



Shape and Dynamics of Thermoregulating Honey Bee Clusters

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A model of simple algorithmic “agents” acting in a discrete temperature field is used to investigate the movement of individuals in thermoregulating honey bee (*Apis mellifera*) clusters. Thermoregulation in over-wintering clusters is thought to be the result of individual bees attempting to regulate their own body temperatures. At ambient temperatures above 0°C, a clustering bee will move relative to its neighbours so as to put its local temperature within some ideal range. The proposed model incorporates this behaviour into an algorithm for bee agents moving on a two-dimensional lattice. Heat transport on the lattice is modelled by a discrete diffusion process. Computer simulation of this model demonstrates qualitative behaviour which agrees with that of real honey bee clusters. In particular, we observe the formation of both disc- and ring-like cluster shapes. The simulation also suggests that at lower ambient temperatures, clusters do not always have a stable shape but can oscillate between insulating rings of different sizes and densities.

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1. Introduction

The primary aim of mathematical modelling is to capture the features of a natural system as a simple set of rules. Often, these rules take the form of differential equations describing the temporal and spatial evolution of a set of variables which characterize the state of the system. These can either be analysed directly or used to create a computer simulation which reflects—and possibly predicts—aspects of the system’s behaviour. So successful has this approach been that it is sometimes difficult to see beyond the limitations. Thus, although differential equation models have been applied to the dynamics of animal societies since the 1920s (Murray, 1989), they are, by their nature, restricted to providing information about

averaged quantities such as populations or densities of populations. Generally, this type of information fails to capture the contribution of each individual to the behaviour of the society as a whole (Drogul & Ferber, 1992; Minar *et al.*, 1996; Taylor & Jefferson, 1995).

In this paper we propose an agent-based model. The underlying principle of such a model is that the rules reflecting the system’s behaviour are defined in terms of the autonomous entities (agents) which constitute the system. Agent-based simulations therefore encompass a number of different modelling paradigms including cellular automata, object oriented models and certain discrete event simulations. These models remove many of the limitations of differential equations by allowing the investigation of how the behaviour of individuals—and the rules governing their interaction—generate patterns of global behaviour. This is particularly useful for modelling animal societies.

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Honey bee colonies consist of tens of thousands of individuals all acting autonomously but as part of a complex society. One example of an apparently coordinated colony level response to changing conditions is the formation of spherical clusters and, thereby, the regulation of nest temperature during cold weather. It has been suggested that cluster thermoregulation is the result of the colony acting as a superorganism, capable of adjusting its shape and size to suit temperature conditions (Southwick, 1991). However, it has been demonstrated that in honey bee swarms the bees in the centre (core) do not communicate with those on the surface (mantle) (Heinrich, 1981). This seems to support the hypothesis that the formation and behaviour of the cluster is the result of independent actions by individual bees. The investigation of this hypothesis is a natural application of the agent-based simulation technique.

Previous models of temperature distributions inside winter clusters have used differential heat equations to predict changes in cluster width and core and mantle temperatures over time (Basak *et al.*, 1996; Lemke & Lamprecht, 1990; Myerscough, 1993; Omholt, 1987). Most begin with the assumption that the metabolic heat production at any point in the cluster is a function of the distance from the centre. This presupposes spherical symmetry and a given density distribution of bees within the cluster. The question of how the bees actually arrange themselves into such a configuration—surely an interesting question—is thus avoided.

Watmough & Camazine (1995) improved on this basic model by treating the bee density at different points inside a spherical cluster as a dynamical variable. In this model, heat production depends on the density of bees at any given point—heat diffuses in the cluster and bee densities change according to the local temperature. An individual bee's behaviour is not expressed explicitly but is reflected in density changes as bees move along the temperature gradient toward the point where their temperature is ideal. An unsatisfactory aspect of this model is that it still assumes that the bees always form a spherical shape. In this paper, we introduce an agent-based model which spontaneously produces this global behaviour as a consequence of simple rules

followed by each individual bee in the colony. An unexpected consequence of our model is that it suggests a new dynamical phenomenon: clusters which are seen to pulsate.

2. Problem Description and Model

2.1. MODEL ASSUMPTIONS

The computer model we use is based on the following assumptions about the behaviour of individual bees:

1. Each bee bases her behaviour exclusively on her local temperature.
2. Bees have a preferred range of temperatures. Inside this range a bee moves randomly. When she is outside this range she will move in the appropriate direction along the temperature gradient.
3. Below a lower threshold temperature a bee will go into a “chill coma” and will be unable to move.
4. A bee's heat production is based on her metabolic rate which is an increasing function of temperature. Bees in a coma generate no heat.

Assumptions 1 and 4 are similar to those made in Watmough and Camazine. Assumption 2 is a small generalization of their model since it replaces a single preferred temperature with a preferred temperature range. This allows for bee activity—other than temperature optimization—to take place when the bees are in their preferred temperature range. In our simulation, this other activity is modelled by the bees performing random walks.

In this paper, we confine our attention to the behaviour of clusters at ambient temperatures above 0°C. Below this temperature the cluster diameter reaches a lower limit and some of the clustering bees adopt a new kind of behaviour; shivering their wing muscles to generate heat. Restricting attention to higher ambient temperatures allows us to focus on a simpler model while still producing interesting and realistic cluster behaviour.

In addition to individual bee behaviour we must also represent the transport of heat within

the hive. Following Watmough and Camazine we introduce the following additional assumptions:

5. Heat transfer through the hive is due to diffusion.
6. Diffusion is reduced by *still* bees.

Assumption 6 is a modification of an assumption of Watmough and Camazine. At temperatures below 15°C it is observed that bees huddle close together preventing convection through the cluster (Heinrich, 1981), Watmough and Camazine incorporated this by assuming that all bees have an insulating effect. Here, it is assumed that only stationary bees have an insulating effect. On the contrary we assume that moving bees can contribute to the heat flux by causing local mixing of the air.

2.2 THE FORMAL MODEL

We consider a two-dimensional region which represents the gap between two honeycomb layers in, say, a commercial bee hive. In reality, these gaps are about two or three bee widths wide (Winston, 1987) but we shall assume that no more than a single bee may be found at a given point. Furthermore, we shall assume no heat loss through the honeycomb.

Each bee agent, labelled b , is a computer program containing variables (x_b, y_b) representing its coordinates. We shall constrain the bees to move on the vertices of a finite square lattice, that is, x_b and y_b are integers which satisfy the conditions: $0 < x_b < x_{max}$ and $0 < y_b < y_{max}$. It will be convenient to think of $b \in B$, where B is the ordered set of all bee agents in the hive. By writing $b(t)$ we mean the position of b at time $t \in \mathbb{Z}^+$. This agent definition implies bees which have no memory in the sense that all the relevant information about a bee may be derived from knowledge of her current position.

Before we define how a bee behaves in time and space we must specify its environment. The temperature field is defined as a real-valued function on the lattice $\{(x, y) \mapsto T_{xy} : x \in \{0, \dots, x_{max}\}, y \in \{0, \dots, y_{max}\}\}$. (Note that this lattice is slightly larger than the one that the bees inhabit to allow us to fix the boundary conditions on T_{xy} .) It will sometimes be convenient to use the notation

$T_{xy}(t)$ to denote the temperature at position (x, y) and time t .

2.2.1. Individual Bee Behaviour

The behaviour of a given bee depends on the position of the other bees and on the temperature field. We let T_{coma} denote the temperature below which a bee will enter a chill coma, and T_{minI} and T_{maxI} denote, respectively, the lower and upper bounds of the preferred temperature range of the bees. We now define bee behaviour which incorporates assumptions 1–3. We write a single bee movement as, $b(t) \mapsto b(t + \tau)$, with the integer constant $\tau \geq 1$, defined as a bee time step. Physically, τ can be thought of as the time it takes a bee to move her own body length when crawling about the hive. For any $b(t) = (x_b, y_b)$, if $T_{x_b, y_b}(t) < T_{coma}$ then $b(t + \tau) = b(t)$. Otherwise, consider the set of all positions, (x, y) such that $|x_b - x| \leq 1$ and $|y_b - y| \leq 1$, which do not contain another bee and are within the preferred temperature range (T_{minI}, T_{maxI}) . If this set is not empty then $b(t + \tau)$ is a position picked at random from this set. Otherwise, $b(t + \tau)$ is taken to be one of the positions, (x, y) , containing no other bee, which has T_{xy} nearest to $T_{meanI} = \frac{1}{2}(T_{minI} + T_{maxI})$. In order to resolve conflicts which might arise in the implementation of these rules should more than one bee attempt to occupy a given site, the bee movements are considered serially. At each bee time step the order in which the individual bees are considered is randomized.

2.2.2. Temperature Field

The factors affecting the evolution of the temperature are: the local production of heat by individual active bees, and diffusion effects which tend to make the temperature field more uniform. To avoid numerical artefacts we determine the diffusion of the temperature field on a finer lattice than the one on which bees move. On this lattice we denote the temperature as $\{(i, j) \mapsto T_{ij}^g : i \in \{0, \dots, gx_{max}\}, j \in \{0, \dots, gy_{max}\}\}$ where g is a positive integer which denotes the relative length scales of the lattices. The temperature field experienced by the bees is the local average of the fine scale temperature field

$$T_{xy}(t) = \frac{1}{g^2} \sum_{i=gx}^{(g(x+1)-1)} \sum_{j=gy}^{(g(y+1)-1)} T_{ij}^g(t).$$

The fine scale temperature field is updated using a discrete form of the diffusion equation with a non-constant diffusion coefficient:

$$T_{xy}^g(t+1) = T_{xy}^g(t) + \Delta^2(x, y, t) + f(x, y, t). \quad (1)$$

This equation clearly contains a first-difference approximation of the time derivative of the temperature field and a term, $f(x, y, t)$, which represents heat sources corresponding to the current locations of the bees. The remaining term, $\Delta^2(x, y, t)$, is a discrete (second-difference) form of the diffusion operator acting on the temperature field.

$$\begin{aligned} \Delta^2(x, y, t) = & \frac{1}{4} \sum_{\substack{|x-x'|+ \\ |y-y'|=1}} \mathbf{D}(x, y, x', y', t) \\ & \times (T_{x'y'}^g(t) - T_{xy}^g(t)). \end{aligned}$$

Here $\mathbf{D}(x, y, x', y', t) = \lambda(x, y, t)\lambda(x', y', t)$ is the non-uniform diffusion coefficient written in terms of site-dependent heat transport coefficients. If there is a *stationary* bee on site (x, y) at time t we assume an insulation effect and take $\lambda(x, y, t) = \lambda_{bee}$, otherwise we just set $\lambda(x, y, t) = \lambda_{air}$, the heat transport coefficient of free air. Generally, it is assumed that $\lambda_{bee} < \lambda_{air}$.

The source term of eqn (1) is a nonlinear function of the local temperature which models the observation that a bee's metabolic rate is an increasing function of temperature—see assumption 4. If site (x, y) is empty at time t then $f(x, y, t) = 0$. Otherwise

$$f(x, y, t) = h_{q20} e^{\gamma(T_{xy}^g(t) - 20)}, \quad (2)$$

where h_{q20} is the temperature increase made by a passive bee at 20°C and the exponent, γ , has been determined experimentally to be $\sim \ln(2.4)/10$ (Omholt, 1987).

In order to be able to solve eqn (1) we need to specify boundary conditions on the fine scale lattice. The most natural way to do this is to constrain the temperature at the boundaries of

the region to be some fixed ambient temperature, T_A ,

$$T_{0y}^g(t) = T_A, \quad t \geq 0, \quad y \in \{0, \dots, gy_{max}\},$$

$$T_{x0}^g(t) = T_A, \quad t \geq 0, \quad x \in \{0, \dots, gx_{max}\},$$

$$T_{x_{max}y}^g(t) = T_A, \quad t \geq 0, \quad y \in \{0, \dots, gy_{max}\},$$

$$T_{xy_{max}}^g(t) = T_A, \quad t \geq 0, \quad x \in \{0, \dots, gx_{max}\}.$$

We have now specified a discrete, stochastic dynamical system. Given initial data—an initial temperature field and the set B giving the initial distribution of bees—we can, in principle, follow the evolution of the temperature field and the bee distribution forward in time. For simplicity, we shall assume that the initial temperature field is uniform and set to the ambient temperature

$$T_{xy}^g(0) = T_A, \quad x \in \{0, \dots, gx_{max}\}, \quad y \in \{0, \dots, gy_{max}\}.$$

The initial distribution of bees is sampled at random from the uniform distribution over the entire lattice of possible bee positions.

In practice, we use this formalization as a definition of an agent-based computer simulation of the model. The results which follow in the next section were obtained by a simulation implemented using Swarm simulation libraries for Objective-C (Minar *et al.*, 1996).

2.3. MODEL PARAMETERIZATION

We need to choose model parameters to reflect the real behaviour and physiology of individual honey bees within a cluster. This must necessarily involve a degree of interpretation of experimental data to relate, for example, information about the clusters to parameters characterizing individual behaviour. It follows, therefore, that we should avoid analysing fine details in the simulations we make, rather we look for qualitative behaviour which does not depend sensitively on the actual values of the parameters used.

The parameters which govern bee behaviour are T_{minI} , T_{maxI} and T_{coma} . We set $T_{minI} = 18^\circ\text{C}$ since this is the value at which bees are seen to start clustering (Winston, 1987). Below 18°C an

individual bee has difficulty activating her flight muscles (Heinrich, 1996). Bees can perform most of their normal functions at temperatures up to 35°C. However, experimental data on individual bee behaviour is unreliable when applied to the social situation since we must account for the shared honey resources. A higher body temperature implies a greater metabolic rate and hence greater energy usage. Keeping a relatively low body temperature will reduce the usage of honey resources. With this in mind we set $T_{maxI} = 23^\circ\text{C}$. In nature $T_{coma} = 8^\circ\text{C}$ [below T_{coma} individuals are unable to move to form any cluster (Winston, 1987)].

It has been observed that a passive bee generates $q_{20} = 1.2 \text{ mW}$ at 20°C (Lemke & Lamprecht, 1990). The temperature increase due to a single bee at 20°C per unit time step, h_{q20} , is dependent on the size of the hive (x_{max} and y_{max}), insulation of air and passive bees (λ_{air} and λ_{bee}), the time between bee movements (τ) and the volume associated with an individual bee (g^2). Furthermore, in the simulation we use roughly two orders of magnitude fewer bees than are found in a real hive. We set h_{q20} to produce a global behaviour which is consistent with a well understood aspect of hive behaviour. Specifically, we ensure that for our standard colony—which contains 100 bees—the mean core temperature of the hive is 21.3°C at an ambient temperature of 18°C (Southwick & Mugaas, 1971).

It remains to fix the physical parameters of the system. As we stated earlier, we associate τ with the time it takes a bee to move its own length. Nominally, we might say that this is of the order of 1 s. Thus, times from simulations given in bee time steps can be thought of as being given in seconds. The rest of the physical parameters concern heat transport within the hive. We choose units so that the parameter $\lambda_{air} = 1.0$. In line with observations (Southwick, 1985), we should set $\lambda_{bee} \geq \sqrt{0.3} \sim 0.55$ but this does not result in simulated clusters which can survive at low ambient temperatures. This is probably because we are simulating smaller clusters than would be found in nature. We therefore set $\lambda_{bee} = 0.45$. The qualitative aspects of the simulation described in the next section are similar to those for a higher value of λ_{bee} . The complete parameterization of the simulation described below is summarized in Appendix B.

3. Cluster Formation

We are particularly interested in the behaviour of bees when the ambient temperature, T_A , is less than T_{minI} but greater than T_{coma} . That is, when the ambient temperature is too low for the individual bee to be happy but high enough for her to be able to move to a more comfortable location. The striking—but perhaps unsurprising—characteristic of all our simulations of this situation is that bees started at random, uniformly distributed locations tend to move together to form clusters.

In the simulations it is possible to identify three qualitatively different types of cluster.

1. “Droplet” clusters in which the distribution becomes separated into many small independent clusters. In this configuration very few—if any—bees are active.
2. The disc cluster, where the bees are distributed uniformly on a single, roughly circular disc within which many bees are active.
3. The ring cluster, which is similar to the disc cluster except that there are fewer bees at the centre than at the circumference of the disc.

These clusters may occur either as transient structures, or as time independent, equilibrium distributions representing a final, stationary state of the simulation. An example of each of these is given in Fig. 1 which shows three equilibrium clusters produced by varying the ambient temperature and the total number of bees.

It is useful to specify these different cases more rigidly in terms of various statistical characterizations of the bee distribution. In the first instance, we should like to distinguish clustering as some kind of non-uniformity. To this end we propose the following χ^2 test which allows us to assess if bees are distributed uniformly on each row of the hive. We define

$$X_U^2(t) = \sum_{y=1}^{y_{max}-1} \frac{(n_y(t) - E)^2}{E}, \quad (3)$$

where $n_y(t)$ is the number of bees in row y at time t , and E is the expected number of bees in each row—assuming a uniform distribution (i.e. $E = |B|/(y_{max} - 1)$). The statistic X_U^2 has a χ^2 distribution with $y_{max} - 2$ degrees of freedom.

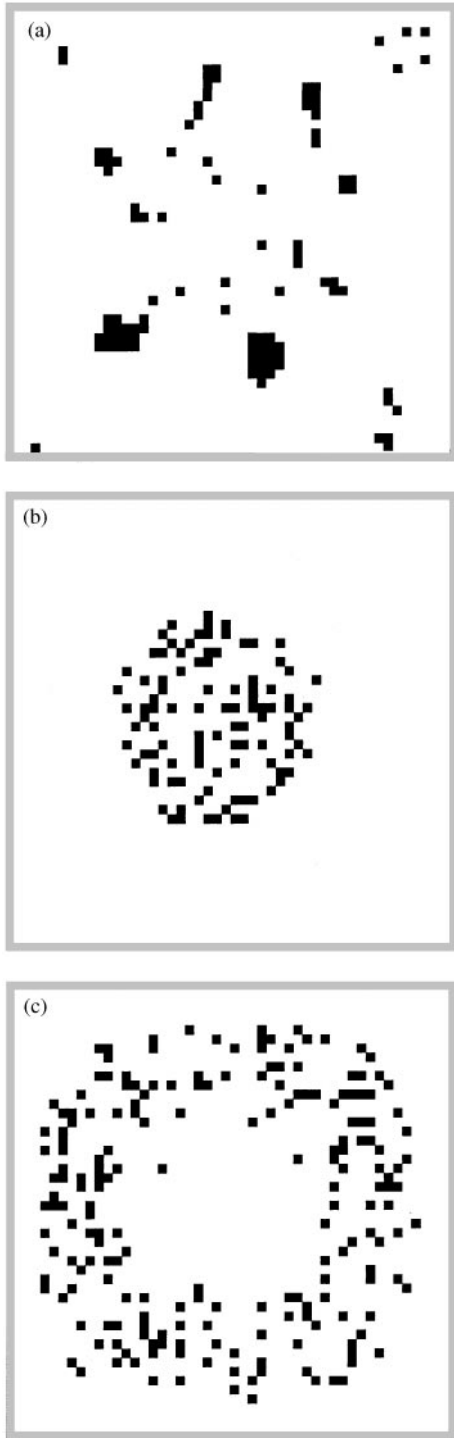


FIG. 1. The equilibrium distribution resulting from simulation runs of 100 or 200 bees at various ambient temperatures. The bees were initially distributed uniformly at random. (a) Droplet clusters: 100 bees at $T_A = 9^\circ$. All bees are inactive. (b) Disc cluster: 100 bees at $T_A = 12^\circ\text{C}$. Over 90% of the bees are active. (c) Ring cluster: 200 bees at $T_A = 13^\circ\text{C}$. Over 90% of the bees are active.

3.1. DROPLET CLUSTERS

When starting the simulation with the bees sparsely distributed and $T_A \leq 12^\circ\text{C}$, the bees can arrange themselves, through some initial activity, into an equilibrium state in which none of them is able to move. Applying the X_U^2 test to the resulting distribution of still bees reveals that they are no longer uniformly distributed across the hive. In fact, nearby bees have moved together to form the small groups we call “droplet” clusters. This situation arises when the heat generated by each individual bee and her immediate neighbours is larger than the heat detectable from any other source. In clusters such as these every bee is below her range of ideal temperatures. In nature, if bees are split into small but relatively close groups outside the hive, it is observed that these groups will remain separate and—in cold weather—the bees within them may enter a chill coma (S. Martin, pers. comm.). This does not occur inside the hive and we note that in our simulation if we repeat the experiment with the bees initially closer together they never appear to come to equilibrium in the droplet state. We also observe that, similarly, if we start with a uniform distribution of bees but reduce the ambient temperature slowly the bees do not end up in the droplet state. This case is discussed in Section 4.

3.2. FORMATION OF ACTIVE CLUSTERS

An important characteristic of ring and disc clusters which distinguishes them from droplets, is that they consist of moving bees. In this section we wish to study the formation of these active clusters. We do this by computing various statistics which summarize aspects of a simulation run. We have already mentioned the first of these, X_U^2 . We now define $N_a(t)$, the number of active bees at time t , as

$$N_a(t) = |\{b \in B : b(t) \neq b(t - \tau)\}|. \quad (4)$$

Taken together these statistics allow us to make a crude distinction between the various clusters which arise—even transiently—during a simulation:

$$\text{Initial distribution} \quad X_U^2 < \chi_{y_{\max}-2}^2(0.05) \quad N_a = 0,$$

$$\text{Droplet clusters} \quad X_U^2 > \chi_{y_{\max}-2}^2(0.05) \quad N_a < \frac{1}{2}|B|,$$

TABLE 1

The mean times, over 20 simulation runs, for 100 bees started uniformly at random to pass to each stage of cluster formation. t_1 is the mean time, in bee step units, till the bees enter a—possibly transient—droplet cluster. Similarly, t_2 is the mean times till the cluster becomes a disc shape. $t_2 = \infty$ implies that the cluster remains as an equilibrium droplet cluster. The $T_A \geq 16^\circ\text{C}$ are sufficiently large that the cluster is spread uniformly across the hive for the duration of the simulation

T_A ($^\circ\text{C}$)	Mean t_1	$T_C(t_1)$ ($^\circ\text{C}$)	Percentage $t_2 = \infty$	Mean t_2 ($t_2 < \infty$)	$T_C(t_2)$ ($^\circ\text{C}$)
8	73.5	8.28	70	2410	22.18
9	79.1	9.36	50	2091	22.02
10	86.8	10.38	45	1863	18.30
11	70.5	11.36	45	1998	18.78
12	74.5	12.40	25	1265	17.93
13	88.0	13.61	0	1263	18.52
14	67.0	14.39	0	909	17.85
15	72.0	15.52	0	609	18.19
16			0	466	17.97
17			0	275	18.02
18			0	0	18.0

Disc and ring clusters $X_U^2 > \chi_{y_{\max}-2}^2(0.05)$

$$N_a > \frac{1}{2} |B|,$$

where $\chi_v^2(\alpha)$ is the value of the χ^2 distribution with v degrees of freedom which is exceeded with probability α . A cluster is deemed to have changed from one stage to another when both conditions are fulfilled for five consecutive time steps.

When the distribution of bees evolves to an active cluster we observe that the bees are able to influence the temperature of their environment. As a measure of this we define the core temperature at time t as $T_C(t) = T_{xy}$ where $(x, y) \in B$ is the position of the nearest bee to (x_c, y_c) , the mean position of all bees. Table 1 summarizes the results of a series of experiments to study the effect of the ambient temperature, T_A , on cluster formation. All the experiments used 100 bees initially distributed uniformly on a 50×50 lattice.

In the table, t_1 is the mean time—averaged over 20 runs—for the system to appear to be in a—possibly transient—droplet state according to the X_U^2 statistic. For $T_A < 16^\circ\text{C}$, these times are essentially independent of T_A . Our interpretation of this effect is that these values of t_1 represent the

time it takes for non-uniformities to develop in the temperature field and for the bees to respond by moving towards each other along the temperature gradients produced. At higher ambient temperatures, $T_A \geq 16^\circ\text{C}$, no transient droplet clusters are seen.

The process of active cluster development is associated with the generation of a non-uniform temperature distribution. In the final stages, this is generally peaked in the centre of the hive. A measure of how far this process has progressed is the difference between T_C —which represents the temperature at the centre of mass of the bees—and the fixed value of the temperature, T_A , at the boundary. In the case of droplet formation, we see that $T_C(t_1) \approx T_A$ indicating that as yet no global pattern has formed in the temperature field.

The rest of table 1 is concerned with passage to the active cluster stages. The time t_2 is defined—similarly to t_1 —as the average time until N_a exceeds half the total bee population. For ambient temperatures in the range $8^\circ\text{C} \leq T_A \leq 12^\circ\text{C}$, t_2 can sometimes be longer than the length of the simulation because the bees form an equilibrium droplet configuration. Whether or not this occurs depends on the random starting configuration.

In calculating the average for t_2 we disregard those runs which resulted in equilibrium droplet states. An arresting fact is that the core temperature at the time the cluster becomes active is, to a good approximation, 18°C, the lower bound of the bee's preferred temperature range. Excepting the lowest values of T_A —where many complications can arise due to the potential stability of droplet formations—this result is independent of the value of T_A . This suggests that the bees cannot form an active cluster until they have heated the hive sufficiently. Naturally, this takes longer at lower ambient temperatures and we find a roughly linear dependence of t_2 on T_A .

These simulations all show that the first active cluster to form is a disc. When the condition $T_C = T_{minI}$ is met, individual bees aiming to achieve their local goal—to be within their preferred temperature range—create the circumstances whereby the global goal of all the bees—to move around an area of the hive freely—can be achieved. Bees inside the disc are within their preferred temperature range and therefore become uniformly distributed across the disc. We find that for small numbers of bees (between 70 and 120 on the 50×50 lattice) this disc shape is an equilibrium.

3.3. FROM RINGS TO DISCS

Figure 1(c) shows that 200 bees at 13°C form a ring rather than a disc. A distinguishing feature of this ring is that the bee nearest to the centre of the cluster will be significantly further away from the centre than if the bees were uniformly distributed on a disc. Let us use this simple observation to develop a statistic which is sensitive to the transition between discs and rings.

Imagine a disc of radius R in which there are $|B|$ bees distributed uniformly. Consider the centre of the disc and draw the smallest circle needed to contain at least one bee. Let this circle have radius r . Since the density is assumed to be uniform this construction gives us a simple measure of the density of the bees $\rho \approx 1/\pi r^2$. Another estimate of the bee density comes from the observation that we have $|B|$ bees in a disc of radius R so that $\rho \approx |B|/\pi R^2$. Equating these shows that $|B|(r/R)^2 \approx 1$ for bees uniformly distributed on a disc.

We define our estimate of $|B|(r/R)^2$ at a given time t as $D_C(t) =$

$$|B| \frac{\min\{(x' - x_c)^2 + (y' - y_c)^2 : (x', y') \in B\}}{(\text{Cluster radius at } t)^2}. \quad (5)$$

When the bees are clustered uniformly in a disc, D_C should be approximately unity and independent of the number of bees. Figure 2 shows the mean core temperature and the mean value of D_C for various numbers of bees once an equilibrium state has been reached. For $70 \leq |B| \leq 120$, D_C is constant and of the order of unity. Observation of the simulation shows that these sized clusters are clearly in a disc shape similar to that shown in Fig. 1(b). As $|B|$ increases beyond 130 the values of D_C grow rapidly, indicating a significant change in the clustering behaviour of the bees. Rather than being uniformly distributed on a disc the bees are now found distributed on a ring. The larger values of D_C show that radius of the circle at the centre of the disc which contains just one bee, r , is an increasing fraction of the radius of the whole cluster, R . Observing the evolution of such clusters from an initially uniform distribution reveals the bees moving through both droplet clusters and disc shapes to finally come to equilibrium as a ring.

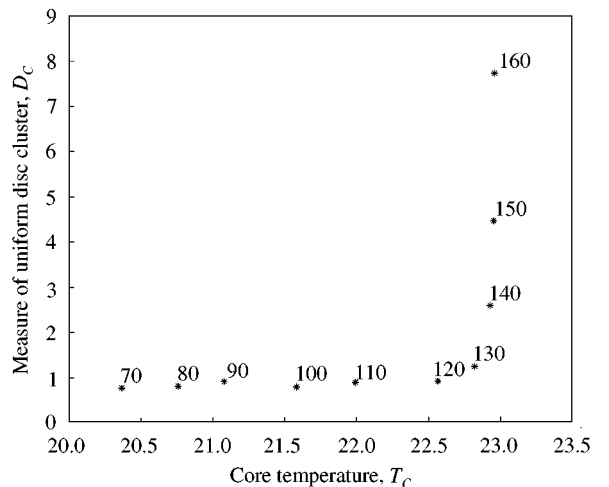


FIG. 2. The mean core temperature, T_C , plotted against the mean D_C , the measure of the nearest bee to the centre of the cluster for differing numbers of bees. These values were obtained by varying the number of bees between 70 and 160 at an ambient temperature of 13°C then running the simulation until the cluster reached equilibrium. The means were found over 5000 bee time steps at equilibrium.

Clusters with a value of D_C inconsistent with a disc shape have a mean core temperature very close to the ideal maximum for an individual bee, $T_{maxI} = 23^\circ\text{C}$. The bees move into a ring rather than a disc because the centre of the cluster is too hot. The cluster shape “adjusts” to keep bees within their ideal range of temperatures. It is interesting to note that real thermoregulating clusters form both uniform disc shapes and rings with higher bee densities on the mantle (Winston, 1987). The simulation demonstrates that these shapes may be formed by individual bees responding only to their local environment. In this sense, it is possible that cluster shape adjustments are entirely self-organized.

4. Low-Temperature Cluster Dynamics

In nature, when a bee’s body temperature drops below $T_{coma} = 8^\circ\text{C}$ she goes into a chill coma (Winston, 1987). We cannot, therefore,

sensibly study the formation of clusters at ambient temperatures below T_{coma} . In order to examine behaviour at these temperatures, we begin a simulation of 100 bees at a high ambient temperature and gradually lower it to values of T_A between 0 and 8°C . To reduce transient effects, we let each simulation run for 10 000 bee time steps, for each value of T_A , before making any observations.

Figure 3 shows the mean mantle and core temperatures and cluster width plotted against ambient temperature for clusters presumed to be at equilibrium. In real bee nests, as ambient temperatures fall, clusters contract reaching a minimum size at $T_A \approx 0^\circ\text{C}$ (Seeley & Heinrich, 1981). They then exhibit a rise in core temperature accompanied by continued decrease in mantle temperature. Our simulation reaches minimum width at $T_A \approx 9^\circ\text{C}$. Below this temperature it exhibits the increase in core and decrease in mantle temperatures consistent with observations.

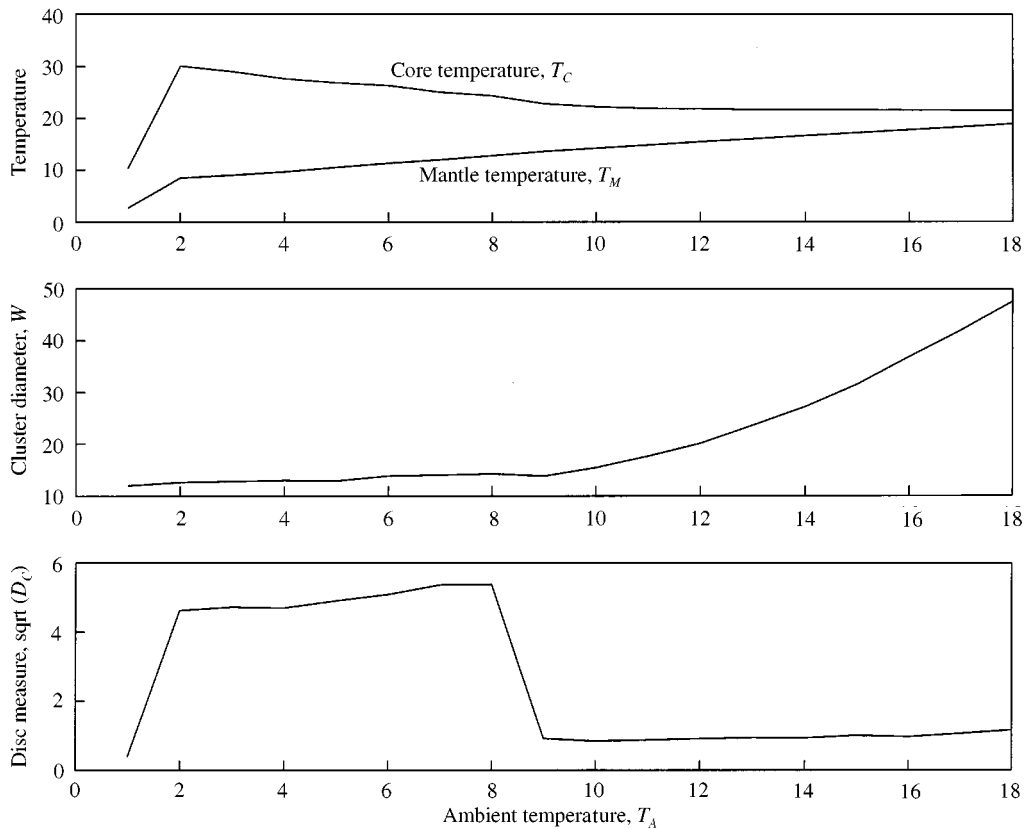


FIG. 3. Mean core temperature (T_C), mantle temperature (T_M), cluster width (W) and the mean value of the D_C test plotted against ambient temperatures.

Although we see increases in core temperature which agree qualitatively with observations of natural bee clusters, our model takes no account of the wing muscle “shivering” mechanism which individual bees employ at ambient temperatures below 0°C (Seeley & Heinrich, 1981). A similar heating effect to ours is observed in Watmough and Camazine’s model, where core temperatures begin increasing as T_A drops below 7.5°C , well above the onset of shivering. These results suggest that an increased core temperature need not be solely a consequence of shivering. Rather we see that it can be a consequence of a positive feedback mechanism; the increased insulation efficiency of a tight cluster of bees leads to a warming effect which in turn increases the heat production since the metabolic rate of the bees is an increasing function of temperature. Indeed, such a feedback mechanism—reminiscent of neutron-induced radioactive decay—could lead to catastrophic temperature increases if it were not for some mitigating mechanism such as, for example, the bees rearranging the configuration of the overheated cluster, thereby allowing it to cool.

4.1. A PULSATING CLUSTER

Once the cluster width reaches a lower limit and the core temperature exceeds 23°C ($T_C > T_{maxI}$) the cluster is no longer a uniform disc (see the mean value of D_C in Fig. 3). Further investigation reveals that unlike the ring cluster observed with larger numbers of bees, the shapes formed in the present case are no longer stable (i.e. they change in time). Figure 4 shows four different shapes observable in a cluster of 100 bees at an ambient temperature of 4°C . The cluster is seen to pulsate as it continuously cycles through these shapes.

The cluster has entered into a *behavioural cycle*. This is not caused by any changes in external conditions but by the behaviour of the individuals in the cluster. Figure 5 shows plots of core and mantle temperatures, bee activity and the number of hot, cold and happy bees over time. Seven complete behavioural cycles can be observed in the plot. In each cycle, we usually observe an initial period of activity with up to 50% of the bees active and the cluster shape is

a disc (shape D in Fig. 4). During this period the core temperature, $T_C \approx T_{maxI}$. However, as the core temperature increases above T_{maxI} the bees move into a ring shape (shape A). The density of bees in the ring is much greater than in the uniform disc and activity drops. The core temperature continues to climb rapidly while the mantle temperature climbs more slowly. Once the mantle temperature rises sufficiently, there is a second smaller peak in activity as the bees on the mantle move outward. This leads to a rapid drop in core temperature since the insulating shape of the ring is temporarily lost as the structure changes. The new structure is similar to shape B in Fig. 4. This shape gives a slower decrease in core temperature and activity is very much reduced. The time for this drop is variable—contrast, for example, the fourth and fifth cycles of Fig. 5—but the rate of heat loss increases as shape B changes to shape C. As the core temperature nears T_{maxI} activity in the cluster increases and the behavioural cycle repeats.

The cycles are of various lengths and not always clearly defined. For example, at the beginning of the second and third cycles the core temperature starts to increase but then decreases again resulting in another activity spike. It is difficult to surmise from the data (or even from direct observation of the simulation) exactly why this occurs. However, since there is a random element in the bee movements it is possible that the positioning of a few individual bees caused the cluster to adjust into a shape which begins to lose heat before a tight ring is formed. This example serves to show that these simple individual bee agents can produce an array of different behaviours, arising both from the randomness in the model and the inherent complexity of the individuals’ interactions.

We know of no observations of such large temperature fluctuations in natural colonies, but there is some preliminary evidence to suggest the possibility of much smaller, regular fluctuations (between 0.1 and 0.2°C) (S. Martin, pers. comm.). Our simulations also show fluctuations in activity and there is more evidence for this in natural colonies. Honey bees are reported to periodically break the cluster, with bees on the mantle entering the core (Winston, 1987). This behaviour has been attributed to the bees in the core allowing

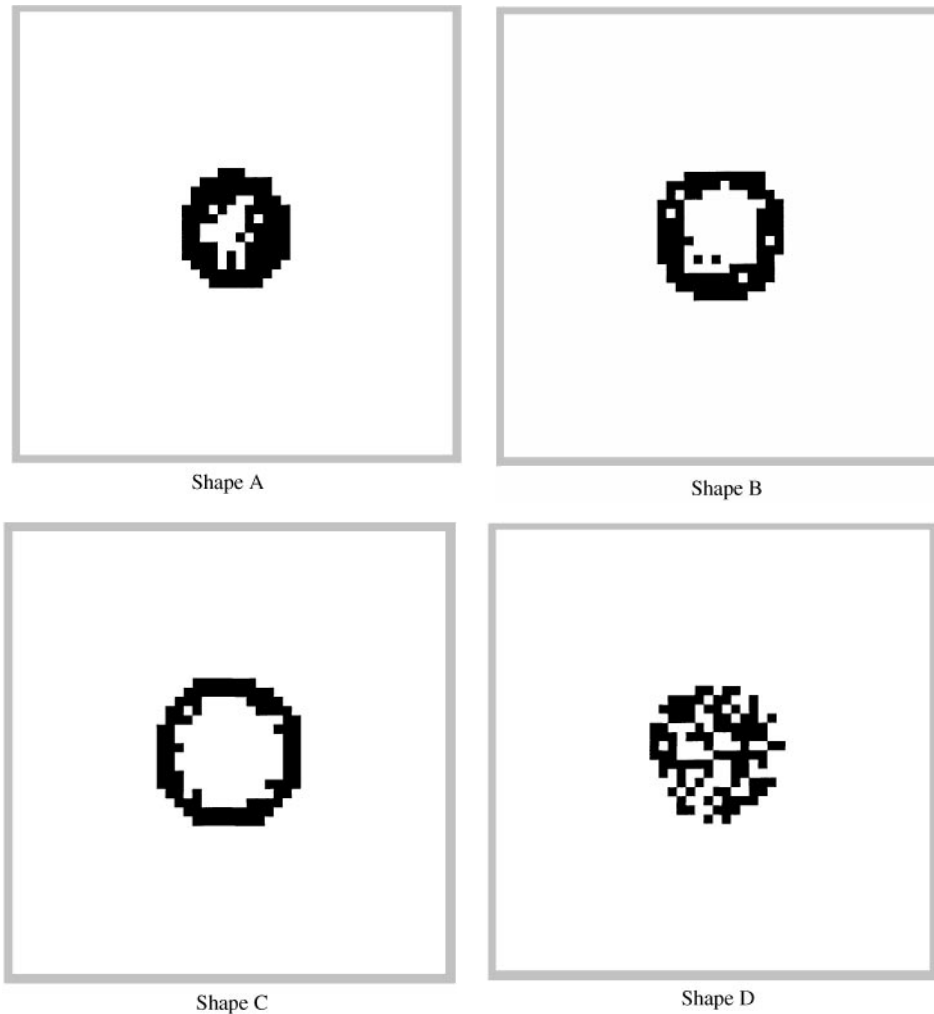


FIG. 4. Cluster shapes found for 100 bees at $T_A = 4^\circ\text{C}$. The cluster cycles through A, B, C and D. The cluster starts tightly packed as in A. This shape leads to fast increases in core temperatures until the cluster expands to shape B, where the core temperatures reach a maximum. In shape B the core temperature falls, falling more rapidly as the cluster expands to shape C. When the core temperature nears T_{maxI} the cluster breaks into activity and shape D is seen. The cycle then repeats as bees become more tightly packed in shape A again.

bees on the mantle to feed on honey (Heinrich, 1981) and increase their body temperature (Winston, 1987). Since our simulation includes no such “altruistic” rules, it suggests that some of the observed breaking and reforming of clusters could actually be a consequence of the interaction between the geometry of the bee cluster and the diffusive heat loss mechanism.

4.2. AMBIENT TEMPERATURES BELOW 0°C

In the pulsating cluster with 100 bees, we find that as the ambient temperature falls the number of bees involved in the bursts of activity

decreases. At 8°C , during a burst of activity, up to 70% of the bees are active. This activity is distributed uniformly throughout the disc (i.e. $D_C \approx 1$). At 3°C , the activity peaks usually involve only 30 bees. At such low ambient temperatures and activities the bees in the cluster are subject to an extreme range of temperatures: those in the core get very hot and those on the mantle become very cold.

Temperatures of 50°C are lethal to honey bees (Heinrich, 1996). If we introduce a maximum temperature at which a bee can remain alive (say, 50°C) then for differing values of the bee insulation parameter, λ_{bee} , the core may overheat with

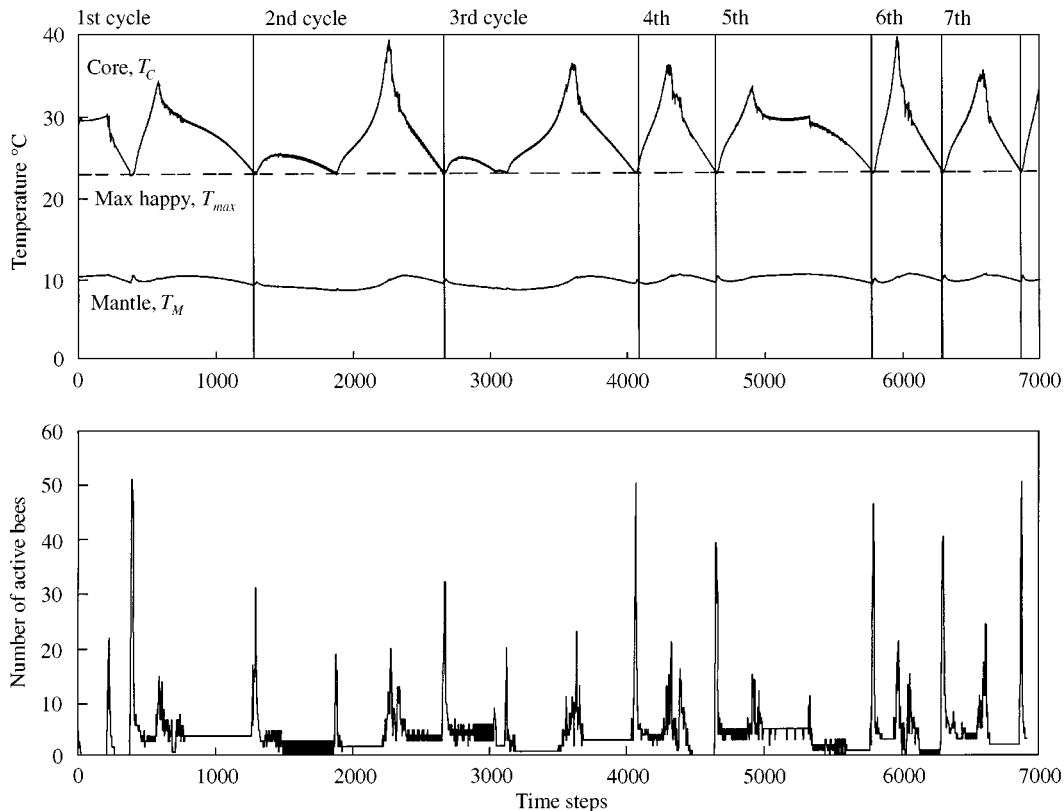


FIG. 5. Plots of core temperature (T_C), mantle temperature (T_M) and bee activity (N_a) as a function of time at 4°C obtained from simulations using 100 bees.

some bees dying or the mantle may become so cold that the bees will fall into a “chill-coma”. A combination of these may also occur with some bees overheating and dying, thus generating no more heat and leading to bees on the mantle entering “chill-coma”. Independent of the value of λ_{bee} the clustering will cease to keep the bees alive at $T_A \approx 1^\circ\text{C}$.

5. Discussion

Partial differential equation models of thermoregulation, which are based on the assumption that bee clusters are spherical, show that the bees may arrange themselves into rings as well as discs (Watmough & Camazine, 1995). Our model here exhibits ring and disc formation without the need to assume an initially spherical cluster. Furthermore, we are able to identify a condition—that the core temperature exceeds the ideal minimum individual bee temperature, T_{minI} —which the bee colony must fulfill in order to spontaneously gen-

erate a single disc of active bees. When the core temperature exceeds the ideal maximum individual bee temperature, T_{maxI} , our model shows that the bees form a ring rather than a disc. These parameters, T_{minI} and T_{maxI} , are therefore of great significance and it would be of interest to see if they can be estimated experimentally. We might expect that these parameters represent some kind of optimum working range determined at the colony level and that they lie well within the range of temperatures at which an individual bee can survive. Considering the essential role that thermoregulation plays in the survival of the colony, the actual values of these temperatures should be understood in the light of natural selection at colony level (Seeley, 1995).

A notable feature of our simulations is that it is possible for clusters to pulsate. In this paper, we have focused on describing a single set of computer experiments; however, we see pulsation over a wide range of parameter values. In particular, provided that the density of bees on the

lattice is relatively low, our preliminary studies indicate that increasing the number of bees in the simulation (we have used up to 2000 bees) does not suppress pulsation. Our understanding of this phenomenon, which is based on bee movements changing the surface area of the cluster, leads us to think that it is something that could be reproduced in continuum models. It would be interesting, therefore, to investigate the possibility of Hopf bifurcations in existing differential equation models of thermoregulation. Such an investigation might give us insight into the role played by the discrete nature of bees in the thermoregulation mechanism.

The experimental observation that bees on the mantle are periodically allowed into the centre of the cluster does indicate the possibility of pulsating clusters. Previously, it has been suggested that cluster breaking is due to the bees feeding and is accompanied by a small rise in ambient temperature. It would be interesting to see experiments at fixed ambient temperatures which measured profiles of cluster temperature and related them to the movement of individual bees. Observations of periodic fluctuations in core and mantle temperatures without corresponding changes in ambient temperatures would provide support for our model. We would hope that such experiments—whatever the outcome—would increase understanding of thermoregulation and provide impetus for new models.

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APPENDIX A

Summary of Symbols

From the Formal Model in Section 2

t	time
(x_{max}, y_{max})	size of the temperature field or hive

B	set of all bees ($ B $ denotes the number of bees in B)	T_A	ambient temperature
$b(t) \in B$	pair (x_b, y_b) of bee coordinates	<i>From the Statistical Tests in Sections 3 and 4</i>	
T_{coma}	lowest temperature at which a bee can move	X_U^2	χ^2 test for the uniform distribution of bees across the hive
(T_{minI}, T_{maxI})	range of temperatures within which each bee wishes to remain	N_a	number of active bees
T_{maxI}	$\frac{1}{2}(T_{minI} + T_{maxI})$	T_C	temperature in the cluster core
τ	time it takes for a bee to make a single discrete movement	D_C	distance to the cluster core to the nearest bee
$T_{xy}(t)$	temperature field from which a bee ascertains her temperature	T_M	temperature in the cluster mantle
$T_{xy}^g(t)$	temperature field from which heat diffusion is updated	W	cluster width
g	granularity of diffusion	APPENDIX B	
λ_{bee}	insulation factor for a single bee	Standard Simulation Parameter Values	
λ_{air}	insulation factor for air	Hive and colony	$(x_{max}, y_{max}) = (50, 50)$ and $ B = 100$
$\Delta^2(x, y, t)$	Laplacian difference operator for diffusion	Bee behaviour	$T_{coma} = 8$, $T_{minI} = 18$ and $T_{maxI} = 23$
$f(x, y, t)$	heat generated by bee per time step	Diffusion rate	$\tau = 8$ and $g = 2$
h_{q20}	temperature increase made by a passive bee at 20°C	Bee insulation	$\lambda_{air} = 1.0$ and $\lambda_{bee} = 0.45$
		Heat generation	$h_{q20} = 0.0037$