OBSERVATIONS ON THE TEMPERATURE REGULATION AND FOOD CONSUMPTION OF HONEYBEES (*APIS MELLIFERA*)

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INTRODUCTION

The ability of a honeybee colony to regulate its temperature enables it to survive conditions to which individual bees succumb. The thermal preference of young bees varies from 35 to 37·5° C. and for older bees from 31·5 to 36·5° C., and depends to some extent on the temperature to which they have been previously conditioned (Heran, 1952).

In summer the temperature of the brood-nest of a colony is maintained at about 34–35° C. and fluctuates very little (e.g. Gates, 1914; Himmer, 1932). The bees normally prevent it from rising above this level by some or all of the following methods: the evaporation of droplets of water which they spread over the comb; the evaporation of water by manipulation of drops in their mouthparts; the creation of currents of air by fanning their wings; a proportion of them leaving the hive (e.g. Himmer, 1932; Lindauer, 1954).

Bees in the hive form a cluster which, as Gates (1914) noted, contracts and expands with decrease and increase in environmental temperature. The temperature in the centre of a broodless cluster in winter usually lies within the range 20–30° C. and is more often nearer to 30° C. than to 20° C. (e.g. Gates, 1914; Wilson & Milum, 1927; Corkins, 1930).

In the present experiments bees have been kept in groups of from 10 to 200 bees, at different environmental temperatures, and the temperatures maintained by the groups, and the amount of sugar syrup and water they consumed, were periodically measured. Records were also made of the approximate percentage of the bees of each group which were clustering together, and of the number which had died. All experiments were carried out during the winter months.

METHOD

The bees were kept in well-ventilated Perspex cages (6 × 5 × 9 cm. high). A thermometer, a glass gravity feeder containing sugar syrup (2 parts sugar : 1 part water by weight), and another containing water, were inserted through the roof of each cage at such angles that the ends of the feeders and the bulb of the thermometer nearly met at a point 1·5 cm. below the centre of the roof. Six wax-coated nails driven into the underside of the roof, so as to form a circle round the ends of the feeders and thermometer, provided additional footholds for bees clustering there. A graduated scale attached to each feeder enabled the consumption of syrup and water to be measured.

Six cages containing 0, 10, 25, 50, 100 and 200 bees, respectively, were used in each experiment. The bees were collected at random from a hive. The cages containing the bees were kept at 30° C. for 1 hr. before being transferred to a cabinet at the experimental temperature, at which they remained for 3 days. Three experiments were carried out at each of a range of temperatures from 0–40° C. at intervals of 5° C.; only the mean results obtained at each temperature are given below.

On the first day of an experiment the cages were transferred to the appropriate constant temperature cabinet at 11.30 hr. and readings taken every subsequent hour until 17.30 hr. On the two following days readings were taken hourly from 09.00 to 17.30 hr. and on the final day of the experiment from 09.00 hr. to 14.30 hr. The temperatures inside the cages did not approach stability until an hour or so after they had been placed in the cabinet, so readings taken before 14.30 hr. on the first day have been ignored unless otherwise stated. Whenever possible, the data given for each experiment are those obtained during three consecutive 24 hr. periods (to be referred to as days 1, 2 and 3, respectively) starting at 14.30 hr. on the first day. Experiments at the three lowest temperatures or at the highest temperature often had to be discontinued before the 3 days had elapsed owing to the inability of the bees to survive.

No attempt was made to control humidity during the experiments.

RESULTS

Death-rate

The mean percentage of bees dead or immobile at the end of day 1 is given in Table 1. In the temperature range of 25–35° C. the percentage was low and about

Table 1. *Mean percentage of bees dead or immobile at end of day 1*

Environmental temperature (° C.)	No. of bees in a group				
	10	25	50	100	200
0	100	100	100	100	90
5	100	100	100	100	34
10	100	73	43	42	5
15	10	21	11	9	3
20	10	12	6	4	3
25	3	3	1	1	2
30	20	11	3	4	1
35	3	0	3	4	2
40	10	12	9	14	47

the same in groups of different sizes. (The relatively high death-rate in the cages containing 10 and 25 bees at 30° C. is mostly due to the large percentage that died in one experiment—50% and 16% respectively.) It was found that, below 25° C., the larger the number of bees in a cage, the greater the percentage surviving at the end of day 1. However, at 40° C. relatively fewer of the bees kept in groups of 200 survived than those kept in smaller groups, although in no instance significantly so. Only in one of the three experiments at 40° C. did more than 50% of the bees kept in groups of 200 survive day 1, and even then over 100 bees were dead by the end of day 2.

At 15–35° C. most groups survived until the end of day 3, but at 10° C. and below only few of the groups did so. The exact number of hours from the time they were first placed in the experimental cabinet, before the bees in the different groups all became dead or immobile, is not always known since this often occurred outside the hours of observation. However, at 0° C. groups of 10 or 25 bees only survived 1 or 2 hr., and sometimes only half an hour, groups of 50 or 100 bees survived about 4–5 hr., and groups of 200 bees over 6 hr. but generally less than 21½ hr. At 5° C. groups of 10 bees still survived 1 or 2 hr., groups of 25 bees about 5 hr., groups of 50 or 100 bees over 6 hr., but generally less than 24 hr., and groups of 200 bees for 2 or 3 days. At 10° C. groups of 10 bees survived about 5 hr., groups of 25 bees 1 or 2 days, and the larger groups generally survived all 3 days of an experiment.

Temperatures of the groups

The temperatures maintained by groups of different sizes at different environmental temperatures are shown in Fig. 1. Whenever possible the data presented are the mean group temperatures recorded during days 1, 2 and 3. However, as noted above, groups kept at 40° C. or at 10° C. and below often succumbed long before 3 days had elapsed. Consequently, at these environmental temperatures only the mean temperature in each cage 3 hr. after introduction to the cabinet concerned is given (i.e. the mean temperature at 14.30 hr. on day 1).

The temperatures of the groups increased with the environmental temperature. At temperatures ranging from 0–30° C. they kept themselves above the temperature of the environment for as long as they survived—in general the lower the environmental temperature the greater the difference between it and that of the groups of bees. Thus on the three occasions that a group of 200 bees was kept at 5° C. its mean temperature during days 1 and 2 was 20·5° C., i.e. 15·5° C. higher than the environment.

It is apparent that the larger the group the higher its temperature above that of the environment. The difference between the temperatures of the larger and smaller groups in each experiment decreased with increase in environmental temperature. At 35° C. or 40° C. all groups were at approximately the same temperature, i.e. at or slightly below the environmental temperature.

Percentage of bees clustering

During hourly readings the approximate percentage of bees clustering round the ends of the feeders and the bulb of the thermometer in each cage was recorded. The mean percentage of bees in the different groups that were clustering at each environmental temperature is given in Table 2. The results presented for the experiments at 40° C. are those obtained on day 1 only, and the data given for 10° C.

are from the one experiment in which the groups of 50, 100 and 200 bees survived without considerable loss until the end of day 3.

In the temperature range of 20–40° C. the percentage of bees clustering increased with increase in the size of their groups. At 15° C. and below there was a marked

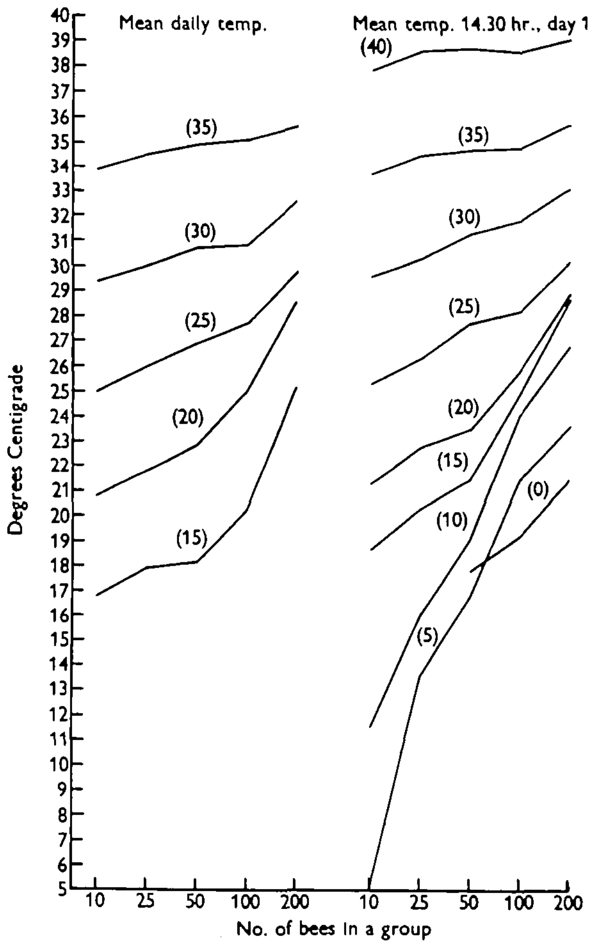

Fig. 1. Temperatures of groups at various environmental temperatures (environmental temperatures in parentheses).

Table 2. *Mean percentages of bees recorded clustering*

Environmental temperature (° C.)	No. of bees in a group				
	10	25	50	100	200
10	—	—	99	99	98
15	70	81	73	78	81
20	1	2	40	48	48
25	0	1	20	47	64
30	1	2	23	46	57
35	0	4	24	48	55
40	0	0	11	44	56

increase in the percentage of bees clustering in groups of all sizes, particularly in the cases of bees in groups of 10 or 25 which at higher temperatures clustered little if at all. At environmental temperatures of 10° C. and below usually well over 90% of the bees clustered before they became chilled and dropped on to the floor of their cage.

Amount of syrup and water consumed

The amounts of syrup and water consumed daily per bee in the different groups at different environmental temperatures are given in Tables 3 and 4 respectively. The data presented for experiments carried out at temperatures from 15–35° C. are the mean of those obtained on 3 days, whereas the data for experiments at 10 and 40° C. represent those obtained on 1 or 2 days only, depending on the survival time of the groups concerned.

Table 3. *Amount of sugar syrup (mm.³) consumed daily per bee*

Environmental temperature (° C.)	No. of bees in a group				
	10	25	50	100	200
10	—	39·9	50·2	50·2	50·8
15	47·5	52·4	58·4	54·6	55·7
20	39·9	45·9	38·2	37·7	37·7
25	30·0	30·6	27·8	21·3	22·4
30	32·8	23·5	13·6	11·5	17·5
35	22·9	15·8	18·0	18·6	14·2
40	3·3	1·6	6·0	5·5	11·5

Table 4. *Amount of water (mm.³) consumed per bee*

Environmental temperature (° C.)	No. of bees in a group				
	10	25	50	100	200
10	—	0·3	0·0	0·0	0·0
15	0·0	0·0	0·0	0·0	0·0
20	0·0	0·0	0·0	0·0	0·3
25	0·5	0·5	0·5	0·3	0·3
30	0·0	0·0	0·5	0·5	0·8
35	5·8	9·8	10·9	10·1	11·4
40	10·1	20·4	29·7	16·7	21·7

In each experiment the amount of syrup or water consumed in the different cages was corrected for evaporation from the feeders and change in volume according to temperature, by subtracting from the results obtained the amount lost from the feeders in a control cage without bees. The amount of syrup or water consumed daily per bee is calculated on the mean number of bees alive in the group concerned during each day.

In all groups the amount of syrup consumed decreased with increase in environmental temperature. When the environmental temperature was 15° C. there was no correlation between the size of a group and the amount of syrup consumed per bee. However, at environmental temperatures of 20–35° C. bees in groups of 10 and 25 tended to consume more syrup than bees in larger groups; this is probably related to the fact that bees in the smaller groups clustered little, if at all, at these temperatures. At 40° C. there was, in general, a marked reduction in the amount of syrup consumed.

Negligible quantities of water were drunk at 10, 15 or 20° C., and only small amounts at 25 or 30° C., but at 35 and 40° C., relatively enormous quantities were taken.

DISCUSSION AND CONCLUSIONS

Pirsch (1923) found that the temperatures of the bodies of bees that were permitted limited movement only were similar to that of the air at about 30–40° C., but at an air temperature of 5·5° C., the bees' temperatures averaged 4·7° C. higher. Himmer (1925) found that the temperature of a resting bee approached that of its surroundings, although the temperature of an active bee rose considerably higher, differences of as much as 20° C. being found at times.

Himmer (1926) reported that individual bees lose motility at 11–12° C. and become rigid at 6–7° C. The authors (unpublished) have found that the temperature at which bees enter chill coma varies between 9 and 12° C. The present results illustrate the ability of a comparatively small number of bees to raise their surrounding temperature, and consequently to increase their survival time, although to a relatively small extent in comparison with a colony of normal size. Thus Corkins (1932) found that two-thirds of the members of a colony of about 17,500 bees survived after it had been kept at a mean temperature of −15° C. for 329 hr.

Various observers have reported that bees form a cluster within the hive when the outside temperature drops to below 15° C. (e.g. Phillips & Demuth, 1914; Himmer, 1926), although bees may start to cluster when the outside temperature is 18° C. (Wilson & Milum, 1927). The present results explain these observations but show they are incomplete; with decrease in the environmental temperature from 20–15° C. the percentage of bees clustering increased markedly and practically all the bees of a group were clustering at 10° C. At 20° C. and above, however, although bees in groups of 10 or 25 showed little tendency to cluster, the proportion clustering in the larger groups increased with the size of the groups. In such circumstances, therefore, clustering is not in response to low temperature, but is the result of the mutual attraction of the bees to one another. The larger the group of bees forming a cluster, the more bees are attracted to join it. These results confirm and extend those of Lecomte (1950) and Free & Butler (1955).

Many workers (e.g. Gates, 1914; Himmer, 1926; Wilson & Milum, 1927) have concluded that there is, at times, an inverse relationship between the temperature in the centre of a broodless cluster and that of the outside air, and Himmer (1932) postulated that this resulted in the maintenance of the minimum temperature necessary for movement on the outskirts of the cluster. But this relationship appears to be a short-term one only, and although the cluster temperature remains fairly constant regardless of outside temperature, such changes as do occur are directly related to the environmental temperature (e.g. Corkins, 1930; Lavie, 1954). During the present study the temperature within the cages increased both with the number of bees present and with the environmental temperature.

There are two ways by which bees in a winter cluster may possibly compensate for a decrease in environmental temperature. First, by reduction of heat loss, both by contraction of the cluster which, as Corkins (1930) pointed out, decreases its cooling surface and, secondly, by increased heat production, i.e. increase in the bees' metabolic rate. Although the latter method has been assumed to occur by many workers who have studied the behaviour of the winter cluster (e.g. Phillips & Demuth, 1914; Himmer, 1926), the present results provide the first real evidence that bees will respond to decreased environmental temperature by increased metabolism and heat production, and consequently by increased food consumption.

In the present experiments bees drank very little water at environmental temperatures of 30° C. and below, although their food was highly concentrated sugar syrup. Considerable quantities were drunk at 35° C. and nearly twice the amount at 40° C. There appear to be two possible explanations of this. It could have been the result of the bees consuming water which was subsequently manipulated and evaporated between the mouthparts as happens within the hive when outside temperatures reach 32° C. (Lindauer, 1954). However, above temperatures which are critical for each species, the wax layer of the epicutule of insects becomes permeable to water and their transpiration rate increases very greatly (Wigglesworth, 1953). Probably, therefore, the high water consumption by bees when kept at 35 and 40° C. was associated with a high rate of water loss through the cuticle.

The temperatures within the cages were only slightly below that of the environment at 40° C., so that any evaporation of water that occurred was relatively ineffective in lowering the temperature surrounding the bees. In contrast, Lindauer (1954) found that at an outside temperature of 40° C. the temperature within a hive containing a colony of bees was 36° C.

The high death-rate of bees kept at 40° C. may partially have been a consequence of the temperature itself, or the temperature combined with a high relative humidity which, as Wolfenbarger (1934) and Woodrow (1935) have shown, alone adversely affects longevity by causing dysentery.

SUMMARY

1. Bees have been kept in groups whose numbers ranged from 10 to 200 bees, at temperatures ranging from 0–40° C.

2. At 40° C. bees in groups of 200 had a higher death-rate than bees in smaller groups. At temperatures of 25–35° C. the death-rate was low and about the same in all groups. Below 25° C. the more bees in a group, the longer they survived.

3. The temperatures of all groups increased with that of their environment, the larger a group, the higher its temperature. The difference between the external temperature and that of the groups decreased with increase in the former until at 35 and 40° C. groups of all sizes were at or slightly below environmental temperature.

4. At temperatures from 20–40° C. the percentage of bees in a group that were clustering was directly related to the size of their group, bees in groups of 10 or 25 hardly clustering at all. At each temperature at 15° C. or below, about the same high percentage of bees clustered in all groups.

5. The amount of food (sugar syrup) consumed per bee increased with decrease in the environmental temperature. Very little water was drunk at environmental temperatures of 25° C. or lower but, at 35° C. and above, relatively enormous quantities were taken.

6. These results have been discussed especially in relation to information on the temperature regulation and food consumption of colonies in winter.

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