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Body Temperature and Flight Performance of Honey Bees in a Servo-mechanically Controlled Wind Tunnel

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Summary. 1. Workers of *Apis mellifera ligustica* were tethered to an aerodynamic balance in front of a laminar wind tunnel. They had control over the tunnels wind velocity. Lift, wind speed, wingbeat frequency, thorax and air temperature, and the action potentials in the fibrillar dorsoventral (DV) and dorsolongitudinal (DL) flight muscles were continuously recorded. The air temperature in the tunnel could be controlled. Correlations between all mentioned parameters and the thorax temperature were analyzed.

2. Animals that assumed flight position and flew for more than thirty seconds disregarded optical inputs. They did not respond to changes in speed or direction of an optical pattern, and flew even in complete darkness.

3. In flights that started with thorax temperatures at environmental values, temperature differences between thorax and environment reached 5.2 °C after 4.5 min of flight (Fig. 1). In animals with body temperatures above 36 °C, active temperature regulation could be observed: A large drop of fluid appeared between the ventral side of the head and the thorax, and the front legs frequently rubbed the fluid over the ventral part of the thorax.

4. The average wingbeat frequency showed a linear increase from 136 Hz at a thorax temperature of 24 °C, to 194 Hz at thorax temperature of 33.5 °C. A further increase of the thorax temperature from 33.5 °C to 38 °C was correlated to an increase of the wingbeat frequency to 202 Hz. This increase had a much smaller slope (Fig. 2).

5. The average lift increased from 28.5 dynes at 24 °C to 78.5 dynes at 33 °C (body angle 0°). The lift stayed practically constant from 33 °C to 38 °C (Fig. 2). The lift at thorax temperatures between 33 °C and 38 °C would keep the empty body weight aloft. The flight velocity increased from 0.8 m/sec, thorax temperature at 24 °C, to 3.3 m/sec, thorax temperature at 38 °C (Fig. 2).

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6. The average action potential frequencies (APF) in the fibrillar flight muscles rose from between 8 and 9 Hz at thorax temperatures of 24 °C to between 12 and 13 Hz at thorax temperatures of 38 °C. In the range of biggest change in lift and thrust, at thorax temperatures between 26 °C and 31 °C, the APF in the dorsoventral muscles stayed constant, while it rose only one Hz in the dorsolongitudinal muscles (Fig. 2).

7. The increase in lift showed a linear relationship to the increase in wingbeat frequencies between 122 Hz and 158 Hz. Between 158 Hz and 208 Hz the gain in lift was bigger. From 208 Hz on the lift stayed constant. The flight velocity rose linearily with wingbeat frequencies from 122 Hz to 208 Hz (with some irregularities near 140 Hz) and with a steeper increase at wingbeat frequencies over 208 Hz (Fig. 3).

8. It was concluded that the large increase in the power output of the flight motor that occurred with rising thorax temperatures was mostly caused by an augmentation of the efficiency of the flight system and not by an increase in neural activation.

A. Introduction

Insects have at least two basically different methods to vary flight power output: They can change the form of the wingbeat and thus alter the power output *per wingbeat* (wing loading). Corrections of power output can be made at a constant wingbeat frequency. Secondly, power output might be increased by a rise in wingbeat frequency, while the power output per wingbeat is not altered. Honey bees use both methods.

In a previous study (Esch et al., 1975) changes in lift and thrust were induced by sudden alterations in the optical field of experimental animals. Wingbeat frequencies changed, if at all, only slightly. Lift and thrust must have been altered by changes in wing loading. But it was noted that wingbeat frequencies varied slowly in longer flights. The changes were positively correlated to variations in the thorax temperature. We suspected that differences in thorax temperatures were responsible for the difficulties we incurred, when we tried to calculate unequivocal "power output"/"action potential frequency" ratios.

The flight muscles of a number of insects work most efficiently at temperatures between 30 °C and 40 °C. Most individuals warm their thorax in preparation for take-off, and keep a temperature difference between thorax and environment during flight. Sotavalta tethered several species of Hymenoptera, Diptera and Lepidoptera to a roundabout, with thermistors fixed to the thorax, or suspended them by thin wires, as to allow flight "on leash". He found an average temperature difference of 10–13 °C or slightly less between thorax and environment in *Bombus, Apis* and *Vespa* (Sotavalta, 1954). References for additional studies on the subject can be found in an article by Heinrich (1974).

The optimal flight temperature is determined by the mechanical resonance frequency of the flight apparatus and by temperature dependent physiological properties of the fibrillar muscles, that drive the wings. The viscous modulus of the stimulated muscles has to reach the most negative value possible to allow a maximum power output. Its magnitude depends on the stretching frequency of the muscles and on their temperature: If one varies the stretching frequency from very low to high values, the viscous modulus first falls to a negative minimum and then rises into the positive range. The frequency at which its minimum occurs – and at which the power output is maximal – rises with increasing muscle temperature. Thus, by increasing the thorax temperature from low to high levels, physical and physiological properties of the flight motor can be matched optimally at one point (Machin et al., 1962). The flight motor does not operate efficiently if this matching is not proper, and animals might not be able to fly.

Individuals on a flight balance in front of a servo-mechanically controlled wind tunnel frequently fly with lifts that are not sufficient to keep them aloft in free flight. The temperature of the thorax rises slowly, and the aerodynamic output increases. It was the objective of this study to quantify the increase in the aerodynamic power output occurring at rising body temperatures, and to investigate the role of neural activation in the fibrillar flight muscles during this process.

B. Materials and Methods

The honey bees (*Apis mellifera ligustica*) came from the apiary of the Department of Biology at the University of Notre Dame.

A description of the servomechanically controlled wind tunnel and the aerodynamic two component balance is given in an earlier publication (Esch et al., 1975). Alterations were made at some critical points (the letters refer to Fig. 1 in the above mentioned publication). The transducer T 1 was replaced by a Harvard Apparatus, model 363, isometric transducer. To reduce the thermal drift in the sensitivity range necessary for our observations (0 to 200 mg), a thermistor (Fenwal type GB 41 J1) was fixed to the transducer lip and used in a compensation circuit at the input of amplifier A1. Temperature changes of 15 °C caused thermal drifts smaller than 10 mg/h.

The universal joint (k1, k2) was replaced by a small universal joint from a US Navy, type MK 35 mod. 3, gyro. This made mechanical damping unnecessary. The crystal X was omitted, since the wingbeat could be recorded directly from the output of amplifier A1. The response time of the lift measuring system was reduced to about 10 ms. The output of amplifier A1 was fed through a variable filter, so that unwanted vibrations could be eliminated, if necessary.

The lift measuring device is very sensitive to building vibrations. It was necessary to place it on a heavy balance table. A foam rubber pad, 4 cm thick, on top of which a partly inflated inner tube of a car was set, provided a further mechanical isolation of the balance from the balance table. All electrical connections to the balance had to be made through very thin, spiraled wires to avoid conduction of vibration to the balance.

A box was built around the balance (length 100 cm, height 60 cm, width 60 cm). The wind tunnel blew into this box from one side. We attached an air return duct (diameter 12 cm) to the opposite side. This duct brought the air back to the inlet of the tunnel. A thermostatically controlled electric heater was inserted into the return duct. Air temperatures between 20 and 36 °C could be maintained in the tunnel, if the air circulated with speeds between 10 and 20 cm/s between flights.

Wind velocity, air temperature 2 cm behind the bee, thorax temperature and lift were continuously recorded with a Beckman 4-channel, type S II-Dynograph strip chart recorder. These parameters, together with the action potentials in the fibrillar dorsolongitudinal and dorsoventral muscles, were at the same time recorded on magnetic tape with a Precision Instrument, model 6104, tape recorder in FM-mode for later analysis with a Nova 1200 digital computer.

The surface of a cylinder (diameter 107 mm, length 135 mm) was marked with alternating black and white stripes (stripe width 33.6 mm). It rotated under the bee, so that the stripes moved from front to back at a rate of 10 stripes per s. The cylinder was made from clear plastic and it was illuminated with a 60 watt light bulb from the inside. The experimental animal saw front and back edge of the cylinder under an angle of 70° from the vertical. Experiments were conducted in a dark room, the cylinder provided the only illumination. Optical conditions were very similar to those described by Heran (1955) for investigations in which he studied the wind compensation of flight speed in bees.

All other technical details are described in an earlier publication (Esch et al., 1975).

C. Results

a) General Observations on the Flight Behavior

The angle between body length axis and wind tunnel length axis is called "body angle". All animals were attached to the flight balance at body angles close to 0 degrees. This is the body angle most frequently observed in straight, level flight (Esch, unpublished). The body angle determines the fractions of the total flight power output that are used for lift or thrust (Esch et al., 1975).

Many animals hesitate to assume flight position (abdomen held horizontal, legs folded upwards and backwards close to the body) in the first 30 s of flight. In this period they respond to optical stimuli, as changes in the velocity or direction of rotation of the striped cylinder, or nearing of the hands or head of the experimenter, by changing lift and thrust and varying of the positions of the different parts of the body. If the velocity of the striped cylinder is increased in the direction from front to back, the abdomen is raised, if it decreases or even changes direction, the abdomen is lowered. After this initial period, however, most individuals assume flight position and disregard optical inputs. They even fly in total darkness. These flights last from minutes to hours.

b) Temperature Difference between Thorax and Environment and Flight Time

Most flights were stimulated by pulling a piece of paper from the legs of the experimental animals ("tarsal reflex"). Individuals with thorax temperatures close to environmental temperatures were not ready to fly. The wingbeat fre-

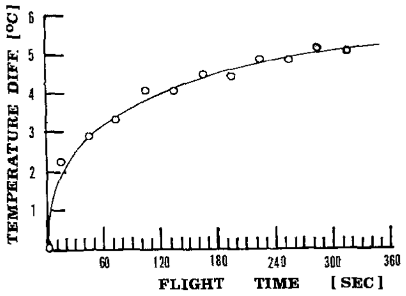

Fig. 1. Temperature difference between thorax and environment in relation to flight time. Standard errors omitted because they were very small ($\leq \pm 0.32$ °C)

Table 1. Data plotted in Figure 1. Measurements from 9 individuals. Mean and standard error are given

Flight time (seconds)	Temp. diff. (°C)	Number of measurements (*N*)
15.0 ± 1.02	2.33 ± 0.22	69
44.4 ± 0.76	2.94 ± 0.20	40
76.0 ± 1.22	3.30 ± 0.16	54
104.0 ± 0.82	4.20 ± 0.20	33
136.0 ± 1.40	4.10 ± 0.19	42
165.0 ± 0.90	4.50 ± 0.26	29
195.3 ± 1.44	4.40 ± 0.24	36
224.0 ± 1.12	5.00 ± 0.30	18
254.8 ± 1.74	4.80 ± 0.26	23
283.6 ± 1.25	5.22 ± 0.32	14
315.0 ± 2.36	5.06 ± 0.32	13

quency of bees with low thorax temperatures increased continuously for several minutes in undisturbed flights. The body temperature rose slowly over the environmental temperature (Fig. 1). The values for Figure 1 were averaged from all flights available, regardless of environmental temperature. No significant differences can be found if one groups data from environmental temperatures above 30 °C versus data from environmental temperatures below 30 °C. The thorax temperature increases exponentially to a difference of about 5 °C after 4.5 min of flight. Table 1 gives the data used to construct Figure 1.

c) The Relationship between Body Temperature and the Different Flight Parameters

1. The Wingbeat Frequency

All measurements related to 2.5 °C intervals in body temperature, beginning at 22.5 °C, were used to draw Figure 2. The means and the standard errors are plotted. This graph is especially interesting since average lift, flight velocity and action potential frequencies in the fibrillar flight muscles can be derived from the same data set. We find a practically linear increase of the wingbeat frequencies with thorax temperature from 136 Hz at 24 °C to 194 Hz at 33.5 °C, and from there with a smaller slope to 202 Hz at 38 °C.

2. Lift and Flight Velocity

Lift and thrust increase with the wingbeat frequency (Hocking, 1953; Weis-Fogh, 1973). The wingbeat frequency depends on the thorax temperature. Thus we can expect an increase in lift and flight velocity with a rise of the thorax temperature. This is shown in Figure 2. The flight velocity increases with the body temperature through the whole range tested, from 0.8 m/s at 24 °C to 3.3 m/s at 38 °C. The average lift rises from 28.5 dynes at 24 °C to 78.5 dynes

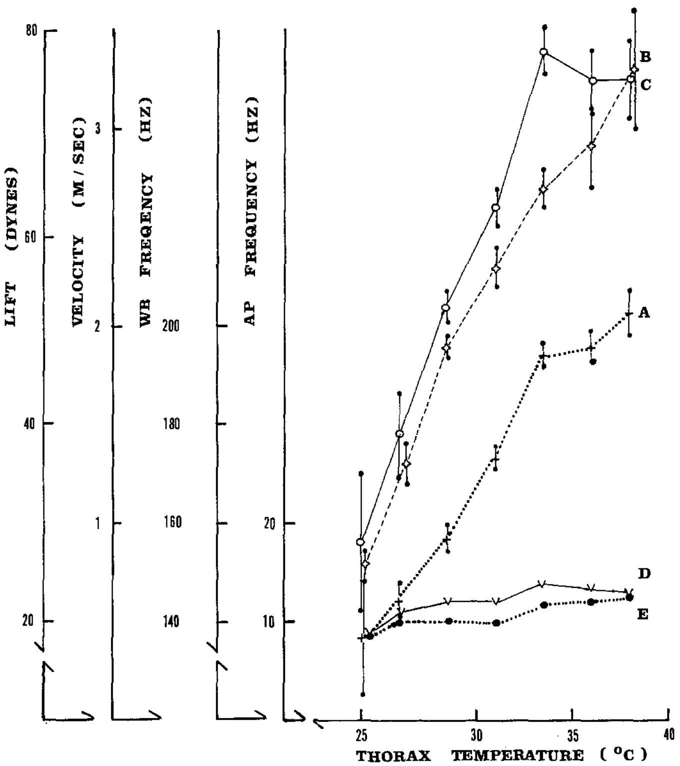

Fig. 2. Different flight parameters versus thorax temperature: *A*, wingbeat frequency (crosses and dotted line); *B*, flight velocity (hollow crosses and dashed line); *C*, lift (circles and solid line); *D*, DL action potential frequency (v and solid line); *E*, DV action potential frequency (solid circle and dotted line). Standard errors are given for each point, except for action potential frequencies, where they are very small (≦ ±0.5 Hz, except for 23.9 °C at which DL = ±1.8 Hz and DV = ±1.9 Hz)

at 33 °C, and then stays constant to 38 °C. The lift at lower temperatures would not be sufficient to keep an animal aloft in free flight. But between 33 °C and 38 °C it would support the empty body weight. The choice to change the body angle exists in free flight, and individuals could sacrifice flight velocity for additional lift and extend the range of environmental temperatures and body temperatures under which they could fly (Esch et al., 1975). Also, the maximum possible power output is probably not produced in our experiments since individuals reach flight speeds of 8–9 m/s in free flight (v. Frisch, 1967).

3. Action Potential Frequencies in the Fibrillar Flight Muscles

Two sets of big fibrillar muscles provide the power for flight, the dorsal longitudinal muscles (DL, wing depressors, muscle 71 in Snodgrass, 1956) and the dorsal ventral muscles (DV, wing elevators, muscle 72 in Snodgrass, 1956). We had found earlier that sudden increases in lift and thrust are accompanied by a

Table 2. Various flight parameters and thorax temperature (Fig. 2). Data from 9 individuals, except for 23.9 °C with only one animal. Mean and standard error given for each data point

Thorax Temp. (°C)	Wingbeat Frequency (Hz)	Flight velocity (m/s)	Lift (dynes)	Action Pot. Frequency		Number of Measurements *N*
				DL (Hz)	DV (Hz)	
38.0	202.6±3.9	3.3±0.3	75.0±4.1	12.4±0.5	12.4±0.4	28
36.0	196.9±3.1	2.9±0.2	75.0±2.8	13.0±0.5	12.1±0.5	43
33.5	194.2±2.2	2.7±0.1	78.3±2.4	13.7±0.3	11.7±0.3	106
31.0	173.5±2.3	2.3±0.1	62.0±2.0	12.1±0.3	9.5±0.3	107
28.5	157.5±1.6	1.9±0.1	52.0±1.3	12.0±0.2	10.0±0.2	153
26.2	144.8±4.6	1.3±0.1	39.0±4.4	11.1±0.3	9.9±0.4	33
23.9	136.0±9.9	0.8±0.1	28.4±7.7	8.5±1.8	8.4±1.9	3

distinct rise in action potential frequencies in these muscles (Esch et al., 1975). The changes occurred at practically constant body temperatures. When lift and flight velocity change together with the thorax temperature, the variation in the action potential frequency is missing (Fig. 2). In the range of a huge increase in power output between 26 °C and 31 °C, action potential frequencies in the DV muscles stay constant, while frequencies in the DL muscles increase only insignificantly. The muscles are not "activated" more frequently, yet power output increases. Their efficiency is presumably augmented with rising thorax temperatures. One possible reason for such a behavior was discussed by Machin and Pringle (Machin et al., 1962). Table 2 lists all the data used to draw Figure 2.

d) The Relationship between Wingbeat Frequency and Different Flight Parameters

1. Lift and Flight Speed

In the past, several investigators attempted to calculate the aerodynamic output and the efficiency of insect flight motors from the wingbeat frequency (Hocking, 1953; Weis-Fogh, 1973). The dependence of lift and flight velocity on the wingbeat frequency cannot be simple in bees, since these animals have the capability to change the form of their wingbeats (Pringle, 1974). The results of our experiments are depicted in Figure 3. Only data from animals in flight position were used. The lift–wingbeat relationship has three sections: A linear increase in the lift with wingbeat frequencies rising from 122 Hz to 158 Hz, a steeper but linear growth from 158 Hz to 208 Hz, and a range of constant lift from 208 Hz to 227 Hz. The lift generated at wingbeat frequencies above 208 Hz would keep the empty weight of a bee aloft.

The flight velocity deviates from a linear increase (toward higher values) between 122 Hz and 158 Hz, shows a practically linear increase between 158 Hz and 208 Hz and a steeper linear increase from 208 Hz to 227 Hz. Beginning at 208 Hz practically all the additional flight energy produced seems to be invested into thrust. An extrapolation of the flight speed into the range of higher wingbeat frequencies reveals that flight velocities of 8 m/s, as they have

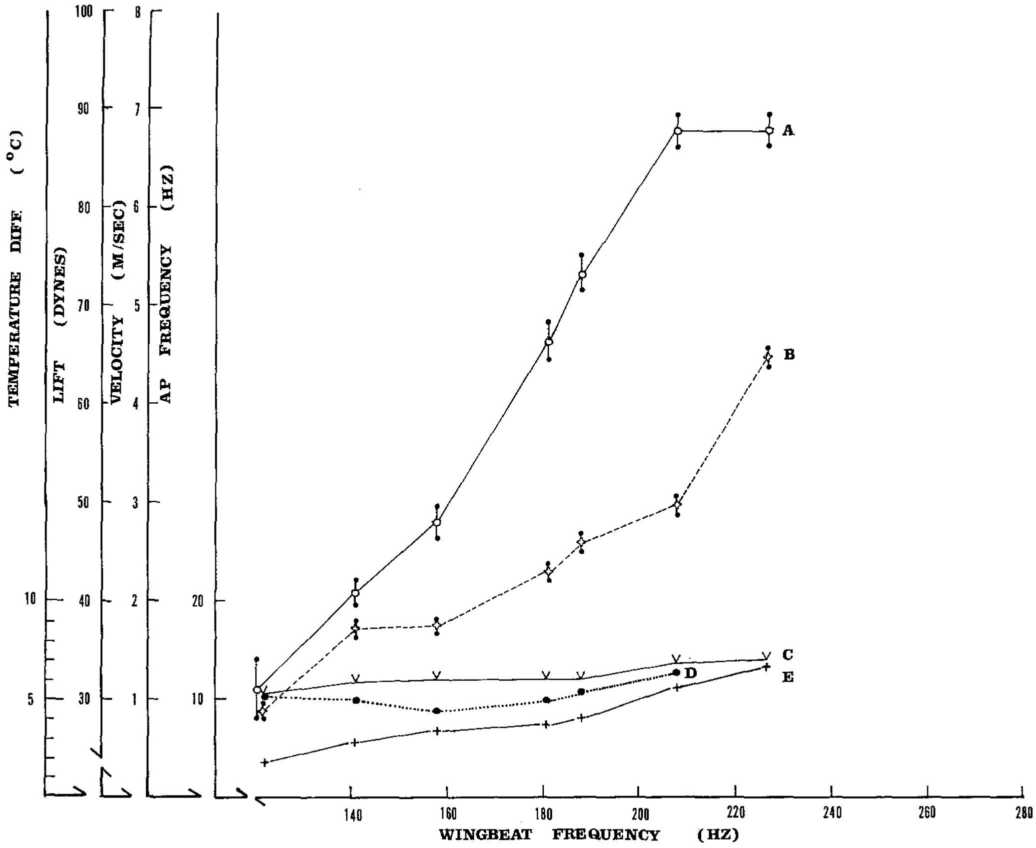

Fig. 3. Different flight parameters versus wingbeat frequency: *A*, lift (circles and solid line); *B*, flight velocity (hollow cross and dashed line); *C*, DL action potential frequency (v and solid line); *D*, DV action potential frequency (solid circle and dotted line); *E*, temperature difference between thorax and environment (cross and solid line). Standard errors given for each point, except for action potential frequencies where they are very small ($\leq \pm 0.6$ Hz)

been reported by v. Frisch and collaborators in free flight (v. Frisch, 1967), could be reached by our animals at wingbeat frequencies between 270 Hz and 280 Hz. Wingbeat frequencies as high as 277 Hz have been reported in the literature (Sotavalta, 1947, as cited in Heran, 1959).

2. Temperature Difference between Thorax and Environment

We saw the correlation between the aerodynamic power output and the wingbeat frequency in the last paragraph. From the same data set used there, one can calculate how the power output and the temperature difference between thorax and environment are correlated. The results are also shown in Figure 3. The amount of heat produced must increase rapidly with a rise in the wingbeat frequency, especially if one considers that at higher wingbeat frequencies more

Table 3. Various flight parameters and wingbeat frequency (Fig. 3). Data from 9 individuals. Mean and standard error given for each data point

Wingbeat Frequency (Hz)	Lift (dynes)	Flight velocity (m/s)	Action Pot. frequency DL (Hz)	Action Pot. frequency DV (Hz)	Temp. Diff. (°C)	Number of Measurements (N)
227.0±0.9	88.5±1.4	4.5±0.1	–	13.7±0.2	6.8±0.1	20
208.0±0.5	88.4±1.4	3.0±0.1	14.2±0.3	12.8±0.3	5.6±0.1	98
188.6±0.5	73.5±1.5	2.6±0.1	12.3±0.2	10.6±0.2	4.0±0.1	113
181.6±0.6	66.4±1.9	2.3±0.1	12.2±0.2	10.2±0.3	3.6±0.1	92
158.4±0.5	48.3±1.4	1.8±0.1	12.1±0.3	8.6±0.2	3.4±0.1	100
142.0±0.5	40.7±1.0	1.8±0.1	11.9±0.2	10.1±0.3	2.8±0.1	93
122.0±1.3	30.7±3.8	0.9±0.1	10.7±0.5	10.5±0.6	1.7±0.2	22

heat is removed from the thorax per unit of time by the higher wind velocity. By extrapolation to higher wingbeat frequencies one can see, that temperature differences of about 10 °C could be expected at wingbeat frequencies between 270 Hz and 280 Hz, if no other changes would take place in the control of the flight system. We know from earlier results (Fig. 2) that thorax temperatures above 40 °C are required for such high wingbeat frequencies under our experimental conditions. Thus full power output could not be reached at environmental temperatures under 30 °C. On the other hand, if full power output would be desired at environmental temperatures higher than 36 °C, active cooling must be employed to prevent the thorax from overheating.

3. Action Potential Frequencies in Fibrillar Flight Muscles

We noted before that the action potential frequency in the fibrillar flight muscles does not change significantly with the body temperature. Similar results can be obtained for the action potential-wingbeat relationship (Fig. 3). The action potential frequency changes only 3.5 Hz maximally in the whole range of wingbeat frequencies between 120 Hz and 230 Hz. It stays constant over big stretches from 140 Hz to 190 Hz. This result seems to be at variance with earlier findings (Esch, 1964; Bastian and Esch, 1970) and it will be discussed again later on.

D. Discussion

1. Changes in Optical Responsiveness

We know from earlier investigations that proper optical and mechanical sensory inputs are necessary to sustain flight over longer spans of time in bees: Freely flying animals dive in narrow spirals to the ground when the lights in the flight-room are turned off (Faust, 1952). Tethered individuals, exposed to moving optical patterns without adequate wind stimulation, fly only an average of

20 s (Schaller, 1960). Our experiments indicate that the different sensory inputs do not control the flight behavior in a rigid, reflex-like fashion. They are weighted according to their momentary importance. In the beginning of flight, optical orientation is indispensable to attain the right flight attitude and course. When mechanical sense organs indicate that the flight efforts result in "proper" sensory inputs, the importance of optical information is reduced. Our experimental animals could even disregard optical information and fly in the dark at this point. On longer flights, optical inputs seem to gain importance only if there is a disagreement between flight efforts and mechano-receptive inputs. This had to be the case in most previously published experiments. Only a servo mechanism that allows the flight efforts to feed back on the mechano-receptive input, can avoid that. If a stable situation can be reached in which the optical inputs become unimportant, bees might fly for several hours until they run out of fuel.

2. Thorax Temperature, Wingbeat Frequency, Lift and Flight Velocity

The relationship between thorax temperature and wingbeat frequency has been described by Sotavalta (Sotavalta, 1954). If we regard the thorax temperature as an independent variable and examine its influence on the wingbeat frequency, our observations generally agree with his data (Fig. 2). An increase in wingbeat frequency under otherwise constant conditions has to lead to a bigger aerodynamic output (Hocking, 1953; Weis-Fogh, 1973). The boost in lift and flight velocity with rising body temperature (Fig. 2) can be explained through an increase in wingbeat frequency (Fig. 3) that in turn is caused by a rise in body temperature.

As lift reaches the magnitude of the "empty body weight", it does not rise further with the wingbeat frequency. Additional energy produced is now invested into thrust, as the increase in the slope of the flight velocity indicates (Figs. 2, 3). We had found earlier that a change in the body angle is an effective way to alter the distribution of the total power output between lift and thrust (Esch et al., 1975). However, such a mechanism cannot be used in the experiments described here. Our animals probably change the form of the wingbeat by activating direct flight muscles (Pringle, 1974). It remains unclear how they determine that their lift is equal to the empty body weight. Freely flying individuals frequently try to lift off and fail. They try again and again, until they stay airborn. Animals at the flight balance lack this opportunity. The tryout for lift, necessary to stay aloft, and the increase in lifting capability with a rising thorax temperature can also be found in bumble bees. Unsuccessful flyers keep increasing their thorax temperature in successive trials until they can lift off (B. Heinrich, personal communication). Individuals carrying heavier loads have higher thorax temperatures, independent of environmental temperatures (Heinrich, 1975). The stepped-up flight velocity at wingbeat frequencies above 208 Hz (Fig. 3) leads to an increase in the removal of heat from the thorax. Average body temperatures are above 37 °C at these frequencies. A higher cooling rate might prevent a climbing of thorax temperatures to unfavorable values. Frequently the heat production must increase faster than the cooling rate, and an active cooling process is employed: A large drop of fluid appears between the ventral part of the head and the anterior ventral part of the thorax. The individuals remain in flight position. The front legs start to brush the liquid over the ventral part of the thorax as far as they can reach, if one increases the environmental temperature in this situation. Otherwise normal flight is continued. A similar behavior is used to cool an overheated bee colony: Many workers distribute a liquid from their mouth parts over the surface of the combs. They evaporate the liquid by beating their wings and producing an air stream (Lindauer, 1954). Bumblebees also regurgitate a fluid and "leash" their tongue when exogenously heated, besides other measures, to prevent overheating (B. Heinrich, in press).

The maximal average temperature difference between thorax and environment of about 5 °C (Fig. 1) is much smaller than the average 9–10 °C Sotavalta reports (Sotavalta, 1954). The body temperature at the beginning of flight and the moment during flight when the temperature is taken are critical: If an animal decides on its own to fly, the thorax temperature is preheated to 36 °C. If such a flight is performed at environmental temperatures of 20 °C, a temperature difference between 10 and 15 °C might be measured in the first minute of flight. At flight velocities of about 1.5 m/s, as they are usual for roundabouts of the type used by Sotavalta, the temperature difference drops within several minutes to values between 3 and 9 °C (Esch, 1960, p. 323). A similar situation can be found in bumble bees. The thorax temperature of a queen might decline from 36.6 °C to 30.7 °C in 3 min of uninterrupted flight, when the animal is suspended from threadlike thermocouple leads (environmental temperature 23 °C), (Heinrich, 1972); but free flying individuals can show temperature differences of 33 °C between thorax and environment, if they make maximal flight efforts (environmental temperature 2 °C) (Heinrich, 1975). In the experiments reported here, all animals started with thorax temperatures at *environmental* levels. The body temperature rose, but so did the flight velocity and the cooling rate. After a few minutes individuals lifted their empty body weight at a flight speed of about 3.5 m/s. Compared to the maximal possible aerodynamic output in free flight, the values measured in our experiments are low: Flight velocities between 8 and 9 m/s can be reached (v. Frisch, 1967), and loads equal to the empty body weight might be lifted. In this case more heat is produced and the temperature difference between thorax and environment has to be higher. The low aerodynamic output is caused by the unwillingness of the experimental animals to change the form of the wingbeat and to activate the indirect flight muscles at higher action potential frequencies (see next paragraph).

3. *Action Potentials in Fibrillar Muscles and Aerodynamic Output*

Recordings of electrical activity from the fibrillar flight muscles of flies (Nachtigall and Wilson, 1967) and honey bees (Bastian, 1972; Esch et al., 1975) have shown that changes in the aerodynamic output of the flight system can be positively correlated to variations in action potential frequencies of these muscles. Our present results seem to be at variance with this: Average wingbeat frequencies could rise from 120 Hz to 190 Hz, the lift could more than double and the flight velocity nearly triple, while the action potential frequencies did not change significantly in any of the fibrillar muscles. We suggest that there are at least two methods by which the power output of the flight system can be altered: (1) In the cases mentioned at the beginning of this paragraph, changes in the sensory input of the experimental animals led to *sudden* variations of the aerodynamic output. Since the wingbeat frequency is not increased significantly (Bastian, 1972; Esch et al., 1975) additional power must have been produced by an increment of the wing-loading. Direct flight muscles can accomplish the necessary corrections in the form of the wingbeat (Pringle, 1974). The concurrent increase of the action potential frequency in the fibrillar muscles insures that enough power per wingbeat is available. If an increase in wing-loading does not occur in this situation, the wingbeat frequency increases with the action potential frequency as it was noted in earlier experiments (Bastian and Esch, 1970). (2) In the experiments conducted for this investigation, it was tried to keep the sensory inputs constant. The wingbeat frequency rose *slowly* with the thorax temperature over several minutes. The efficiency of the fibrillar flight muscles must have increased with the temperature. This allowed a big change in power output under constant neural activation. One way to achieve a higher efficiency with increasing muscle temperature is to shorten up- and downbeat of the wing and to avoid an overlapping of contractions in antagonistic muscles (Heinrich, 1974). Machin et al. (1962) give a physico-chemical explanation for an increase of muscle effectiveness with temperature.

Observations on freely flying animals strongly support the notion that efficiency of the flight apparatus depends on its temperature. They are described in many publications (for instance: Heinrich, 1974). Honeybees with thorax temperature near 20 °C do not take off immediately, if they are intensely disturbed at the entrance of a hive. They have to raise their thorax temperature to nearly 30 °C before they can fly and attack (Esch, unpublished). Von Frisch remarks that honey bees need more time to return from a feeder than for the flight out. "That is connected with the fact that with their burden they do not infrequently stop to rest" (quote from v. Frisch, 1967). The animals do not actually rest, but show very active pumping of the abdomen that is indicative of flight muscle activity and heat production (Krogh and Zeuthen, 1941). The body temperature in flight must have decreased to a point where the forager could no longer stay aloft, because the flight apparatus became too inefficient. During the stop the body temperature is raised and flight might continue. Heinrich reports similar behavior for bumble bees. Some animals, especially small workers, cannot fly for longer periods in a temperature controlled room if the temperature was lower than 10 °C. They land, display an increasing respiratory activity and take off again. Thus they can stay active at low environmental temperatures by "behavioral thermoregulation" (Heinrich, 1975).

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