.* **79**, 193–230.