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VENTILATION IN A BEE-HIVE DURING SUMMER

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I. INTRODUCTION

In literature on bees the desirability of ventilation of the hive is often stressed, but many authors do not state clearly whether, in their opinion, the renewal of the air is necessary for concentrating the honey, for cooling, or for respiration. Moreover, it is not always clear whether the word ventilation is applied to air-currents which are independent of the activity of the bees, or, on the other hand, to those that are caused by the special wing movements (so-called '*fanning*') of the workers. Of the works consulted by the author, Freudenstein's book (1938) is the only one which explicitly states that the air-current caused by the fanning workers has all three of the functions just mentioned, viz. cooling, respiration, and concentration of honey. Obvious though this may seem, yet it is not more than a hypothesis, which, to my knowledge, has not yet been verified experimentally.

Extensive investigations have been carried out on temperature regulation in bee colonies. Here, however, attention has almost always been concentrated primarily on the question as to what degree the temperature is kept constant, and far less, or not at all, on the means used by the bees to achieve this. In particular the question whether the fanning activity at the hive entrance increases when the temperature in the hive rises to too high a value has not been investigated experimentally. [1]

Very little is known as to the regulation of the respiration of a bee colony as a whole. As far as I know, even the simplest experiment, the analysis of the air in the hive, has never been made. Bees, just as other insects, undoubtedly have mechanisms for the regulation of their individual respiration. The intensity of the respiratory movements of the abdomen varies in accordance with the greater or lesser need for ventilation of the air in the tracheal system. However, what has up to the present remained unknown is the existence, in addition to the individual regulation, of a *social* regulation of the respiration, effected by the fanning activity at the entrance or elsewhere in the hive, of a group of workers, varying in numbers with the need for ventilation. [2]

Another problem on which no experimental data are extant is whether there is increased fanning during and after a period of rich bee forage. It is true that simple observations show that there is more fanning, and a louder buzzing noise, in a hive during a period of warm summery weather, and rich bee forage, than in cold and wet weather. But no

[1] Fanning as a reaction to heat has been demonstrated in several insects related to the honey bee, and with a similar social organisation, viz. in the wasps *Polistes gallica* (Steiner, 1930*b*) and *Vespa crabro* (Himmer, 1931) and in the bumblebee *Bombus agrorum* (Himmer, 1933). Moreover, it appeared in the case of *Polistes* that in hot weather the wasps carry water to the nest, spread it over the combs, and then cause it to evaporate quickly by intensive fanning. The honey bee, too, is known to carry water to the hive in hot weather, and the assumption is obvious, that here again fanning is used for cooling purposes, but so far this had not been actually proved. Steiner (1930*a*) and Himmer (1932) do state that the honey bee, too, reacts to high temperatures with fanning, but this is not more than a plausible supposition. Hess (1926) had already shown that a bee colony managed to keep the temperature of the brood combs below 36,5°C when the environment was heated to 40°C. He concluded that the bees must have achieved this cooling by the evaporation of water carried to the hive, but he does not mention fanning.

[2] About 240 years ago, Gödart noted that a single fanning bumblebee could sometimes be found at a bumblebee nest early in the morning. Because of the loud humming noise made by such a bee, Gödart thought that it was waking the others. For that reason it was called a "trumpeter bumblebee". Later workers, e.g. Sladen (1912) and Friese (1923), have rightly rejected this view and suggested that the fanning has a respiratory function. The latter view is in good agreement with the fact that this fanning occurs mainly in densely populated, subterranean bumblebee nests. The matter has never been investigated experimentally. Yet, on the basis of my carbon dioxide tests (see below, p. 355), I consider it probable that this fanning could be released at any time also in thinly populated nests, by the administration of carbon dioxide.

conclusion can be drawn from this with any certainty. The increase in fanning activity might well be due to a greater oxygen want of the active colony, or to a greater need for cooling.

It is the great number of uncertainties we meet with in this field that stimulated the author to make an experimental study of the problem of fanning. The following pages contain a short description of the results of this investigation.

II. METHODS

A necessary requirement for the planned experiments was a bee hive in which the temperature, the composition of the respired air, and the amount of air flowing through the hive could be both measured, and influenced at will. For this purpose we adapted an ordinary "W.B.C.-lichtkast", supplied by Mellona Ltd., Santpoort, Holland, in the following ways. [1]

A. *Temperature measurements.*

The temperatures were measured by means of a thermo-electric method: The very weak currents arising in a circuit consisting of two different metals, if there is a temperature difference between the two points where these metals are in contact with each other, were measured with a sensitive galvanometer. We had 49 contact points between copper and constantan, 48 of which were mounted inside the hive, whereas one was kept outside for purposes of calibration and checking. Each of the contact points was connected with a multiple switch by means of a 15 m long telephone cable with 50 copper channels. By means of the switch, any one of the 49 contact points could be connected with one pole of the galvanometer. All 49 constantan wires met in a single common contact point where they made contact with the copper wire leading to the other pole of the galvanometer. This common contact point was kept at a constant temperature by means of running tap water. This temperature was read with an accuracy of 0.1° C by means of a mercury thermometer. This reading formed the basis for the calculation of the other temperatures from the galvanometer readings. The 49th contact point (see above) was kept at the same temperature as the common contact point, both being immersed in the same water. Switch and galvanometer were mounted in one of the rooms of the laboratory. As a temperature difference of 1° C corresponded with a galvanometer reading of about 18 mm, the temperatures could easily be measured with an accuracy of 0,1° C. It did not take more than only about 3 or 4 minutes to read the temperatures of all 48 contact points.

[1] The "lichtkast" (light-hive) is a hive with an entrance of 1,2 × 3,5 cm, 10 combs of 20 × 35 cm, "cold way", and with glass windows of 8 × 32 cm in both the front and the back walls of outer and inner cases. The entrance can be narrowed at will by means of two sliding pieces of wood (20 × 1,9 × 2,1 cm), one at each side. For some experiments a portable observation hive, constructed according to von Frisch's (1923) directions, was used.

The arrangement of the 48 contact points in the hive was as follows. Points nrs. 1—16 were located between combs nrs 4—5; points 17—32 between combs 5—6, and points 33—48 between combs 6 and 7. Number 1 was at the back and at the top of the hive, number 2 below 1, number 3 below 2, and number 4 below 3. Point 5 was above again, but 8 cm farther forward than nr. 1; 6, 7 and 8 were below 5. Point 9 was above again, and again 8 cm farther forward than point 5; below it 10, 11 and 12 were located. Contact point 13 was located above and in front, 8 cm in front of point 9. Points nr. 14, 15 and 16 were below 13. The distance between two vertical rows was 8 cm, that between two horizontal ones 6 cm. Contact points 17—32 were distributed in an entirely similar way between combs 5 and 6, and points 33—48 between combs 6 and 7; i.e. nrs. 1, 17 and 33 were located at the same height, and at equal distances from the entrance; the same applies to nrs. 7, 23, and 39, etc. The frames nrs. 4, 5, 6, and 7, moved in two zinc grooves, one on the front wall, and one on the hind wall of the hive, and therefore could be removed for inspection quite as easily as the other frames. From each contact point, two wires, one copper and one constantan, ran downward under a slight angle. They passed through the bottom of the hive, and from there the copper wires were connected with the switch via the cable, whereas the constantan wires went to the common contact point. The diameter of copper and constantan wires was .7 and .8 mm respectively. They were enamelled for insulation.

The arrangement of our contact points is reminiscent of that used by HESS (1926). However, an important difference is that HESS mounted his 27 contact points in the middle wall of three of the combs (i.e. inside the artificial comb), whereas ours were located in the interspaces between four out of the ten combs. We shall see later that this has a marked influence on the results.

B. *Temperature control.*

The hive could be cooled by leading cold tap water through a 4,5 m long copper tube with an internal diameter of 9 mm. This tube was fixed to the underside of the roof with both ends projecting outside the hive. The hive was heated by means of two electric heaters, one on the right and one on the left in the interspace between inner and outer wall of the brood chamber. The heaters were connected in such a way that currents of 10, 30, 50, 99, 132 or 192 Watts could be used. Beneath the oilcloth covering the inner wall of the super, there was a frame covered with metal gauze. It was possible, therefore, to remove the oilcloth and the layer of felt, in order to increase the effect of heating or cooling in the chambers where the bees were, without giving the latter a chance to enter the space between inner- and outer wall of the brood chamber.

C. *Quantitative analysis of the air in the hive.*

Forty-eight copper tubes with an internal diameter of about 1 mm

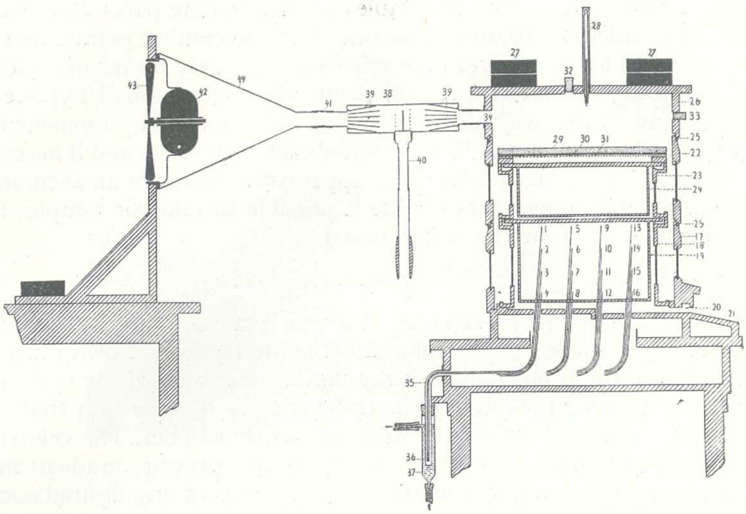


Fig. 1. Vertical section through the middle of the bee hive, the anemometer, and the ventilator. The diagram contains 16 contact points (nrs. 1—16). From each contact point, a constantan wire and a copper wire run downwards. For the sake of clarity, all copper wires have been omitted from the diagram. Of the 16 constantan wires, only those coming from 1 and 2 have been reproduced in full, viz. until the common contact point (nr. 36), where all 49 constantan wires make contact with a copper wire, coming from the galvanometer. For reasons of space, the copper tubes (for taking gas samples), ending just below each of the contact points, have also been omitted. Explanation of numbers: 1—16 = contact points for temperature measurement; 17 = brood chamber (outer wall); 18 = brood chamber (inner wall); 19 = brood frame; 20 = entrance; 21 = flight board; 22 = super (outer wall); 23 = super (inner wall); 24 = honey frame; 25 = rubber tube, sealing the cracks between 17, 22 and 26; 26 = roof; 27 = pieces of lead securing 25; 28 = thermometer for space under roof (in metal holder); 29 = felt plate; 30 = oil cloth; 31 = metal gauze; 32 = upper opening; 33 = front opening (practically always closed); 34 = rear opening, fitted with metal tube to which 38 can be attached; 35 = metal holder for common contact point (in reality, 49 constantan wires meet here with one copper wire); 37 = glass mantle for leading water around 36 (and afterwards past contact point no. 49); 38 = Albrecht anemometer; 41 = rubber connection between 38 and 44; 42 = motor for 43; 43 = ventilator; 44 = zinc funnel.

made it possible to take air samples from different parts of the hive. Each tube ended 6—10 mm below one of the 48 contact points, its other end projected low down from the side of the hive. By means of a piece of rubber tubing the latter end was connected with a small hypodermic syringe, and in this way a sample might be taken at any moment from any tube. The samples were analysed for carbon dioxide, and if necessary for oxygen, by means of a Haldane apparatus. This gave an accuracy of 0,03 %. Similar copper tubes made it possible to take air samples from the entrance or from the flight board.

D. *Control of the composition of the air in the hive.*

Pure carbon dioxide, and gas mixtures rich in CO_2 but poor in oxygen, or even oxygen-free, could be led into the interspace between inner and outer wall of the brood chamber through a tube through the roof of the hive. By removing the felt plate and the oilcloth, we saw to it that these mixtures could penetrate freely into the brood chamber. The velocity of the current was measured by means of a simple pressure gradient meter (calibrated with a 20 l. gasometer). Gas mixtures of any desired composition could also be given in or near the entrance.

E. *Measurement of the air-currents through the hive.*

During these measurements only the entrance and the opening in the roof were left open. All other slits and cracks were closed as carefully as possible by means of molten paraffin wax, or with thin rubber tubing (outer diameter 4 mm). Pieces of lead, to a total weight of 14 kg, were put on the roof to squeeze down the rubber tubing as tightly as possible. A horizontal copper tube (internal diameter 7 cm) was attached to the opening at the back of the roof, and an Albrecht anemometer was connected to this tube. This anemometer is based on the following principle. Several very thin platinum wires, heated by an electric current, project into the air current. The stronger the latter, the more the platinum wires will be cooled. This cooling entails a change in their electrical resistance, which can be mesured by means of a sensitive galvanometer. We calibrated the apparatus by means of a gasometer with a volume of 10 l. We found that it had a very high sensitivity for velocities from 0 up to about .5 or 1 l per second. At higher speeds, the sensitivity was much less, esp. at speeds over 2 l per second. Six thin copper lamellae, projecting into the tube on either side of the anemometer directed the air stream, and ensured its even distribution over the whole tube. Air-currents in both directions could be measured with the same degree of accuracy.

F. *Control of the air-currents through the hive.*

By means of a zinc funnel, a strong ventilator could be attached to the same tube as the anemometer. It could be worked at three different speeds. When working at maximal speed, it blew, or aspirated, about 7 l of air per second through the hive.

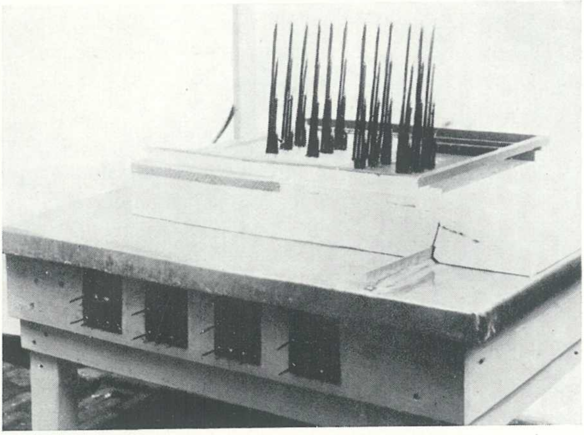


Fig. 2. Floor of the hive, with the 48 contact points, and 48 gas sampling tubes. The other ends of the latter can be seen under the zinc covered table.

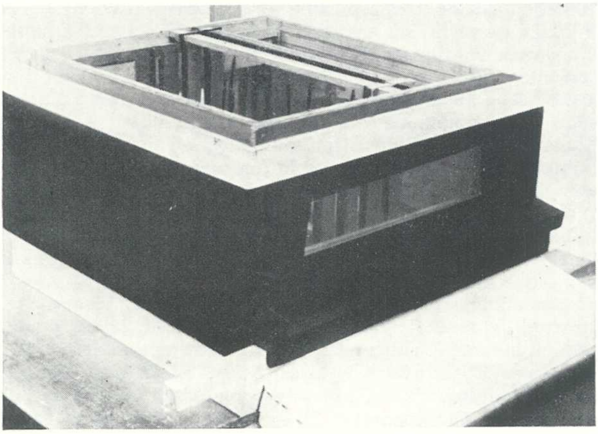


Fig. 3. Brood chamber (inner and outer wall), with flight board, and entrance which can be closed by means of the two sliding pieces of wood. In the cabinet, the zinc grooves for brood frames 4, 5, 6, and 7 can be seen. The (empty) frames nrs. 6 and 7 are in their places.

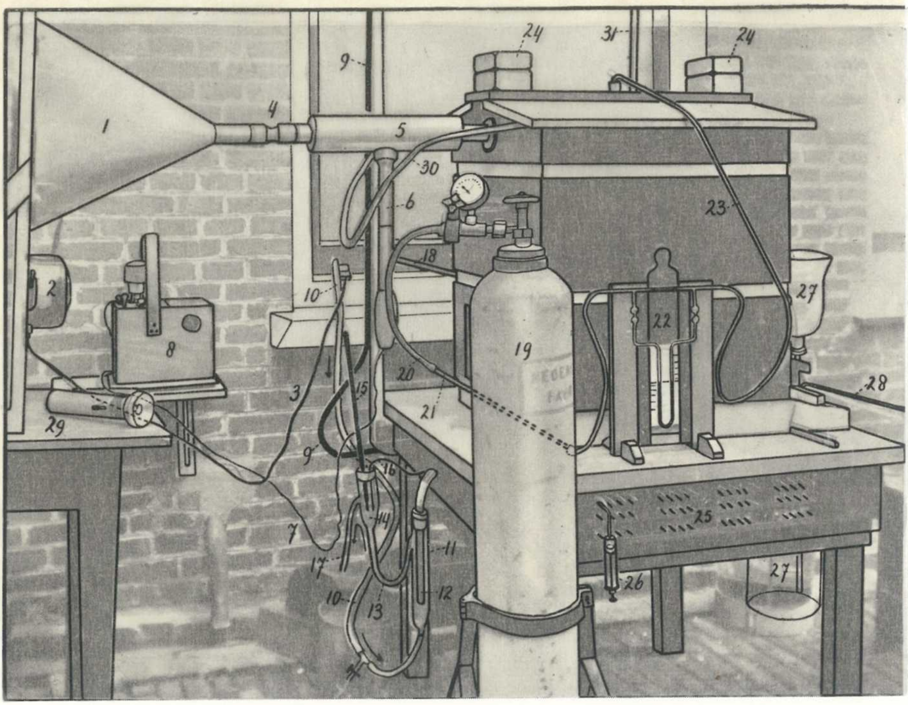
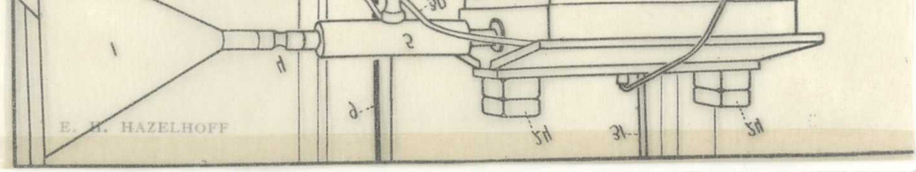
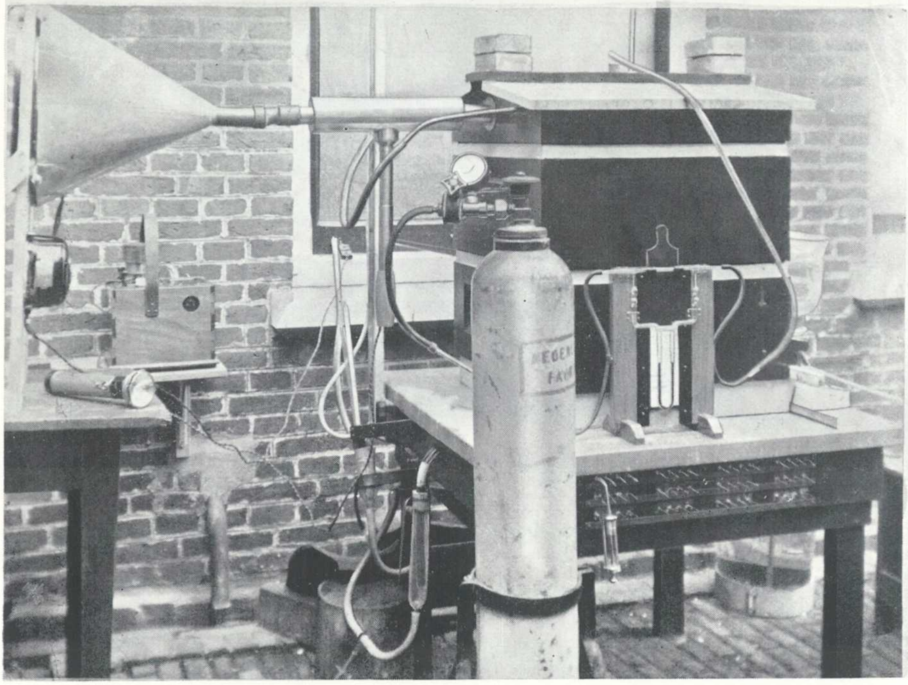


Fig. 4. The complete set up, seen from the side. The anemometer, the ventilator, the carbon dioxide cylinder, and the tubes leading water past the common contact point, and contact point nr. 49 are clearly visible. Explanation of the numbers: 1 = zinc funnel with ventilator; 2 = variable resistance for ventilator; 3 = flex, supplying current to ventilator; 4 = rubber connection between 1 and 5; 5 = anemometer tube; 6 = anemometer; 7 = low voltage lead from accumulators (in 8) to 6, and back to galvanometer (on console against wall); 9 = telephone cable, connecting the 49 contact points with a galvanometer installed in the laboratory; 10 = water supply to 11 (can be emptied in freezing weather by means of the tap); 11 = glass mantle around 12 (same as fig. 1, nr. 37); 12 = brass mantle containing the common contact point (same as fig. 1, nr. 35); 13 = water supply from 11 to 14; 14 = glass tube, containing 15 and 16; 15 = mercury thermometer; 16 = contact point nr. 49; 17 = water drain; 18 = flex supplying electric heaters in the interspace between outer and inner walls of the brood chamber; 19 = carbon dioxide cylinder with manometer; 20 = rubber tube from 19 to 21 and 22; 21 = glass capillary, ensuring an even flow of carbon dioxide past 22; 22 = current meter, with adjustable scale; 23 = rubber tube from 22 to space under the roof of the cabinet; 24 = pieces of lead; 25 = ends of the gas sampling tubes; 26 = syringe for taking gas sample from tube nr 1; 27 = gasometer; 28 = tube for leading carbon dioxide mixtures into the entrance; 29 = pocket torch; 30 = copper tube for leading cold water through the space under the roof; 31 = thermometer.





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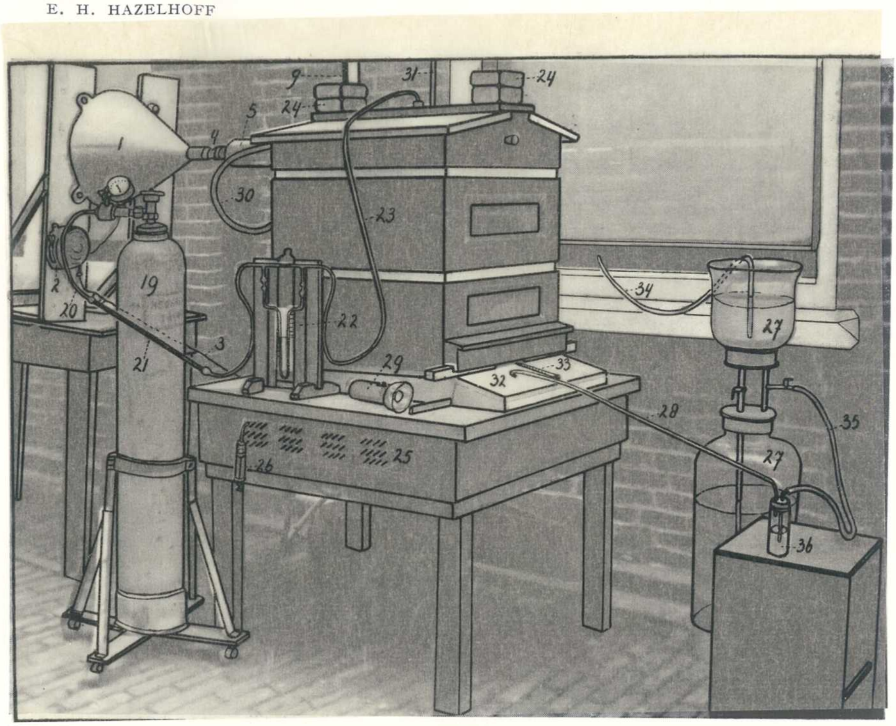
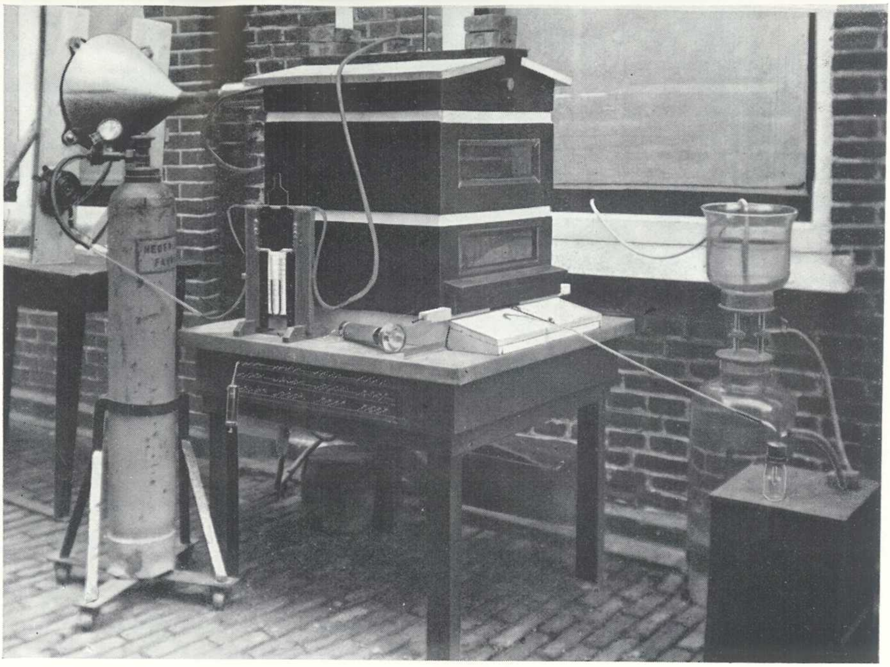


Fig. 5. The installation seen from in front. Explanation of figures: nrs. 1—31: see fig. 5; 32 = flight board; 33 = thermometer; 34 = water supply; 35 = rubber tube to 36 and 28; 36 = water filled tube, regulating the speed of the current through 28.



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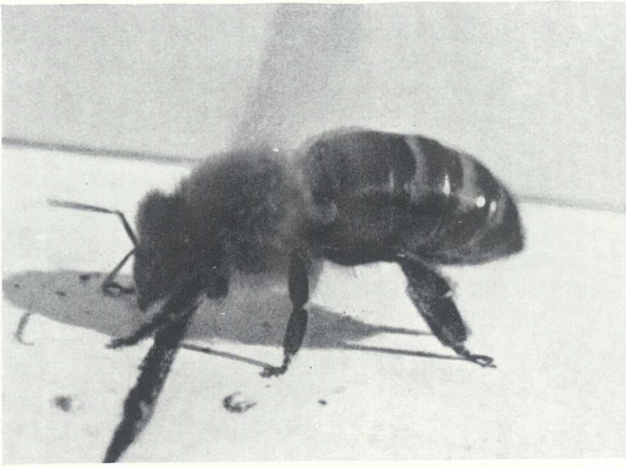

Fig. 6. Fanning bee. The body is slightly curved, the abdomen is pointed (scent gland not extruded). The joint between femur and tibia of the third pair of legs is held close to the body. The rapidly moving wings are hardly visible in figs 6 and 7.

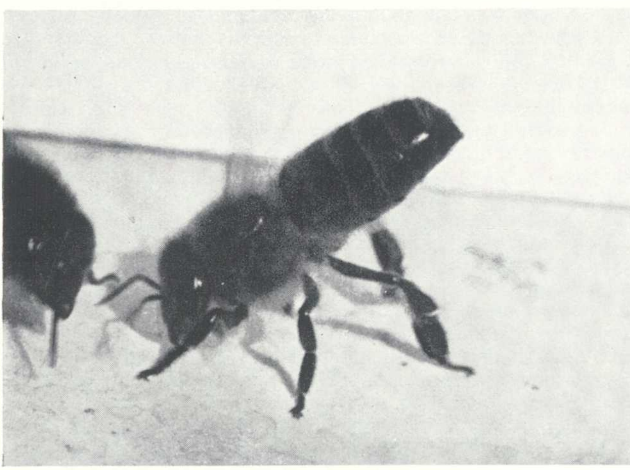

Fig. 7. Scent-fanning bee. The body is rigidly stretched, and the abdomen points upwards as much as possible. The abdomen has a truncate end, because the scent gland is extruded. The distance between the abdomen and the joint between femur and tibia of the third pair of legs is much greater than in the fanning bee, because the body is stretched upwards.

III. RESULTS

A. *The ventilation of the bee-hive during summer.*

Apart from the entrance at the underside, our hive was provided with two other openings, one in the front and one in the back of the roof. Of these two, the former was almost constantly kept closed with a cork stopper, but the latter was fitted with an 8 cm long copper tube (internal diameter 32 mm), to which the anemometer tube could be attached by means of a bayonet fitting. This opening, too, could be closed with a cork stopper. Unless the contrary is stated, the queen excluder, the super (10 combs of 12 × 35 cm.) and the frame with metal gauze, the oilcloth and the felt plate were present during the experiments. Under certain circumstances, not a single fanning bee is to be seen at or near the entrance. Yet as a rule there is a rather considerable current of air through the hive, not only in windy weather, but also during complete calm.

1. In calm weather, it appeared that the air-current always left the hive through the upper opening. The aromatic smell of bees and honey could clearly be perceived here. This air-current is easily strong enough to move a sensitive windvane. An about 1 cm long beard of a down feather, glued with one of its very thin and supple branches to a piece of wood or wire supplies a simple windvane which is very useful because of its high sensitivity. It will clearly indicate the direction of the air current leaving the hive through the upper opening, as well as that of the stream entering the hive at the entrance.

The hypothesis is obvious that this rising air current is caused by the heat production of the bees. Just as in a stove, which is also provided with an upper opening, a draught will occur in the hive, due to the lower specific gravity of hot air as compared with cold air. It is true that the specific gravity of the air, both in the hive and in the stove is increased by its higher carbon dioxide content, but evidently this factor is far outweighed by the lowering of specific gravity, due to the rise in temperature.

On analysis the air leaving the hive through the upper opening in calm weather when no bees were fanning, was found to contain 0,6—0,7% carbon dioxide (Aug. 4th, 1940, 6.33 a.m.). Inside the hive, a similar concentration of carbon dioxide was found. At the entrance, of course, the air did not contain more than the normal percentage of carbon dioxide of atmospheric air (0,03 %).

The intensity of the air current in calm weather could well be measured with the hot wire anemometer. It was found to vary between 0,1 and 0,2 l per second, with an average of 0,17 l per second, i.e. over 600 l per hour. From this quantity, and the carbon dioxide content of 0,6—0,7 %, it can be calculated that the carbon dioxide production amounts to about 4 l per hour. [1]

[1] An adult human being produces about 15 l of carbon dioxide per hour when resting, and up to 100 or 120 l per hour during heavy physical work.

2. Wind, whether weak or stronger, has a marked influence on all this. Direction and speed of the wind in the courtyard where we had installed our hive were extremely variable. The same was true of the air currents through the hive as was shown clearly by the movements of the windvane, and by the anemometer. The air current changed its direction very frequently. Its intensity was also very variable. In weak winds, (wind speed 1—2 m per second), it was in the order of 1,5—2 l per second.

3. Fanning. We must now discuss the air currents caused by the fanning of workers in the entrance (drones never take part in this activity). The workers take a good grip of the substrate with their legs, and move their wings as though they were going to fly away. As a consequence, they do not dart forward themselves, but send an air current backwards. They always orient themselves with the head towards the inside of the hive, and consequently the air current leaves the hive through the entrance. With a pocket torch one can easily observe, that often a number of workers are fanning inside the hive as well, esp. on the bottom floor. These, too, are always oriented so that they propel the air current caused by their wings towards, and through, the entrance. One would expect therefore that whenever bees are fanning an air current would enter the hive through the upper opening. However, this is by no means always true. Even in completely calm weather, the air current at the upper opening will sometimes be entering into, but at other times leaving the hive, as can be demonstrated with a wind vane. Although this may seem unexpected, the explanation is simple. If so many bees are fanning, that they occupy all or nearly all the entrance, the air current always enters the hive through the upper opening. However, if fewer bees are fanning so that they occupy only one half or one third of the entrance, the rest of the latter will give access to a considerable stream of air, and the normal rising air current, caused by the heat production in the hive, will leave the hive through the upper opening. A simple experiment shows convincingly that this is really the true state of affairs. If the right half of the 20 or 25 cm wide entrance is occupied by fanning workers, the air current at the upper opening can be made to enter or leave the hive by closing or opening the other half of the entrance, respectively.

When intensive fanning is going on all over the entrance, an air current of 0,4—0,5 l per second, i.e. 1440—1800 l per hour, can be drawn through the hive. In one experiment, in which a dozen strongly fanning bees occupied the whole 25 cm wide entrance, the air movement even amounted to 0,8—1,0 l per second, that is 2880—3600 l per hour. JESSUP (1925) states that he has recorded air currents of 18—20 cubic meter [1] per hour (with a maximum of as much as 22,9 m^3). His measurements were made with a winged-wheel anemometer, mounted in front of one of the two round entrances of his hive. It seems, however, that JESSUP has not ensured an even distribution of the air current caused by the bees over

[1] ZANDER (1936) erroneously mentions 20 cm^3.

the whole of his anemometer. In my opinion, therefore, the values mentioned by him may well be too high.

Under certain circumstances, fanning may cause a measurable pressure deficit in the hive. If the upper opening is closed, an open paraffin manometer connected with the interior of the hive indicates a pressure deficit of 1.5—2 mm paraffin during intensive fanning. Even with the upper opening closed, the bees achieve quite a reasonable ventilation of the hive, as may be seen from the fact that the carbon dioxide content of the air remains low under these circumstances. Presumably the air now enters between or over the fanning bees, and leaves very close to the same bees. [1]

4. The stimuli which cause fanning. As has been said in the Introduction already, it may be expected that the following factors will cause fanning:

a. high temperature inside the hive.

b. high carbon dioxide content, or low oxygen content, of the air in the hive.

c. rich bee forage.

The first two factors were investigated by us in a series of temperature experiments and experiments with carbon dioxide and oxygen.

a. Temperature experiments. Heating with 192 Watt current during 30 minutes caused a noticeable increase in the number of fanning bees. After 60 or 90 minutes, fanning was intensive, not only at the entrance, but in the hive (on the floor) as well, and even outside the hive on the flight board. If the felt plate was removed, the effect of heating made itself felt somewhat earlier. The results of the temperature experiments are summarized in Table I.

From 9.46 until 10.11, a steadily increasing buzzing was heard, caused by the increasing number of fanning workers. From 10.11 until 10.47 the buzzing remained very loud, after that it decreased gradually. From 10.18 until 10.35, more than three quarters of the whole entrance was occupied by fanning bees, and by 10.38 even the whole of the entrance. At 10.01, the entrance was narrowed several times from 25 to 17 cm, without disturbing the fanning bees. This each time caused an increase from .3—.5 to .5—.7 l per second in the air current entering the hive through the upper opening. This shows again that the part of the entrance not occupied by the fanning bees acts as a "leak". Therefore, our anemometer readings give minimum values!

In moments of calm, a quite warm current of air could clearly be felt by a hand held behind the fanning bees. This current passed low over the flight board. About 2 cm above the latter, it was hardly noticeable. Even in a soft wind, it could be felt.

It follows from Table I that heating causes very intensive fanning, and that in this way the bees achieve such a strong cooling effect that

[1] We do not doubt that in a normal hive ventilation will as a rule be much less difficult than in our hive during the experiments.

Table I. Temperature experiment, 21st Aug. 1940. Upper opening open, and fitted with anemometer. No felt. Width of entrance 25 cm. Cloudy weather, with occasional light rain; weak wind. Heating from 9,15 until 10,31.

	Temperature (°C) of			Number of contact points in hive with a temperature of . . .				Number of bees fanning			Air-current through upper opening	
Time	Air outside	Entrance	Space under roof	35,0—35,9° C	34,0—34,9° C	30,0—33,9° C	25,0—29,9° C	in hive	in entrance	on flight board	l. per second	Direction
9.04	13.9	17.4	17.7					2	3	0	0.04—0.5	usually inwards
9.11	14.0	17.7	17.8	0	4	34	10	3	2	0	id.	
9.15 beginning of heating (192 Watt)												
9.19	14.0	18.2	26.1					2	2	0	,,	
9.28	13.8	16.5	35.1					5	2	0	,,	
9.41	13.7	17.2	43.9					4	2	1	,,	
9.46	15.0	20.1	46.2					4	6	0	,,	variable
9.51	15.0	22.4	47.0					> 10	5	1	,,	
10.01	15.1	26.2	48.1	0	16	29	3	many	9	1	0.3—0.5	always inwards
10.11	14.3	27.1	49.2					many	8	2	id.	
10.18	14.1	28.6	49.9					many	7	8	,,	
10.26	14.4	29.0	49.5	12	12	20	4	many	13	6	,,	
10.31 heating stopped												
10.32	14.9	29.8	44.0					many	10	6	0.35—0.55	
10.38	15.2	30.1	32.5	5	20	19	4	many	12	4	0.5—0.6	
10.41	15.3	30.2	30.1					> 15	12	4	0.3—0.5	variable
10.47	15.3	25.2	27.9	4	21	18	5	> 12	6	3	0.1—0.3	
10.52	15.1	23.3	26.0	0	23	21	4	10	6	0	id.	
10.58	15.0	22.1	24.4	0	21	23	4	8	5	0	,,	
11.04	15.0	20.3	23.9	0	17	26	5	6	5	0	0.1—0.2	usually outwards
11.09	15.2	19.2	23.3	0	12	30	6	2	4	1	id.	
11.15	15.2	18.0	22.9					4	3	0	,,	
11.22	15.5	17.8	22.0					3	3	0	,,	

the temperature between combs 4, 5, 6, and 7 remains much lower than in the space under the roof, where there are no bees. Apparently the air current, after passing through the roof space, where it is heated, is cooled again by the evaporation of water. Probably the greater part of this water will be supplied by still uncovered honey. Some of it, however, may originate from the bodies of the bees.

It might be supposed that the higher temperature in the hive, leading to increased metabolism, resulted in increased carbon dioxide production, and that the latter must be regarded as the real cause of fanning. This, however, cannot be true, for the carbon dioxide content of the air in the hive actually was considerably lowered by the intensive fanning. A mixed sample, taken from sampling points 18, 20, 21, 23, 26, 28, 29, and 31, (that is from 8 out of the 16 sampling points between combs 5 and 6), at 10.43, i.e. at a moment when fanning was still intensive, contained only 0,27 % carbon dioxide (instead of 0,7—1,0 %). The same conclusion, that the carbon dioxide content is lower instead of higher during and after heating, can be derived from another experiment, in which no anemometer readings were taken, but a great number of gas analyses were carried out instead (Table II).

Table II. Temperature experiment, 26th Aug. 1940. Upper opening closed. Felt plate fitted. Width of entrance 25 cm. Cloudy, fairly calm weather. Heating (192 Watt) from 11,00 until 12,08. Gas sample A was taken from the middle of the entrance; B is a mixed sample from sampling points 16, 32 and 48 (i.e. the three points closest to the entrance); C is a mixed sample from sampling points 18, 20, 21, 23, 26, 28, 29, and 31 (all between combs 5 and 6).

	Temperature (°C) of			Number of contact points in hive with a temperature of . . .				Number of bees fanning			Carbon dioxide content of samples		
Time	Air outside	Entrance	Space under roof	35,0—35,9° C	34,0—34,9° C	30,0—33,9° C	25,0—29,9° C	in the hive	in entrance	on flight board	A	B	C
10.00				0	4	33	11						
10.55	17.3	27.2	18.6					4	2	0	0.77	1.00	0.71
11.00 beginning of heating (192 Watt)													
11.15	17.5	27.4	35.2					8	3	0	0.54	0.59	0.40
11.30	17.8	28.5	43.9					> 15	4	1	0.33	0.36	0.28
11.45	18.0	30.1	46.2					many	3	2	0.25	0.21	0.26
12.00	18.3	33.2	40.3	2	22	23	1	many	4	9	0.39	0.25	—
12.08 heating stopped													
12.35	18.8	34.1	28.6	32	5	11	0	many	5	8	0.31	0.33	0.20
13.25	18.2	31.1	24.0	0	20	28	0	> 12	3	3	0.35	0.31	0.25
14.35	18.4	27.9	21.9	0	11	34	3	9	2	0	0.69	0.62	0.82
16.10	18.4	24.9	21.7	0	22	26	0	4	2	0	0.82	0.68	0.69

This table shows clearly that the carbon dioxide content, both in the hive and at the entrance was markedly lowered at 11.15 already. Even lower figures, not more than about one third of the original values, were found at 11.30 and 11.45. Not till a considerable time after the end of heating (2,5 hours), the carbon dioxide content had returned to normal values. It will be clear that in this experiment fanning was not the consequence of an increase in the carbon dioxide content, but that, in contrast, it caused a marked decrease of the latter, in spite of the fact that the upper opening remained hermetically sealed all through the experiment. In both experiments (Tables I and II), the fanning is a reaction to the rise in temperature itself. It may be regarded as one of the means used by the bee colony to achieve a social temperature regulation.

Finally we must consider what happened if some time after the beginning of a temperature experiment a strong current of air was sucked through the hive by means of the ventilator. The effect was surprising: the number of bees fanning at the entrance, which just before the ventilator was switched on was 18, had fallen to 6 after 20 seconds, to 2 after 40 seconds, and even to 0 after 50 seconds. The cool outer air streaming in through the entrance caused a prompt reduction in the number of fanning bees. Table III gives a summary of one of these experiments.

Table III. Temperature experiment with ventilator, 21st Aug. 1940. Same circumstances as in Table I. Heating from 11,33 until 13,07, (192 Watt). Ventilation from 12,39 until 12,46.

	Temperatures of			Number of contact points in the hive with a temperature of . . .						Number of bees fanning			Air-current through the upper opening	
Time	Air Outside	Entrance	Space under roof	36,0—36,9° C	35,0—35,9° C	34,0—34,9° C	30,0—33,9° C	25,0—29,9° C	< 25,0° C	in the hive	at the entrance	on the flight board	l. per second	Direction
11,33	Heating started (192 Watt)													
12,07	16,4	20,8	44,4							> 15	5	0	0.06—0,5	usually outwards
12,18	16,8	24,3	45,3							> 20	4	0	0,06—0,5	variable
12,22	16,5	25,0	45,7							> 20	5	2	0,25—0,33	inwards
12,32	16,5	27,1	45,8	5	13	12	14	4	0	many	9	4	0,5 —0,6	inwards
12,37	16,6	27,2	45,6							many	10	4	0,8 —1,0	inwards
12,39	Ventilator started (heating continued)													
12,39½	16,3	20,1	43,6	0	4	13	22	7	2	4	2	0	abt. 7[2]	outwards
12,41	16,5	18,9	42,2							0	0	0	abt. 7	outwards
12,43	16,6	18,2	41,1							0[1]	0	0	abt. 7	outwards
12,46	Ventilator stopped (heating continued)													
12,48	16,3	19,1	44,6	1	6	13	20	7	1	0	1	0	0,2—0,5	inwards
12,51	16,5	20,4	45,0	3	12	10	20	3	0	5	0	0	0,3—0,8	inwards
12,54	16,3	20,5	45,0							8	6	0	0,5—0,8	inwards
12,57	16,5	21,1	45,6							> 10	8	0	0,8—1,0	inwards
12,59	16,5	24,0	44,4							many	11	2	1,0—1,4	inwards

[1] At 12,43 the floor of the hive, as far as this could be seen with the aid of a bright torch, was completely left by the bees.
[2] The air-current, caused by the ventilator could not be accurately measured with our anemometer. It was estimated at about 7 l per second.

This experiment demonstrates clearly that fanning is suspended as soon as cold outer air was sucked into the hive by the ventilator. To conclude this chapter, we mention some observations done on July. 18th and Sept. 3rd 1940 with a von Frisch observation hive. If on a sunny day the lid is removed from one side of the hive, the sun rays will illuminate part of the comb occupied by the brood through the two layers of glass. As a result we saw that after 1 minute 4' after 2 minutes 10—12, after 3 minutes 20—25 of the workers walking about on the comb began to fan. This fanning took place practically only on the regions irradiated by the sun. We then closed the hive for 2 or 4 minutes. After this interval fanning was strongly reduced, but had not yet completely ceased. This means that fanning for temperature regulation does not occur only at or near the entrance, but also inside the hive on the brood combs.

b. Carbon dioxide experiments. Intensive fanning was caused after a short time by leading pure CO_2 into the hive through an opening in the roof with a speed of e.g. 3 l per second. Table IV gives further details of these experiments. It shows that fanning had markedly increased already

Table IV. Carbon dioxide experiment, 27th Aug. 1940. Upper opening open, with anemometer attached. No felt. Width of entrance 12 cm. Little wind, and at times almost calm. From 10,20 until 11,03 3 l of pure CO_2 per minute are led into the cabinet through an opening in the roof.

	Temperature of			Average temperature of contact points nrs. . . .				Number of bees fanning			Air-current through upper opening	
Time	Air outside	Entrance	Space under roof	1, 5, 9, 13, etc.	2, 6, 10, 14, 18 etc.	3, 7, 11, 15, 19 etc.	4, 8, 12, 16, 20 etc.	in hive	in entrance	on flight board	l. per second	Direction
10.19	16.4	25.1	16.9	31.28	33.47	32.31	29.13	5	1	0	0.2—1,5	variable
10.20 CO_2 stream started												
10.25	16.6	26.2	16.9					> 10	7	1	0.7—0.9	inwards
10.30	16.8	26.2	16.8	30.98	33.24	32.13	29.18	many	7	5	0.9	
10.35	16.8	26.3	16.8					many	10	3	0.9	
10.40	16.8	26.7	16.9	30.65	33.18	32.04	29.20	many	8	3	0.9	
10.45	17.0	26.3	17.0					many	7	3	0.9	
10.50	17.0	26.1	17.0	30.71	33.26	32.04	29.02	many	8	2	0.9	
10.55	17.2	26.2	17.1					many	10	3	0.9	
11.00	17.3	26.4	17.1	30.53	33.15	31.92	28.73	many	9	2	1.0	
11.03 CO_2 stream stopped												
11.04								many	10	3		
11.05	17.3		17.1					many	8	2		
11.06								> 12	5	1	0.3—0.5	
11.08				30.74	33.25	32.03	28.94	7	4	0	0.2—0.5	
11.20				30.97	33.53	32.39	28.98					
11.30				31.00	33.65	32.55	29.55					
11.40				31.25	33.61	32.60	29.57					
11.50				31.03	33.48	32.54	29.78					

5 minutes after the beginning of the CO_2 current. After another 5 minutes, it had practically reached its maximal intensity. (A loud buzzing noise could be heard at a distance of 2 meters from the hive). By this time (10.30 a.m.), there was a noticeable decrease of the temperature in the hive already. This decrease became somewhat stronger in the course of the next half hour. Five minutes after stopping the carbon dioxide current, fanning had returned to an approximately normal intensity. The temperatures in the hive then showed a clear rise, but had not yet returned to normal values. Contact points 1, 5 etc. did not recover their usual temperature till about 11.40, nrs. 2, 6, etc. about 11.20, nrs. 3, 7, etc. about 11.20, and nrs. 4, 8, etc. about 11.25. In this case, fanning cannot have been due to high temperatures in the hive, because temperatures were actually lowered. Of course, this decrease was the result, and not the cause of fanning. [1]

Fanning, therefore, is caused by an increase in the carbon dioxide content in the hive and at the entrance. In other words, these experiments lead to the conclusion that bees have two mechanisms for the regulation of their respiration, one individual (consisting of rhythmic movements of the abdomen, which renew the air in the tracheal system), and, in addition, a social one (consisting of the fanning at the entrance, and, as we shall presently see, also in the hive, on the combs).

The following data were obtained in the course of the experiment (Table IV) as regards the carbon dioxide content of the air in the hive, and at the entrance. Carbon dioxide content at the entrance: at 10,41: 3,56 %, at 11,04: 1,28 %, at 11,06: 0,39 %, and at 11,14: 0,35 %. At 10,41 the average carbon dioxide content at the sampling points nrs 18, 20, 21, 23, 26, 28, 29, and 31 was 3,36 %. Other, similar experiments also showed always that the bees managed to keep the carbon dioxide content of the air in the hive fairly low, even though large quantities of the gas were led into the hive. In this experiment they sucked so much air through the upper opening into the hive that by their intensive fanning the carbon dioxide was diluted from 100 % to about 3,46 %, that is about 29 times. As 3 l of carbon dioxide were led in per minute, they must have aspirated about 28 times that volume of air, that is about 84 l per minute. [2]

The anemometer readings show that about 0,9 l of air per second entered the hive through the upper opening, i.e. about 54 l per minute. The remainder has probably entered the hive through such parts of the

[1] It must be admitted that the temperature in the entrance was slightly raised. This is not a very significant increase, however, and in my opinion it must not be regarded as the cause of fanning, but as one of its consequences. The lowest contact points in the hive, too, showed a slight *initial* rise of temperature (viz. at 10.30 and 10.40 a.m.). Presumably, this, too, was a result of the fanning, as the hot air was sucked down from the upper parts of the hive in the direction of the entrance.

[2] In this calculation, the quantity of carbon dioxide produced by the bees themselves may be disregarded, as this is very small as compared with the quantity introduced by us (cf p. 349).

entrance as were not occupied by the workers. The carbon dioxide contents, measured at 11,04, 11,06 and 11,14 (1,28 %, 0,39 %, and 0,35 %, respectively) show that within 3 minutes after the introduction of carbon dioxide was stopped, its concentration had regained the normal value.

In the experiment on Aug. 9th 1940, 5 l of carbon dioxide per minute were introduced between 10,00 and 10,08, with the anemometer attached to the open upper opening, and the felt plates removed. The width of the entrance was 6 cm. From 10,02½ until 10,09½ there was a steady state, whereby the bees (four, or sometimes five workers were fanning at the entrance) sucked 0,8—0,9 l of air per second through the hive. The carbon dioxide content of the air emerging through the entrance averaged 6,47 % (6,35 % at 10,03 and 6,58 % at 10,07½). In other words the CO_2 was diluted from 100 % to about 6,47 %, i.e. some 15 times. It follows that about $14 \times 5 = 70$ l of air per minute must have been aspirated. The anemometer registered a current of $60 \times .85 = 51$ l per minute through the upper opening. Probably the rest has again found its way into the hive past the fanning bees.

Even if the temperatures are low both inside and outside the hive, intensive fanning can be provoked by the introduction of carbon dioxide. On Sept. 11th 1940, we began introducing CO_2 (3 l per min.) at 10,20, the upper opening being closed. The outside temperature was 10,2° C, the average temperature of the contact points at the beginning of the experiment was 30.6° C for the top row of 12 contacts, 31,3° C for the next row, 29,7° C for the third row, and 25,7° C for the bottom row. Notwithstanding these very low temperatures in the hive, there was intensive fanning after 15 minutes (many workers were fanning in the hive, 10 at the entrance, and 12 on the flight board). This resulted in a noticeable decrease of the temperatures in the hive (at 10,36: 29,6, 30,3, 28,7 and 26,0° C respectively), so that here again fanning can only be ascribed to the introduction of carbon dioxide. At 10,40 the upper opening was opened, and connected to the ventilator. Twenty seconds after the ventilator was switched on, the number of fanning bees at and near the entrance had decreased from about 25 to 2. After ten more seconds, not one was left!

It may well be asked why the temperatures in the hive are lowered so very little, in spite of the great quantities of cold outer air that are drawn through it (e.g. .9 l per second for more than half an hour, see Table IV). At present no certain answer can be given to this question. It is conceivable, however, that the air streams mainly over the outer combs, and that the temperature here is lowered far more than at our contact points, all of which were located among the inner combs. Further it may be imagined that the bees somehow manage to prevent the evaporation of too much water. This would limit the cooling effect of fanning considerably. Finally, it is conceivable, that strong cooling does indeed occur, but that it is compensated nearly completely by the simultaneous production of heat in great quantities. However this may be, it remains a remarkable fact that even under very difficult circumstances — such as the introduction of great quantities of carbon dioxide — the social regulation of respiration does practically not interfere with the social temperature regulation.

From some experiments made on July 19th and Aug. 13th with the VON FRISCH observation hive, we concluded that fanning provoked by CO_2 is again not restricted to the neighbourhood of the entrance. Into this hive, which has a volume of about 8 l, we led gas mixtures with 30 or 50 % CO_2 instead of pure carbon dioxide. Within a few minutes a number of the workers sitting on the brood comb [1] began to fan.

A few minutes after the CO_2 current was stopped, fanning ceased too, apparently because the carbon dioxide disappeared quickly through the many cracks. In this very small colony, no bees came to fan at the entrance. Probably, the effect of the fanning on the comb will not have been very great in this case. Apart from "social regulation", the "individual regulation" of the bees' respiration came into action too. Almost all bees present in the hive made clearly visible respiratory movements with the abdomen. Table V gives a summary of one of the experiments. The most striking point is that at 11,09, when there was only 7,27 % of CO_2 in the cabinet, fanning was much more intensive than at 11,03, when the carbon

Table V. Carbon dioxide experiment, 13th Aug. 1940, in VON FRISCH observation hive. Upper opening open, no felt. Entrance 1½ × 2 cm. From 11,00 until 11,06, 3½ l per minute of a gas mixture containing 50,3 % CO_2, 10,4 % O_2, and 39,3 % N_2 is led into the hive through an opening in the roof.

Time	CO_2 concentration at centre of comb (%)	Number of bees fanning on one side of comb	"Individual" respiratory movements of abdomen
10.59	2.34	0	absent
11.00	Introduction of gas mixture started		
11.00½		1	absent
11.01		4	weak
11.01½		8	marked
11.02	17.50		deep and rapid
11.03	22.71	12	deep and rapid
11.05		15	deep and rapid
11.05½	24.36		deep and rapid
11.06	Introduction of gas mixture stopped		
11.07		10	deep and rapid
11.08		15	deep and rapid
11.09	7.27	23	decreasing
11.10		10	weak
11.11		8	very weak
11.12		4	doubtful
11.13	1.77	2	absent
11.16		1	absent

[1] There were only very few bees on the other 3 combs.

dioxide concentration was more than 20 %. This suggests that concentrations of CO_2 over 20 % are too high.

In another experiment, also made on Aug. 13th, we gave 2 l per minute of a gas mixture of 36,2 % CO_2, 13,3 % O_2, and 50,5 % N_2, from 12,12 till 12,22 a.m. The number of workers, fanning on one side of the brood comb, was 0 at 12,10, 5 at 12,13, 8 at 12,14, 10 at 12,17, 15 at 12,20, 15 at 12,21, 10 at 12,23, 8 at 12,24, 6 at 12,25, 4 at 12,28, and 2 at 12,32. The carbon dioxide content of the air in the cabinet never rose above 18 % during this experiment.

It follows from these experiments that fanning for the regulation of respiration does not take place only on the place which is the most favourable for ventilation — i.e. at or near the entrance — but also inside the hive, on the combs. As soon as the first bees, reacting to carbon dioxide, have started fanning at or near the entrance, the temperature here will be slightly raised because warm air is aspirated from the interior of the hive. This may stimulate more bees to come and fan at the entrance, than would come without this rise in temperature. This will not occur in the case of bees fanning on the combs, for here the temperature will be lowered (see Table IV).

The following experiment demonstrated very clearly that a rise in temperature is not indispensable for fanning at the entrance to take place. By means of a bent glass tube with an internal diameter of 3 mm (fig 7, 28) we led a gas mixture containing 25 or 50 % carbon dioxide through the entrance (about ½ to 1 l per minute). The end of the tube was only about 5 cm inside the entrance, and the mixture left the hive *via* the entrance. A few seconds or minutes after the beginning of the carbon dioxide current, a worker would start fanning in the entrance at the very spot where the carbon dioxide current came out. When the gas stream was stopped, the worker would soon stop fanning. These experiments were made on days when there was little or no "spontaneous" fanning. The reaction was quite prompt, and especially the fact that the fanning bee would take up a position exactly in the carbon dioxide current was very convincing. This experiment gives the exact proof, that increased carbon dioxide concentration of the air causes fanning, or, in other words, that we may really call this a social regulation of the respiration. The variation in the interval elapsing between the beginning of the CO_2 stream, and the beginning of fanning is due, obviously, to the fact that it may last some minutes, though sometimes much less, before one of the passing bees happens to be hit by the CO_2 stream. Table VI gives further details of one of these experiments.

The interval between the beginning of the carbon dioxide stream, and that of fanning was 210, 5, 60, 8, 30, 53, 15, 20, 5, and 15 seconds, or, on the average, 39 seconds. The interval between the stopping of the stream, and the ceasing of fanning was 125, 135, 20, 150, 95, 15, 115, 20, 10, and 65 seconds, or, on the average, 75 seconds.

The foregoing may be summarized as follows: It has been proved

Table VI. Carbon dioxide experiment, 28th Aug. 1940. 0,5 l per minute of a gas mixture containing 50,6 % CO_2, 10,4 % O_2, and 39,0 % N_2 are led into the entrance via a hook-shaped glass tube. Width of entrance 25 cm, upper opening closed, felt plates fitted, temperature of outer air 15,5°C.

CO_2 stream started	Beginning of fanning	CO_2 stream stopped	End of fanning
11,00'00"	11,03'30"	11,04'25"	11,06'30"
07'03"	07'08"	07'30"	09'45"
20'30"	21'30"	21'50"	22'10"
22'50"	22'58"	23'15"	25'45"
26'00"	26'30"	26'45"	28'20"
28'42"	29'35"	29'45"	30'00"
31'00"	31'15"	31'25"	33'20"
34'30"	34'50"	35'05"	35'25"
35'40"	35'45"	35'50"	36'00"
36'40"	36'55"	37'10"	38'15"
38'30"	38'38"		

experimentally that in bees there is a social regulation of respiration (effected by fanning at and near the entrance, and on the combs, as a reaction to increased carbon dioxide concentration of the air).

c. Experiments on the influence of oxygen deficiency. These experiments were made exclusively with the VON FRISCH observation hive. In one experiment, in the course of 5½ minutes 20 l of a gas mixture consisting of 2,0 % O_2, and 98 % N_2 was led into the hive. By the end of the 5½ minutes, the oxygen concentration in the cabinet had fallen to 10,96 % (the CO_2 concentration was 2,09 %). By that time the individual respiratory movements were hardly visible yet, and only 2 or 3 bees were fanning on the comb (none at the beginning of the experiment; the comb was kept out of the sun!). In another experiment pure nitrogen was led in at a speed of 3 l per minute during 27 minutes, i.e. about 80 l in total. The volume of the hive was about 8 l. Nevertheless the oxygen concentration in the hive did not fall below 5,14 % (CO_2 content 0,77 %). Individual respiratory movements were still weak. The number of fanning bees usually was 3 or 4. We may conclude from these data that the social regulation of respiration can also be set going by lack of oxygen, but much less readily than by an excess of carbon dioxide. Under natural circumstances, lack of oxygen will not play a role in the social regulation of respiration, as the accumulation of carbon dioxide will have caused fanning long before the oxygen concentration has been sufficiently lowered to take effect. This is in good agreement with what is known about the relative influence of oxygen and carbon dioxide on the individual regulation of respiration in various insects (HAZELHOFF, 1926).

B. *Scent-fanning*.

Scent-fanning must be well distinguished from fanning. Both in fanning and in scent-fanning, the bee makes flying movements with its wings, while holding on to its substrate with its legs. The function of fanning, however, is the production of an air current through the hive; that of scent-fanning is the dispersal of a scent secreted by glands of the worker. The profile of the abdomen in a scent-fanning bee is entirely different from that of one that is fanning, because the former extrudes its scent-gland. Moreover, the attitude of the body is different. In a scent-fanning bee, the abdomen points obliquely upwards. The body is stretched as much as possible. In a fanning bee, on the other hand, the body is slightly bent. Fanning occurs on the combs and at the entrance, scent-fanning both at the entrance and, e.g., on places where there is a rich bee pasture. SLADEN (1902) was the first to guess the function of scent-fanning. In 1923, VON FRISCH succeeded in proving Sladens hypothesis correct. A fairly good picture of scent-fanning may be found in VON FRISCH's book (1931). JACOBS (1925) states that bees show scent-fanning, a.o., under the following circumstances: 1) when the swarm moves into a new hive, 2) when, for some reason, it returns to an old hive, 3) if one shakes and upsets a hive, and the bees are crawling up the walls, 4) when returning with honey or pollen to the hive, a worker may, on arrival at the entrance, stop there and show scent-fanning for a moment, and then go on into the hive (this occurs especially in the first flights after hibernation), 5) a worker which has found an exceptionally rich supply of food (e.g. a dish with honey), will, on her return, after emptying her crop and warning her companions, start scent-fanning during flight on approaching the source of food (here, therefore, without a support for the legs!); she will go on scent-fanning for some time, even after the beginning of sucking (cf VON FRISCH's experiments on the "scent language" of bees). In all these cases, the function of scent-fanning is to show the way to other bees, either to the hive, or to the source of food.

I can add that scent-fanning on the flight board is especially intensive when many young bees are making their orienting flights. Further, wholesale and long continued scent-fanning can be provoked at any time during good flying weather by the following simple method. If the entrance is closed for 3 to 5 minutes, and then reopened, a large proportion of the workers present on the flying board (e.g. 50 or 100 or even 200) will start scent-fanning for several minutes. The other bees will enter as though nothing had happened. All the scent-fanning bees are now oriented with their heads towards the entrance. A worker returning now will find it very easy indeed to find the entrance! Gradually the number of scent-fanning bees decreases, and after 5 to 10 minutes the situation is practically normal again.

I thought it a matter of some interest to investigate whether scent-fanning, just as fanning, could be influenced by a ventilator aspirating air through the upper opening. Table VII shows the result of one of these experiments. Comparison with other experiments in which the entrance was closed, but no ventilator was used (which experiments we shall not discuss in detail), shows that the action of the ventilator had no detectable influence on scent-fanning. In this respect too, therefore, scent-fanning differs completely from fanning, which can be caused to cease within two minutes by switching on the ventilator (see Table III).

Table VII. Experiment with closed entrance and ventilator, 22nd Aug. 1940. Entrance closed from 11,03 until 11,08, then opened (width 20 cm). At 11,09, about 60 workers were already on the flight board, in the entrance, and on the floor of the cabinet (the majority on the flight board). A few seconds later, the ventilator was started at full speed, and kept working until 11,19. Outside temperature 15,0°C.

Time	Number of bees scent-fanning			Air-current through upper opening	
	in hive	in entrance	on flight board	l. per second	direction
11.08	entrance opened				outwards
11.09	ventilator started				
11.09½	many	12	abt. 60		
11.10	many	10	abt. 50		
11.10½	many	10	abt. 40	abt. 6	
11.11	many	10	abt. 25		
11.11½	many	8	15	abt. 7	
11.12½	fairly many	6	11		
11.13	fairly many	4	8	abt. 7	
11.14	abt. 15	3	3		
11.15	abt. 15	2	1		
11.16	10	2	0	abt. 7	
11.17	5	1	0		
11.19	0	0	0	abt. 7	

IV. SUMMARY.

1. In completely calm weather, and in the absence of fanning by the bees, a fairly strong current of air passes through bee hives of the type pictured in fig 1 in an upward direction (0,1—0,2 l per second).

2. If a number of bees start fanning at the entrance, a downward air current (of e.g. 0,5—1,0 l per second) will usually pass through the hive.

3. Fanning can be provoked experimentally
   a. by heating
   b. by the introduction of carbon dioxide
   c. by lowering the oxygen concentration.

4. It follows from what has been said sub 3*a*, that fanning has a function in social temperature regulation during summer (prevention of too high temperatures).

5. It follows from what has been said sub 3*b* and 3*c* that bees have a social regulation of respiration (renewal of the air by fanning, at or near the entrance, according to the need of the colony).

6. Even very intensive fanning can be stopped completely within two minutes by the action of a ventilator, aspirating air through the upper opening.

7. Long continued scent-fanning by great numbers of bees occurs when the entrance, having been closed for a period of a few minutes, is reopened.

8. In contrast to what has been said above (6) about fanning, scent-fanning is not influenced by bringing into action a ventilator at the upper opening.

V. RÉSUMÉ

1. Si le temps est absolument calme, et en l'absence de ventilation active par les abeilles, un courant d'air relativement fort passe par une ruche du type fig. 1., en une direction ascendante (0,1—0,2 l. p. sec.).

2. Si un nombre d'abeilles commence à ventiler à l'orifice de la ruche, un courant d'air de 0,5—1,0 l. p. sec. passe par la ruche en une direction descendante.

3. On peut provoquer la ventilation active par les abeilles d'une manière expérimentale

a. par réchauffement

b. par introduction de gaz carbonique

c. par abaissement de la concentration de l'oxygène.

4. Il s'ensuit de l'observation 3*a*, que la ventilation fonctionne dans la régulation sociale de la température.

5. Des observations 3*b* et 3*c*, il s'ensuit qu'il existe une régulation sociale de la respiration (renouvellement de l'air par ventilation près de l'entrée de la ruche, selon les besoins de la population).

6. Une ventilation même intensive peut être terminée brusquement en deux minutes par l'action d'un ventilateur aspirant l'air de la ruche par un trou dans la partie supérieure.

7. Un grand nombre d'abeilles bat le rappel, si l'entrée est réouverte après quelques minutes de fermeture.

8. Le battement de rappel n'est pas influencé par l'action du ventilateur mentionné sous 6.

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