

Why Honeybees Rear Brood in Winter. A Theoretical Study of the Water Conditions in the Winter Cluster of the Honeybee, *Apis mellifera*

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A model is presented describing the water conditions in the winter cluster of the honeybee, *Apis mellifera*. It is based on a specific view of how the thermoregulation of the winter cluster is accomplished. It assumes that the apparently coordinated thermoregulatory responses of the broodless winter cluster are results of the individuals' acting behaviourally and physiologically to regulate their own body temperature. The results include predictions about radial distribution of water evaporation and accumulation per bee, and cluster humidity, as a function of ambient temperature. The main conclusion is that the phenomenon of brood rearing in the winter cluster is likely to be a strategy which the bees have adopted in order to reduce their own water content when this has reached a specific level.

1. Introduction

A clear conception of the water conditions in the winter cluster of the honeybee, *Apis mellifera*, still seems to be lacking. Some understanding has been obtained by the works of Altmann (1956), Altmann & Gontarski (1961), Hallund (1956), Lotmar (1954), Møbus (1980*a, b*), Simpson (1950) and Wedmore (1947), but no one has so far presented the conceptual apparatus necessary for a comprehensive analysis on a quantitative basis.

A mathematical model is presented, based on the works of Omholt & Lønvik (1986) and Omholt (1987), of heat production and thermoregulation in the winter cluster. The model describes different aspects of the water conditions at the individual and colonial level as a function of ambient temperature. The predictions are shown to be consistent with a hypothesis advocated by Møbus (1980*b*), saying that the phenomenon of brood rearing in the winter cluster is a strategy which is adopted by the bees in order to regulate their water content.

The hope is that the model presented in this paper, together with those of Omholt & Lønvik (1986) and Omholt (1987), will motivate a structured and comprehensive experimental approach to the intricacies posed by the winter cluster.

2. Description of the Model

(A) RATE OF WATER EVAPORATION PER BEE

The observation that the humidity level is decreasing from the centre of the cluster and outwards (Simpson, 1950), implies the existence of a radial water transport.

Provided that this transport is mainly due to diffusion (Simpson, 1961), it may be described by Fick's law which says that the water current density at a specific point is proportional to the humidity gradient at that point (Alonso & Finn, 1980), so that (assuming stationary conditions and spherical geometry)

$$\int_0^r 4\pi r^2 D(r, T_a) Z(r, T_a) dr = -4\pi r^2 G(r, T_a) \frac{dW(r, T_a)}{dr} \quad (1)$$

where T_a = ambient temperature outside the cluster surface; $D(r, T_a)$ = bee density per unit volume at a distance r length units from the centre; $Z(r, T_a)$ = rate of evaporation per individual bee; $G(r, T_a)$ = coefficient of diffusion; $dW(r, T_a)/dr$ = humidity gradient.

The radial distribution of the evaporation rate per bee as a function of ambient temperature may then be equated as

$$Z(r, T_a) = -\frac{1}{D(r, T_a)} \left[\left(\frac{2G(r, T_a)}{r} + \frac{dG(r, T_a)}{dr} \right) \frac{dW(r, T_a)}{dr} + G(r, T_a) \frac{d^2 W(r, T_a)}{dr^2} \right]. \quad (2)$$

The humidity profile when $T_a = 5^\circ\text{C}$ ($T_{\max}$) is assumed to be described by the function

$$W(r, T_{\max}) = W_c(T_{\max}) / \left[1 + \frac{W_c(T_{\max}) - W_p(T_{\max})}{W_p(T_{\max})} \left(\frac{r}{R(T_{\max})} \right)^2 \right] \quad (3)$$

where $W_c(T_{\max})$ and $W_p(T_{\max})$ are the humidity levels at the centre and the periphery respectively, and where $R(T_{\max})$ is the radius of the clusters at $T_{\max}$ (Fig. 1).

The coefficient of diffusion is likely to be inversely related to bee density. However, when $T_a = T_{\max}$, the coefficient of diffusion is assumed to be a constant (G_c), due

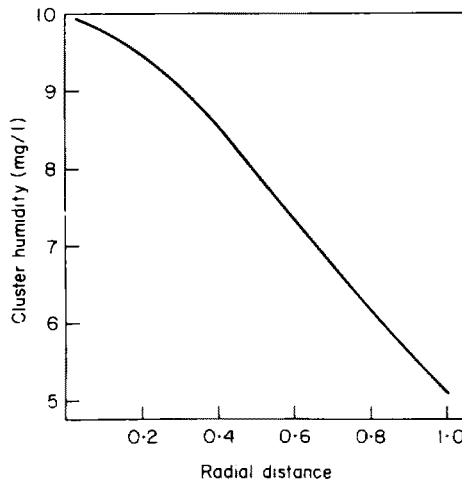


FIG. 1. The presumed radial humidity profile in the winter cluster at an ambient temperatures of 5.0°C and an ambient relative humidity of 60%, which is applied for the calculation of the radial distribution of evaporation rate per bee.

to the rather homogenous cluster structure at that temperature (Omholt, 1987). This enables the quantification of G_c from the relationship

$$G_c = \frac{E(T_{\max})}{4\pi R(T_{\max})^2 \frac{dW(r, T_{\max})}{dr}} \quad (4)$$

where $E(T_{\max})$ is the total amount of water that evaporates from the cluster per unit time at $T_{\max}$.

One may obtain an approximate quantification of $E(T_{\max})$ from

$$E(T_{\max}) = \int_0^{R(T_{\max})} 4\pi r^2 D(r, T_{\max}) \left(\alpha + \frac{\beta}{\delta(1-\beta)} \right) q(r, T_{\max}) dr + E_{\text{calib}} \quad (5)$$

where $q(r, T_{\max})$ = radial distribution of metabolic rate per individual bee at $T_{\max}$; α = the amount of metabolic water produced per unit of energy; β = the proportion of free water per unit weight of honey; δ = the amount of energy per unit weight of pure honey; E_{calib} = a calibration parameter expressing whether there is assumed to be a dehydration (>0), hydration (<0) or a stationary ($=0$) water situation at $T_{\max}$.

(B) SPECIFIC RATE OF ACCUMULATION

The radial distribution of water accumulation per bee as a function of ambient temperature follows directly from eqns (2) and (5), and may be equated as

$$A(r, T_a) = \left(\alpha + \frac{\beta}{\delta(1-\beta)} \right) q(r, T_a) - Z(r, T_a). \quad (6)$$

The accumulation rate for the whole cluster is then given by

$$A(T_a)_{\text{cluster}} = \int_0^{R(T_a)} 4\pi r^2 D(r, T_a) A(r, T_a) dr. \quad (7)$$

(C) CLUSTER HUMIDITY

The cluster humidity as a function of ambient temperature may be obtained from

$$W(r, T_a) = W_p(T_a) + \int_0^{R(T_a)} \frac{j(r, T_a)}{G(r, T_a)} dr \quad (8)$$

where $W_p(T_a)$ = the humidity level at the periphery of the cluster at T_a ; $j(r, T_a)$ = the radial water current density (cf. eqn (1)).

(D) QUANTIFICATION OF PARAMETERS

The ambient temperature range ($T_{\min}$, $T_{\max}$) in this study will be $(-20, 5)^\circ\text{C}$ (see Ohmolt, 1987).

The obtainment of radial distribution of metabolic rate ($q(r, T_a)$) is described in Omholt (1987), and that paper should be consulted for further details. Identical values of the different parameters used for these calculations, will be applied in the following, so that

- (a) the heat flux from the cluster at the ambient temperature limits is 350.0 cal/min ($Q(T_{\min})$) and 80.0 cal/min ($Q(T_{\max})$), when the number of bees (N_b) is 15 000;
- (b) the core temperature at $T_{\max}$ is 24°C, and the temperature at the periphery is constantly 10°C for the whole ambient temperature range;
- (c) the coefficient of heat transfer at the surface of the cluster is linearly decreasing between the $k(T_{\min})$ (0.0106 cal/cm²/min/°C) and $k(T_{\max})$ (0.0076 cal/cm²/min/°C);
- (d) the resting metabolic rates at the core ($q(0)_{\text{rest}}$) and periphery ($q(R(T_a)_{\text{rest}})$) are 0.0295 cal/bee/min and 0.0015 cal/bee/min respectively, and the proportionality constant l_c , which is assumed to define the maximum metabolic levels by the resting metabolic level at a given surrounding air temperature, is 8.75.

The density profiles ($D(r, T_a)$) are obtained in the same way as described in Omholt (1987), where the cluster is divided into a core and a shell with densities 1.25 bees/ml (D_{core}) and 5.5 bees/ml (D_{shell}) respectively, and where the maximum and minimum core size is 12.5 cm ($R(T_{\max})_{\text{core}}$) and 6.0 cm ($R(T_{\min})_{\text{core}}$).

Normally, the water content of the honey (β) varies between 0.15 and 0.20 (Simpson, 1961), and the conservative estimate 0.15 will be applied in the following.

The humidity at the periphery of the cluster ($W_p(T_a)$) is assumed to be 1.0 mg/l above the ambient humidity (Grziwa, 1956; Simpson, 1961), and the latter is assumed to correspond to relative humidity (RH) of 60% for all T_a 's. The calibration parameter E_{calib} is assumed to be 2.5 mg/min, which means that the colony is dehydrated at a rate of 2.5 mg/min when $T_a = T_{\max}$ and the relative humidity is 60%. The core humidity at $T_{\max}$ ($W_c(T_{\max})$) is set to be 10 mg/l, which is in agreement with the observations of Simpson (1950). The minimum and maximum values of the rate of evaporation per bee are assumed to be identical for all T_a 's. However, due to the decrease in $R(T_a)$ with decreasing T_a , the gradient will necessarily become steeper in the outer part of the cluster when the limit values are fixed. This adjustment is done in such a way that the total evaporation is identical for all T_a 's (cf. Omholt, 1987). This is a rather crude approximation because the steeper temperature gradient that arises with decreasing T_a (Omholt, 1987), and the increase in respiration frequency with decreasing T_a , are likely to effect some increase in the evaporation despite the considerable decrease in surface area. This implies that the calculated accumulation rates may represent levels somewhat above what is to be expected. However, the difference between predicted and real values is thought to be relatively modest as long as the relative ambient humidity remain constant, and brood rearing is not initiated (see below). The coefficient of diffusion in the core (G_{core}) is assumed to be constant and identical with G_c (cf. eqn (4)), while G_{shell} is allowed to vary between G_{core} and $0.5 \times G_{\text{core}}$, in order to test the sensitivity of the predictions concerning core humidity.

3. Results

(A) WATER EVAPORATION

The predicted radial distribution of water evaporation per bee when $T_a = 5^\circ\text{C}$, shows that the evaporation decreases very rapidly from the centre towards the periphery (Fig. 2). The graph shows a very rapid decline in the outermost part of the cluster. This is caused by the increase in bee density due to the thin shell that is assumed to have been formed at $T_{\max}$. It is difficult to decide theoretically whether this is a sound prediction or not. (The predictions to follow are rather insensitive to a less rapid decline in the outermost part.)

(B) ACCUMULATION OF WATER

The bees in the core will be dehydrated, while the bees in the shell will be hydrated (Fig. 3). However, even if the hydrated ones share their water surplus with the dehydrated ones in connection with food transfer (see Discussion), the rate of accumulation for the whole cluster will increase considerably with decreasing T_a (Fig. 4).

(C) CORE HUMIDITIES

If the relative humidity remains constant, the model predicts a decline in core humidity with decreasing T_a , with a constant coefficient of diffusion (Fig. 5). When

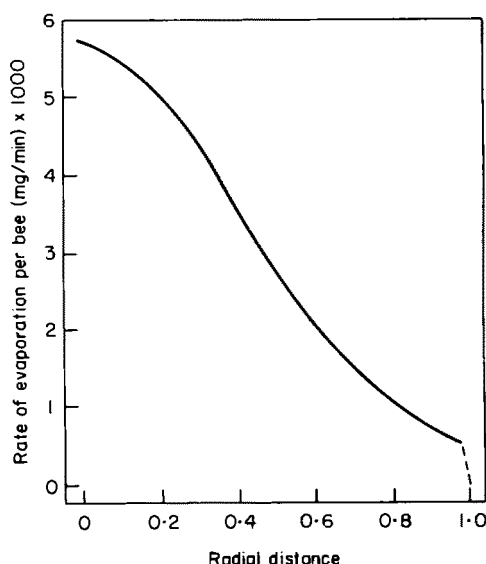


FIG. 2. Predicted radial distribution of rate of evaporation per bee at an ambient temperature of 5°C and an ambient relative humidity of 60%, when $N_b = 15\,000$ bees; $R(T_{\min})_{\text{core}} = 6.0$ cm; $R(T_{\max})_{\text{core}} = 12.5$ cm; $D_{\text{core}} = 1.25$ bees/ml; $D_{\text{shell}} = 5.5$ bees/ml; $T_p = 10^\circ\text{C}$; $q(R(T_a))_{\text{rest}} = 0.015$ cal/bee/min; $q(0)_{\text{rest}} = 0.0295$ cal/bee/min; $I_r = 8.75$; $Q(T_{\min}) = 350.0$ cal/min; $Q(T_{\max}) = 80.0$ cal/min; $k(T_{\max}) = 0.0076$ cal/cm²/min/ $^\circ\text{C}$; $k(T_{\min}) = 0.0106$ cal/cm²/min/ $^\circ\text{C}$; $\beta = 0.15$; $E_{\text{calib}} = 2.5$ mg/min; $RH = 60\%$.

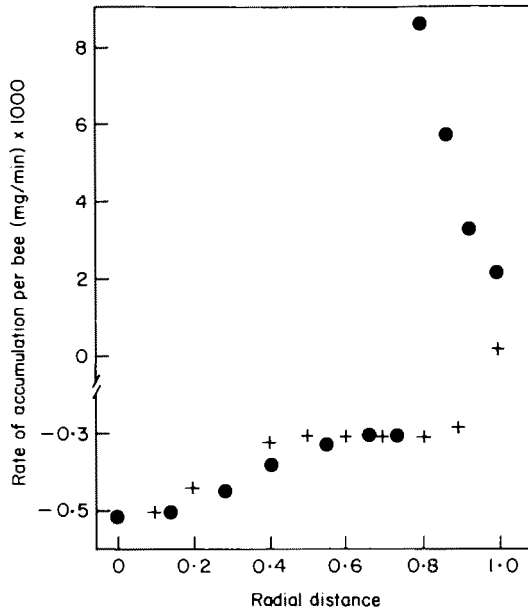


FIG. 3. Predicted radial distribution of accumulation rate per bee at ambient temperatures -20°C (●) and 5°C (+), when $N_b = 15\,000$ bees; $R(T_{\min})_{\text{core}} = 6.0$ cm; $R(T_{\max})_{\text{core}} = 12.5$ cm; $D_{\text{core}} = 1.25$ bees/ml; $D_{\text{shell}} = 5.5$ bees/ml; $T_p = 10^{\circ}\text{C}$; $q(R(T_a))_{\text{rest}} = 0.0015$ cal/bee/min; $q(0)_{\text{rest}} = 0.0295$ cal/bee/min; $l_c = 8.75$; $Q(T_{\min}) = 350.0$ cal/min; $Q(T_{\max}) = 80.0$ cal/min; $k(T_{\max}) = 0.0076$ cal/cm²/min/ $^{\circ}\text{C}$; $k(T_{\min}) = 0.0106$ cal/cm²/min/ $^{\circ}\text{C}$; $\beta = 0.15$; $E_{\text{calib}} = 2.5$ mg/min; $RH = 60\%$.

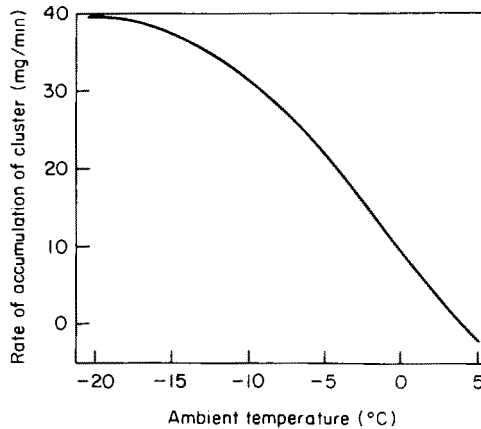


FIG. 4. Predicted rate of accumulation for the whole cluster as a function of ambient temperature, when $N_b = 15\,000$ bees; $R(T_{\min})_{\text{core}} = 6.0$ cm; $R(T_{\max})_{\text{core}} = 12.5$ cm; $D_{\text{core}} = 1.25$ bees/ml; $D_{\text{shell}} = 5.5$ bees/ml; $T_p = 10^{\circ}\text{C}$; $q(R(T_a))_{\text{rest}} = 0.0015$ cal/bee/min; $q(0)_{\text{rest}} = 0.0295$ cal/bee/min; $l_c = 8.75$; $Q(T_{\min}) = 350.0$ cal/min; $Q(T_{\max}) = 80.0$ cal/min; $k(T_{\max}) = 0.0076$ cal/cm²/min/ $^{\circ}\text{C}$; $k(T_{\min}) = 0.0106$ cal/cm²/min/ $^{\circ}\text{C}$; $\beta = 0.15$; $E_{\text{calib}} = 2.5$ mg/min; $RH = 60\%$.

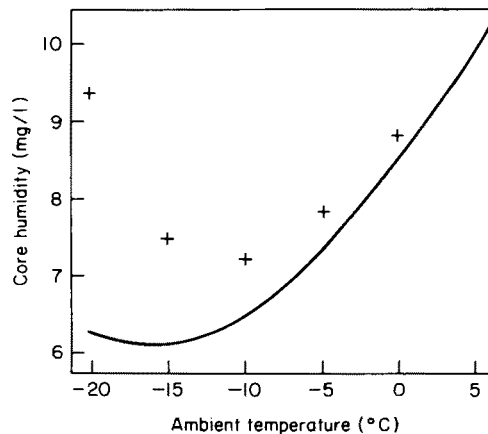


FIG. 5. Predicted core humidity as a function of ambient temperature, when $N_b = 15\,000$ bees $R(T_{\min})_{\text{core}} = 6.0$ cm; $R(T_{\max})_{\text{core}} = 12.5$ cm; $D_{\text{core}} = 1.25$ bees/ml; $D_{\text{shell}} = 5.5$ bees/ml; $T_p = 10^\circ\text{C}$; $q(R(T_a))_{\text{rest}} = 0.0015$ cal/bee/min; $q(0)_{\text{rest}} = 0.0295$ cal/bee/min; $I_c = 8.75$; $Q(T_{\min}) = 350.0$ cal/min; $Q(T_{\max}) = 80.0$ cal/min; $k(T_{\max}) = 0.0076$ cal/cm²/min/ $^\circ\text{C}$; $k(T_{\min}) = 0.0106$ cal/cm²/min/ $^\circ\text{C}$; $\beta = 0.15$; $E_{\text{calib}} = 2.5$ mg/min; $RH = 60\%$; $G_{\text{core}} = G_{\text{shell}} = 0.02$ mg/cm²/min/ $^\circ\text{C}$. The plus signs represent predicted core humidity when $G_{\text{shell}} = 0.5 \times G_{\text{core}}$.

$G_{\text{shell}} = 0.5 \times G_{\text{core}}$, the core humidity will decrease somewhat less. These results are in agreement with the observations of Simpson (1950).

(D) BROOD REARING IN THE WINTER CLUSTER

Møbus (1980b) suggested that the phenomenon of brood rearing in the winter cluster has a definite survival value for a colony with a water problem, as the production of liquid, glandular brood food will remove some of the individually embarrassing surpluses from the bees, and that the increase in core temperature that follows brood rearing will make efficient evaporation possible.

This hypothesis is strongly supported by the predictions given above. Assuming a maximum storing capacity of 40 mg water per bee (Altmann & Gontarski, 1961) and an ambient temperature of 0°C , a cluster of 15 000 bees is expected to start brood rearing about 43 days after their last cleansing flight. This is in clear corroboration with the observations of Avitabile (1978), Jeffree (1956), Møbus (1980a) and Wedmore (1947).

Furthermore, by assuming a water content of 85% in the brood (Lotmar, 1954) and a larval weight just before sealing of 140 mg (Thrasylvoulou & Benton, 1982), a cluster of 15 000 bees is predicted to rear about 12 350 brood in the period from mid-November to the end of February. Avitabile (1978) measured a mean brood production in this period in Connecticut, USA, of 5900 brood for colonies with an old queen, and 11 300 brood for colonies with young queens. The mean temperature in Connecticut during this period is a little below 0°C (Seeley & Kirk Visscher, 1985). Møbus (1980a) reports a mean brood production of 3600 in the same period as above in the North of Scotland. This may be due to a higher mean ambient temperature and/or weaker colonies.

The brood rearing is accompanied by an increase in core temperature to a level somewhere between 31–35°C (Simpson, 1950). At this temperature level the evaporation from the bees increases dramatically (Altmann, 1960; Beament, 1959; Free & Spencer-Booth, 1958; Wigglesworth, 1945). In addition, the saturation deficiency of the cluster air increases. A predicted value somewhat above the observed one is therefore to be expected as long as these effects are not incorporated into the model.

4. Discussion

(A) FURTHER CONSIDERATIONS ABOUT BROOD REARING IN WINTER

Møbus (1980a) reports an experiment where he formed very strong colonies by artificially uniting colonies. After a cold period lasting about three to four weeks, the bees flew out on a day that permitted cleansing flights. In spite of milder temperatures, these bees chilled quickly and died in frightening numbers. Despite that this may be caused by several factors, a natural interpretation of the result is that the bees suffered thirst. This interpretation is substantiated by the fact that the same effect may also arise by keeping hives containing colonies of normal size in beehouses heated by electric means. The relative humidity inside the beehouse will be dramatically reduced compared to the one outside, and abnormally low relative humidities in the clusters (20% or less) have been observed under such conditions (Simpson, 1961). This implies that the evaporation will be much greater than the amount of water produced due to the low metabolism at elevated temperatures. The fact that Pirker (1978) was able to avoid heavy flight losses and to initiate brood rearing in colonies kept in a beehouse at 11°C with an outside temperature of –9.9°C, when he supplied additional humidity to the indoor air by means of an electric humidifier, ought to provide rather conclusive evidence in this connection.

Some workers seem to be of the opinion that the increase in day length after the winter solstice triggers the onset of brood rearing (Avitabile, 1978). However, this hypothesis is not able to explain (as the water regulation hypothesis is) why there is brood rearing in colonies kept in complete darkness in freezing rooms (Free & Simpson, 1963; Villumstad, 1959), why there is such great variation in the time of brood rearing commencement (Jeffree, 1956), or why there are frequent stops in brood rearing in late winter (Jeffree, 1956; Møbus, 1980a). Furthermore, this hypothesis is also weakened by the fact that it seems unnecessary to introduce a photoperiodic regulation mechanism in order to explain the brood rearing cycle in the summer season (Omholt, 1986).

(B) MOVEMENT WITHIN THE CLUSTER

Møbus (1980b) suggested that exchange of bees takes place from time to time, motivated by thirst or water surplus. Bees move from the dehydrating middle to the hydrating shell to take a “metabolic drink”, and bees from the outer shell move inwards to “dry out”.

However, if there is a food transfer from the periphery, where the honey stores are likely to be, and inwards, there may be a water transport by means of diluted

food from the hydrated to the dehydrated bees. This will reduce the need for cluster movement considerably. The existence of such a transport mechanism is strongly supported by the observations of Hallund (1956), which showed no significant difference in fresh and dry rectal weights between bees from the centre and periphery of the cluster.

(C) SUGGESTIONS FOR EXPERIMENTAL RESEARCH

Despite the fact that the predictions presented above seem to agree rather well with empirical observations, the water regulation hypothesis needs further experimental corroboration in order to obtain the status of theory. A rather conclusive test would be to make a simultaneous measurement of the following parameters at different ambient temperatures

- (a) the total heat production;
- (b) the total water loss;
- (c) the humidity profile;
- (d) the temperature profile;
- (e) the cluster radius and the thickness of the shell.

If the time of appearance and the amount of brood rearing can be predicted by the model, this would be a very strong confirmation of the water regulation hypothesis as well as the COFY model (see Omholt, 1987).

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