# PREPARATION FOR FLIGHT BY HAWK-MOTHS

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## INTRODUCTION

The rise in temperature that is normally associated with muscular activity is particularly evident in the pterothorax of large insects where the flight muscles are located. Several authors (Krogh & Zeuthen, 1941; Sotavalta, 1954a; Weis-Fogh, 1956) have investigated the thoracic temperatures of insects during tethered flight and have reported temperatures of 35–42° C. in Hymenoptera, 30–35° C. in Lepidoptera, 35° C. in *Geotrupes* and up to 36° C. in *Schistocerca*.

In some insects this temperature rise may occur during the early period of flight, but Dotterweich (1928) considered that moths belonging to the families Noctuidae, Bombycidae and Sphingidae were incapable of flight until the temperature of the flight muscle had been raised by a preliminary quivering of the wings. In this way the oleander hawk-moth, *Deilephila nerii* L., raised its thoracic temperature to 32–36° C. before it flew, and he recorded a maximum temperature of 41·5° C. during tethered flight. Moths warmed in an oven to 35° C. were found to be capable of immediate flight.

The need for a preliminary warming period suggests that the power that can be produced by the flight muscles at the normal environmental temperatures is insufficient to raise the insect from the ground or sustain it in controlled flight. If one accepts the complex factors of pronation, supination and flexure of the wing, measurement of which is essential for a complete evaluation of the lift and propulsive forces produced during the stroke (Jensen, 1956), the forces generated by the wing will depend basically on the area and length of the wing and the frequency and amplitude of the stroke (Hocking, 1953). It has been calculated that the power required to raise the weight of an insect from the ground rises as the 3·5th power of a linear dimension (Maynard Smith, 1954), whereas the wing area will only increase as the square. One might expect therefore that to raise a heavier moth from the ground would require relatively more work from the flight muscle. This could be obtained by an increase in the frequency and amplitude of the stroke which would in turn be reflected in a greater quantity of heat liberated in the muscle.

In Nigeria climatic factors make it easy to obtain sufficient numbers of any one species to test this hypothesis. The Sphingidae are represented by some ninety species (Boorman, 1960, 1961) which are common at most times of year, several of these being identical with species that occur in Europe. A survey was therefore made, both within a single species and for different genera, of the temperature of the flight muscle when flight took place and this was related where possible to the weight of the moth, its wing area and the frequency of the wing stroke.

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## MATERIAL AND METHODS

The moths were collected with a Phillips 250 W. mercury-vapour lamp operating from an ordinary light socket on a large expanse of wall. Moths could be collected from the wall in the morning and did not suffer the damage normally found in those taken with a conventional light trap. To ensure that the moths were in good condition they were used on the day of capture or released.

For the purpose of the temperature measurements the moths were placed on a horizontal board and the dense hair covering the pterothorax was removed over a
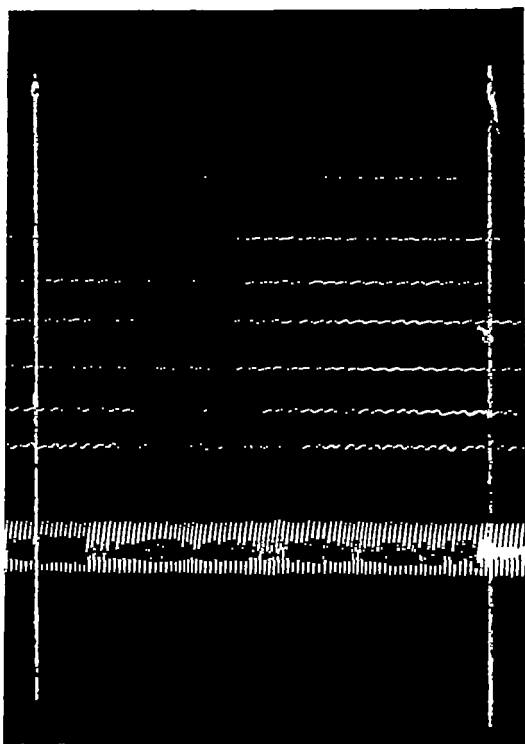


Fig. 1. Extract from a recording of the wing-beat frequency during the warming period of *Deilephila nerii*. Read from above downwards. A period of 23 sec. separates the traces. Time marker, 100 cycles.

small area. The exoskeleton was punctured with a fine needle to one side of the mid-line to avoid damage to the heart and gut and a thermocouple was inserted to a depth of about 4 mm. into the underlying dorsal longitudinal flight muscle. If performed carefully these operations could be completed without anaesthesia and without causing the moths to become active.

The thermocouples were made from 40 s.w.g. copper and constantan wire with leads 10 cm. long. These were soldered to thicker leads for connexion to a switchboard and a galvanometer. In order to reduce heat losses by conduction through the leads, they were insulated with 5 cm. of nylon tubing after leaving the body. The thermo-couple was lightly sealed in place with Copydex and usually broke out of the thorax

as the insect took off. No adverse effect was noticed on the performance or behaviour of any moth that could obviously be attributed to the thermocouple.

The temperature rise was measured with a Cambridge spot galvanometer which had been calibrated against an N.P.L. certified thermometer. The instrument was sensitive to 0·25° C. All the experiments were carried out in an air-conditioned room in which the temperature could be controlled but not the humidity. Unless otherwise stated the experiments were performed at an ambient temperature of 22–23° C.

Measurements of the wing-beat frequency throughout the warming period were recorded kymographically by placing the moths on a light card platform fixed horizontally on the arm of a Palmer isometric muscle lever. A light straw extension and a nylon bristle served to magnify the small vibrations produced by the wings. By lowering the trace at each revolution of the drum an uninterrupted record of the frequency changes during the warming period was obtained. Fig. 1 is an extract of such a record obtained from *Deilephila nerii*. The apparatus proved sufficiently sensitive for moths that weighed more than 0·75 g. and with a thinner-gauge torsion wire would probably be sensitive for moths below this weight. Frequencies measured in this way were at first checked against those measured by direct contact of the wing on smoked paper. In every case the frequencies agreed within narrow limits.

To record the temperature rise it was first necessary to stimulate the moths to become active at times other than those at which they normally fly. This was done by breathing on them (Kalmus, 1948), two or three breaths usually being sufficient to activate them. As they began to warm up the temperature rise was recorded at 15 sec. intervals until take-off.

At the end of the experiment the moth was killed and weighed and its sex was recorded by visual examination or dissection. The wings were cut off and their areas calculated by cutting their shape from a card of known mass per unit area, and then weighing the shapes to the nearest tenth of a milligramme.

## RESULTS

From a preliminary survey it became apparent that the temperature at which flight took place (the term 'flight-temperature' is used in this sense throughout this paper) fluctuated considerably within the species. The behaviour subsequent to stimulation was also erratic; some moths became active quickly whilst others required multiple stimulation and seemed reluctant to fly. If the readiness to fly was being in part determined by some internal factor, it seemed necessary to have some standard by which the temperatures measured could be judged to be those of a normally behaving animal.

On these grounds it was decided to use the oleander hawk-moth, *Deilephila nerii*, for the flight-temperature measurements. It is a large moth, weighing between 1·5 and 3 g., and has a thoracic capsule measuring about 13 mm. across. It has a placid disposition and can normally be handled without causing it to become active. In addition, there are a number of behavioural features that are seen during the warming period which enable an estimate to be made of the normality of the behaviour. Any moths not following the typical behaviour pattern were rejected.

## The behaviour of Deilephila nerii

In the resting position (Fig. 2A) the moth lies on a horizontal or inclined surface with the head depressed between the tibiae. The tarsi of the forelegs are held parallel in front of the head, touching the ground. The second and third pairs of legs are directed laterally and posteriorly. The antennae lie posteriorly along the side of the prothorax with the hooked tips tucked under the base of the forewings. The wings are folded backwards, depressed below the horizontal with the tips touching the ground, giving the moth a typical delta-winged appearance. The thorax and the anterior segments of the abdomen rest on the ground, the last few segments of the abdomen being curled dorsally.
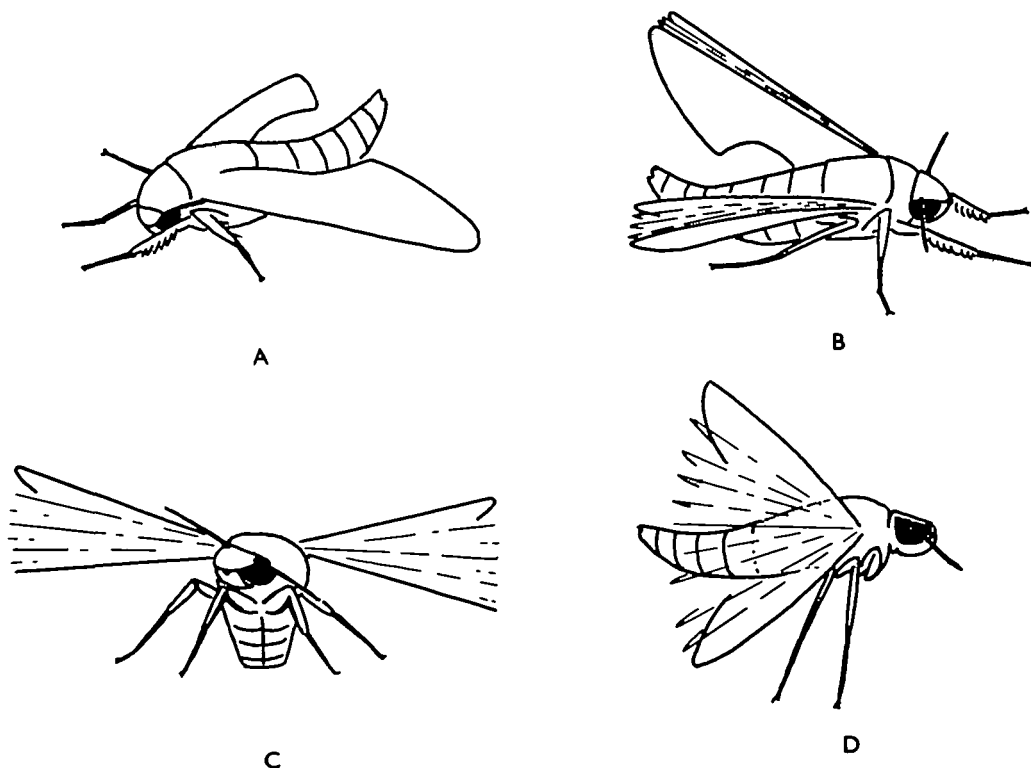
Fig. 2. Behaviour of D. nerii. A, At rest; B, warming up; C, head flicking; D, about to take off.

Following stimulation the moth immediately becomes active. The antennae are swung forward, the head is raised and the first and second pairs of legs are extended slightly, raising the thorax off the ground (Fig. 2B). Under natural conditions the moths become active just as darkness is falling and observation shows that the antennae swing forward shortly before the head is raised and the wings begin vibrating.

The wings are now raised to the dorso-lateral position with the tips level with the end of the abdomen. The vibrations are at first small in amplitude (5°) but as warming continues the amplitude increases and the stroke is brought into the vertical plane, the arc traced by the wing-tip being now level with the thorax. Pulsations of the abdominal air sacs become visible and the abdomen is slowly raised from the ground

As the internal temperature approaches the flight-temperature the moth makes a series of flicking movements with its head, alternately to left and right (Fig. 2C). The intensity of these movements increases as take-off approaches. Their significance is not clear but probably involves an orientation to the available light pattern. Following close upon the head-flicking movements the forelegs are raised from the ground and retracted (Fig. 2D) and the moth takes off. Take-off from a horizontal surface is usually vertical for a short while before a forward component is introduced into the flight.

This type of behaviour might be considered typical of the majority of Sphingidae and was noted in *Euchloron magaera* L., *Hippotion osiris* Dalm., *Pseudoclanis postica* Wkr., and *Herse convolvuli* L. None of these, however, exhibited the pattern as
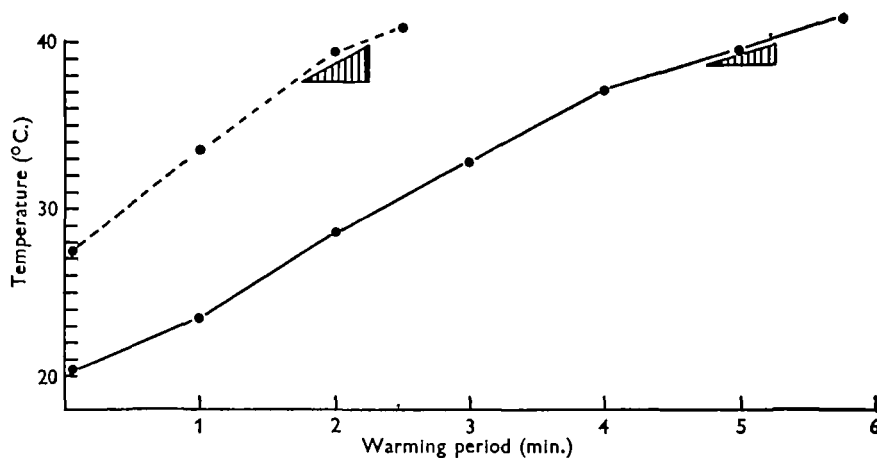


Fig. 3. Temperature rise in the thorax of *D. nerii*. Results of two experiments on the same moth at different ambient temperatures. Broken line, 27·5° C.; continuous line, 19·5° C. Shaded triangles represent the onset and intensity of head flicking.

regularly and as noticeably as *Deilephila*. In contrast with the behaviour pattern described above is that exhibited by the genus *Nephele*. Many moths of this genus appear to be capable of fast and direct flight immediately they are disturbed, the shadow of a hand usually providing sufficient stimulus. When they do warm the flight muscles, they do so by high-frequency vibrations of a very small amplitude and the wings are not raised but remain in the horizontal rest position.

### The flight-temperatures

The temperature rise in the thorax of forty-five individuals of *Deilephila nerii* was measured in the foregoing manner. The temperature of the flight muscle of the insect whilst at rest was usually 1–1·5° C. above the ambient temperature, the difference presumably being due to the resting metabolism of the muscle. Fig. 3 is the typical time course of the temperature rise of a single moth at different ambient temperatures. It was generally found that the flight-temperature was constant for the individual and independent of the environmental temperature over the chosen temperature range. This suggests that the moment at which flight occurs is related to the absolute temperature of the muscle rather than to the temperature in excess of the surroundings.

It is interesting to note that the head-flicking behaviour is initiated at similar temperatures in both experiments.

The mean rate of temperature rise for all the experiments with *D. nerii* was $4.2°$ C./min. The rate is a little faster during the early part of the warming period, falling off at the higher temperatures due to increasing heat loss to the surroundings. The heat losses have been shown by Church (1960a, b) to be principally due to convection, the losses by radiation, conduction and evaporation of water being relatively small. No temperature rise was detected in the abdomen in those moths where this was measured.

It can be estimated from the cooling curves of moths after flight that when the thoracic temperature is about 20° C. in excess of the surroundings heat loss is approaching the rate of heat production. Under natural conditions in Nigeria, the
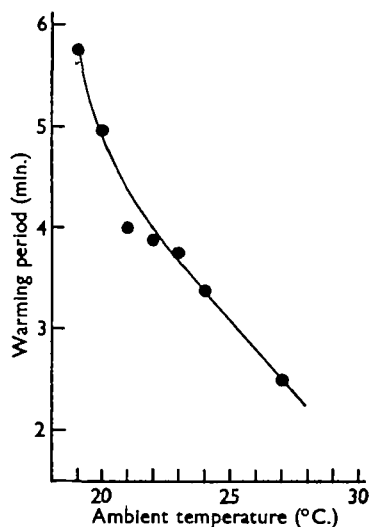


Fig. 4. Relationship between the ambient temperature and the warming period for *D. nerii*. The points represent mean values for several moths.
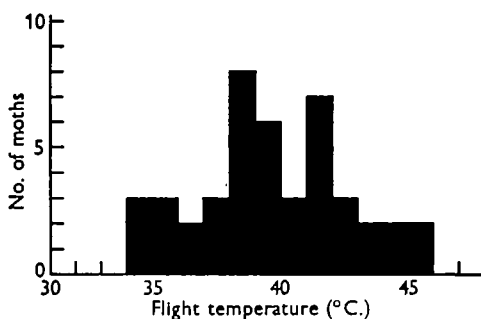
Fig. 5. Distribution of flight-temperatures for forty-five specimens of *D. nerii*.

environmental temperature at the time the moths normally fly is around 25° C. It would therefore seem unlikely both from a physical and from a biochemical viewpoint that the temperature of the flight muscle would ever rise much above 45° C.

Fig. 4 illustrates the effect on the warming period of fluctuations in the ambient temperature. At temperatures above 20° C. the relationship appears to be linear and provides confirmation of the experiments of Dotterweich that showed above 30° C. flight could occur without a period of warming. At temperatures below 20° C. the relationship is no longer linear and becomes exponential in character.

The distribution of the flight-temperatures of the 45 moths used in the experiments (Fig. 5) shows the wide range that may be encountered in moths that are apparently behaving normally. The maximum temperature at $45.5°$ C. is higher than any previously reported and must be approaching the theoretical maximum. No clear distinction can be made between the sexes although several of the moths that took off

temperatures above 40° C. subsequently proved to be gravid females. On several occasions moths were recaptured after a period of flying round the room and the thermocouple was re-inserted rapidly to see if any change had occurred in the temperature within the thorax. Normally no further rise in temperature was detected.

Table 1 contains the average flight-temperatures of other species of Sphingidae. Some of the small moths, in particular *Pseudoclanis postica*, attain temperatures above 40° C. although weighing less than 1 g.

Table 1

| Species | No. in sample | Mean flight temp. (°C.) | Mean temp. excess (°C.) | Mean frequency rise | Av. wt. (g.) |
|---|---|---|---|---|---|
| *Cephonodes hylas* | 1 | 39·2 | 17·8 | — | — |
| *Platysphinx phyllis* | 1 | 39·8 | 16·8 | 18–29 | 0·79 |
| *Pseudoclanis postica* | 5 | 38·6 | 16·8 | 24–43 (2)* | 0·97 |
| *Herse convolvuli* | 8 | 41 | 19·3 | 22–34 (4) | 1·7 |
| *Nephele aequivalens* | 2 | 42·6 | 16·9 | 42–52 (1) | 1·97 |
| *Euchloron magaera* | 7 | 41·3 | 18·8 | 26–43 (2) | 1·8 |

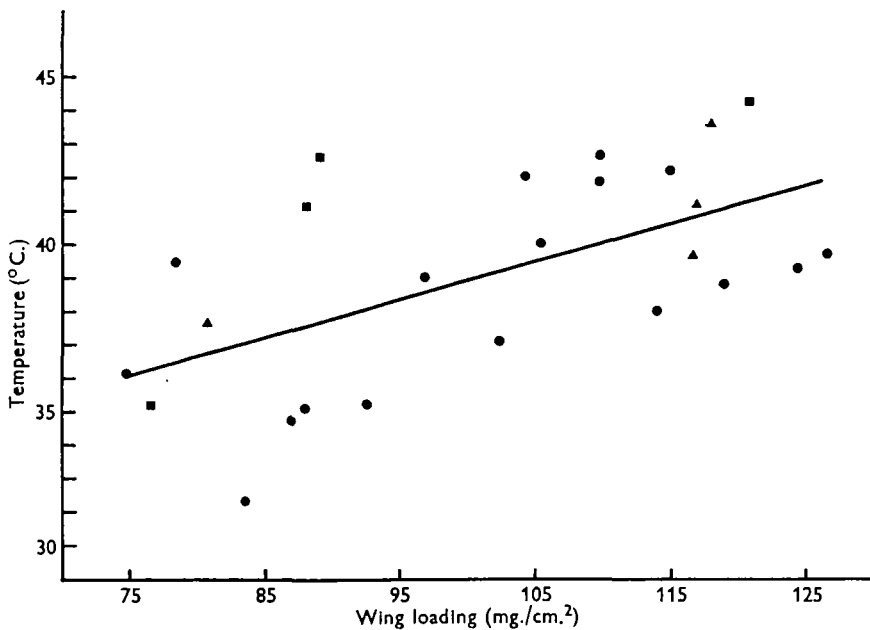\* The figures in parentheses indicate the number of specimens used in the frequency measurements.



Fig. 6. The regression of the thoracic flight-temperature on the wing loading for three genera of Sphingidae ($C = 0.57$, $P = 0.1$%). ●, *Deilephila nerii*, ▲, *Euchloron magaera*, ■, *Herse convolvuli*.

*Wing loading*

Some of the moths used in the flight-temperature experiments were weighed, their wings were removed, and the wing areas calculated. From this it is possible to calculate the wing loading, thereby relating both the weight and the wing area of the moth to the flight-temperature. Fig. 6 illustrates this relationship for *Deilephila nerii*, *Euchloron magaera* and *Herse convolvuli*. The scatter of the points is probably in part due to the
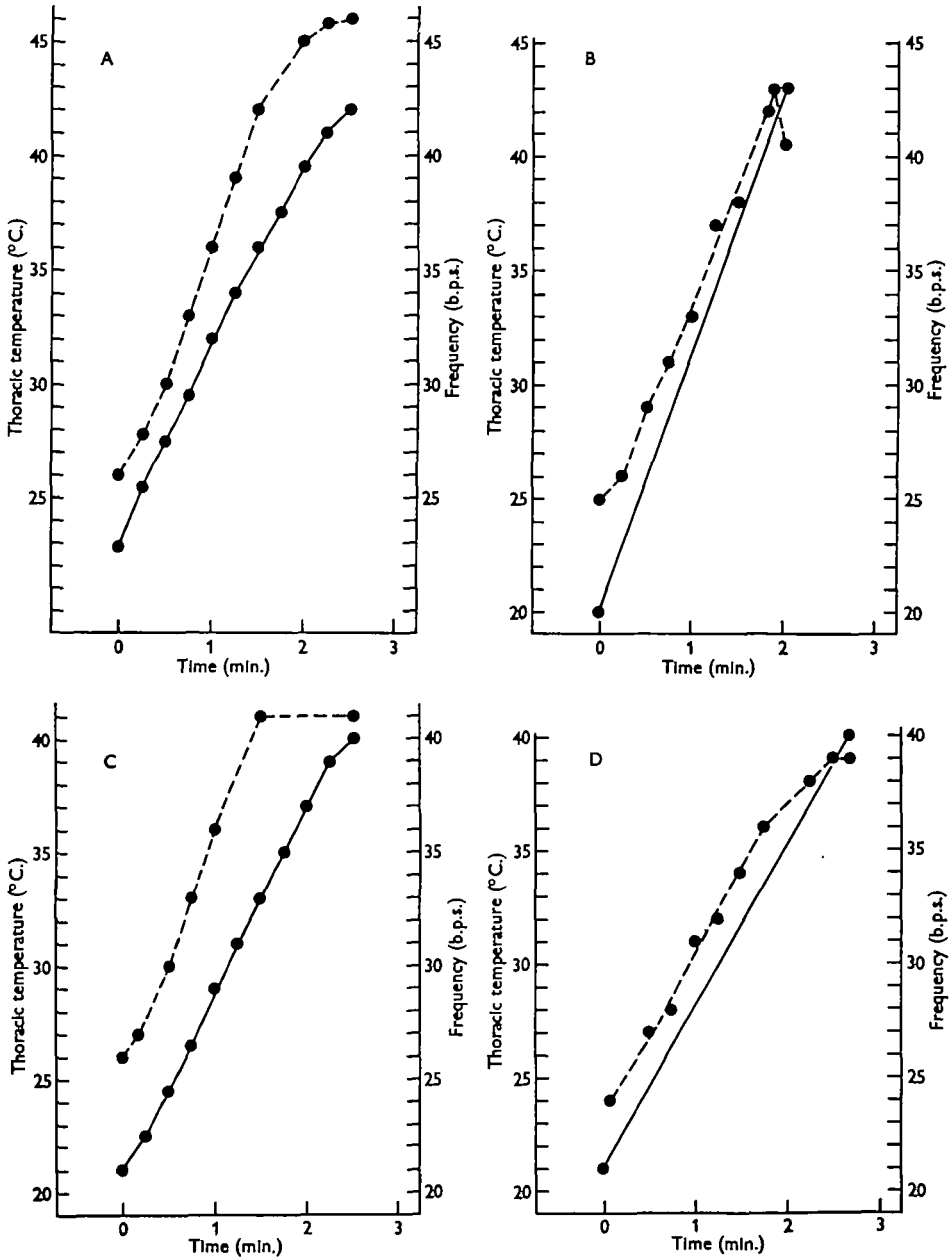
Fig. 7. Relationship of the wing-beat frequency to thoracic temperature during the warming period. Broken line, frequency; continuous line, temperature. A, *Euchloron magaera* (wt. 2·58 g.); B, *Pseudoclanis postica* (wt. 0·75 g.); C, *Euchloron magaera* (wt. 2·52 g.); D, *Deilephila nerii* (wt. 1·74 g.).

fact that both the quantities were determined experimentally and subject to error. The regression of the flight-temperature ($T$) upon the wing loading ($L$) is indicated in the figure and follows the relationship

$$T = 0·11L + 27·9.$$

The flight-temperature shows a positive correlation with the wing loading ($C = 0.57$, $P = 0.1\%$) between the ranges measured here, an increase in the wing loading of 50 mg. corresponding to a rise of 5.75° C. in the temperature of the thoracic capsule at take-off. An analysis of variance of these results indicates that this difference is highly significant.

### Frequency and temperature

The frequency of the wing-beat shows a regular increase during the warming period associated with the rising temperature of the flight muscles (Fig. 7). Observations made on the amplitude of the stroke at this time indicate that this is also increasing although it was not possible to measure this change. There is a noticeable increase in amplitude immediately before take-off which probably coincides with the levelling out or slight drop in the frequency to be noted in the graphs.

### DISCUSSION

Chadwick (1939), Gaul (1951) and Sotavalta (1947, 1952, 1954b) have investigated the effect of density, pressure and temperature of the air and the inertia of the wing on the frequency of the beat. Their experiments were made mostly on Diptera and Hymenoptera, and the conclusions may not be strictly applicable to those insects that do not possess the fibrillar type of flight muscle. Pringle (1957) has suggested that, in those insects where the frequency of the wing-beat is neurogenically controlled, variations in the frequency do not play an important part in the mechanism of flight regulation. Thus in *Schistocerca*, the frequency is set by the physical dimensions of the insect (Weis-Fogh, 1956). The results presented here suggest that this is also true of the Sphingidae, where the frequency of the wing-beat at take-off, which is reflected by the intra-thoracic temperature, is constant in the individual. Within the species the temperature, and by inference the frequency, required for take-off increases with the wing loading and there is some indication that frequency and wing loading in other genera may share this relationship.

Slight variations in frequency may occur in the individual. It appears that just before take-off there is a levelling out or slight drop in the frequency, the lift being sustained by an increase in the amplitude of the stroke. The temperature of the thorax does not fall when the insect is established in forward flight which suggests that the increased lift generated by the movement of the air over the wings is not followed by a lowering of the frequency. Regulation is probably made by means of the stroke amplitude and the other wing-beat parameters.

### SUMMARY

1. Moths belonging to the family Sphingidae are not capable of controlled flight until the temperature of the flight muscle has been raised by a preliminary period of vibrating the wings.

2. The flight-temperature of forty-five specimens of *Deilephila nerii* varied between 34 and 45° C., but individuals always flew at the same temperature.

3. The temperature inside the thorax rose at a mean rate of 4.2° C./min.

4. Alteration of the ambient temperature affects the duration of the warming period but not the flight-temperature.

5. The flight-temperature shows a positive correlation with the wing loading. In *Deilephila* and two other genera of similar dimensions, an increase of 50 mg. in the wing loading corresponds to a rise of 5·75° C. in the flight-temperature.

6. A method of measuring the rise in wing-beat frequency during the warming period is described. The thoracic temperature increases linearly with the frequency.

7. It is concluded that the frequency of the wing beat is determined principally by the wing loading, whilst variations in the other parameters of the wing stroke provide the 'fine control' of flight regulation required during flight and whilst hovering.

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