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Collective ventilation in honeybee nests

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European honey bees (*Apis mellifera*) live in large congested nest cavities with a single opening that limits passive ventilation. When the local air temperature exceeds a threshold, the nests are actively ventilated by bees fanning their wings at the nest entrance. Here, we show that colonies with relatively large nest entrances use an emergent ventilation strategy where fanning bees self-organize to form groups, separating regions of continuous inflow and outflow. The observed spatio-temporal patterns correlate the air velocity and air temperature along the entrances to the distribution of fanning bees. A mathematical model that couples these variables to known fanning behaviour of individuals recapitulates their collective dynamics. Additionally, the model makes predictions about the temporal stability of the fanning group as a function of the temperature difference between the environment and the nest. Consistent with these predictions, we observe that the fanning groups drift, cling to the entrance boundaries, break-up and reform as the ambient temperature varies over a period of days. Overall, our study shows how honeybees use flow-mediated communication to self-organize into a steady state in fluctuating environments.

1. Introduction

Many animal groups are able to solve complex problems using the collective action of many individuals that have access only to local information. These problems often involve spatial scales that are orders of magnitude larger than individuals that typically can sense and respond only locally. Thus, collectively organized solutions to problems such as complex navigation [1], predator avoidance [2] and distributed foraging [3] arise from the active interactions between individuals, which allow locally sourced information to be integrated by the group [4].

Social insects provide many such examples of collective problem-solving in the context of foraging recruitment [5], nest site selection [6] and nest building [7]. Colonies of social insects also perform physiological functions at the colony scale. For instance, honeybee clusters (greater than 10^3 individuals) and army ant bivouacs (up to 10^4 – 10^5 individuals) maintain relatively stable internal temperatures despite dramatic fluctuations in ambient temperature [8–13]. This collective thermoregulation is achieved by modulating the global morphology of the aggregate as a function of the metabolic heat production by individuals [10,14]. Social insects often must coordinate graded responses to fluctuating environmental stressors. These graded responses are often described by response threshold models in which individuals are assumed to execute a given response (e.g. brood incubation or wing fanning) when a stimulus (e.g. temperature) exceeds or falls below the individual's response threshold [15]. Inter-individual variation in thermoregulatory response thresholds allows honeybee and bumblebee colonies to maintain stable temperatures over a broad range of temperatures [16–18].

Many of these behaviours are organized by a process called stigmergy in which individuals interacting with a common environment can lead to an emergent scheme or pattern without direct interaction [19]. In classical examples of stigmergy, individuals deposit static cues in the environment such as pheromones, food stores or building materials that influence future behaviours by

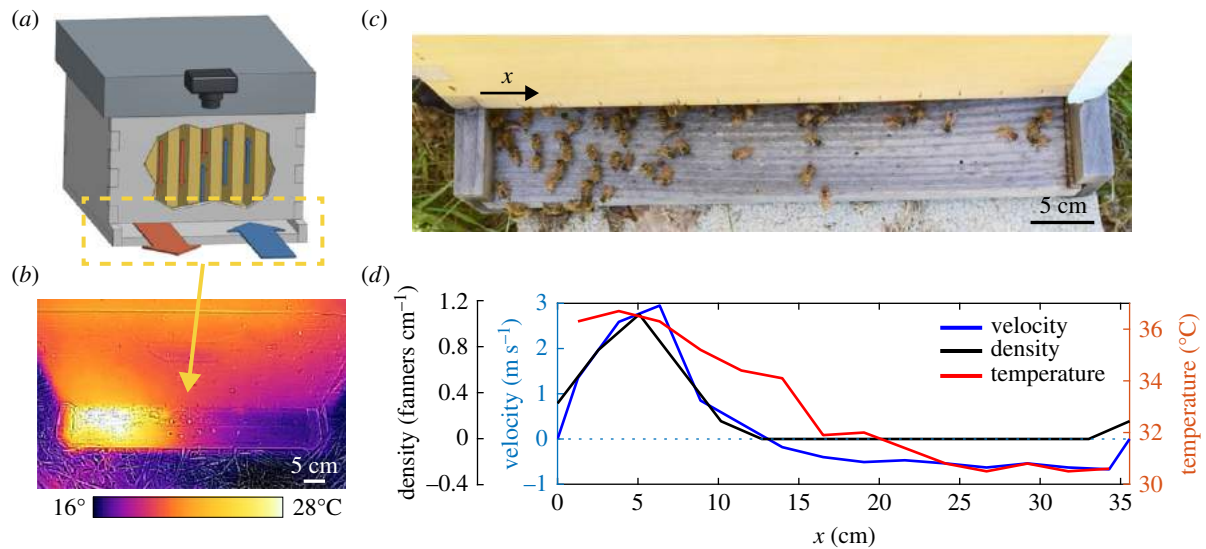


Figure 1. (a) A schematic illustrating the path of air through the hive as induced by fanning bees. Warm, stale air is drawn out of the entrance by fanning bees and relatively cool ambient air enters passively where fanning bees are absent. The camera indicates the viewing angle in (b) and (c). (b) A thermal image of the hive entrance at night when fanning bees are actively fanning. Notice inflowing air at the right of the entrance has cooled the wood and the outflowing air induced by fanning bees on the left has warmed the wood. (c) Honeybees ventilating at the entrance of a hive. Note the dense group of fanning bees at the left of the entrance and the lack of fanning bees at the right of the entrance. (d) The air velocity (blue) and temperature (red) along the nest entrance of a hive. Note that inflow is indicated by negative values and outflow is indicated by positive values. These data demonstrate that the temperature profile along the entrance can be used as a qualitative proxy for flow velocity. (Online version in colour.)

other individuals through positive feedback or recruitment which lead to the emergence of pheromone trails or architectural features such as walls, piles or pillars [4]. In a less commonly studied class of behaviours, individuals interact with a dynamical physical process, such as flow, to structure their behaviour. Experiments on corpse clustering by the ant *Messor sanctus* [20] and nest tube blocking in leaf-cutting ants *Acromyrmex ambiguus* [21] have demonstrated that depositing materials in the environment can modify airflow, which can in turn influence future depositions. Several theoretical studies have suggested that if an individual-level behaviour is responsive to flow-mediated cues and such behaviours manipulate flow, global behaviours can arise that control this flow for adaptive functions such as ventilation or thermoregulation [14,22,23].

A particular instance of this local–global behaviour is seen in the context of thermoregulation and ventilation in European honeybee *Apis mellifera* colonies (greater than 10 000 bees) that often live in congested enclosures such as tree hollows or other pre-existing cavities, where they face the continuous challenge of maintaining relatively stable temperatures (approx. 35–36°C) and respiratory gas concentrations [24,25]. Active ventilation is a natural solution to both problems as it circumvents the limits imposed by impervious walls, small entrances (relative to nest volume) and large colony size. Groups of honeybees near the entrance achieve this by actively pulling air out of the nest by fanning their wings, causing air to be sucked out of the nest [12,26–28]. The resulting colony-level gas exchange with the environment prevents build-up of heat and CO₂ within the nest [29,30]. For this to work over long times requires that air drawn from the nest must be balanced by air flowing into the nest. Seeley & Morse [24] measured the area of entrances of more than 30 feral colonies with entrance sizes varying from 10 to 100 cm². These natural nests also varied substantially in shape, some having a low aspect ratio akin to circular knot-holes and others having a

high aspect ratio akin to slender tree-cracks. Later, Southwick & Moritz [31] observed that colonies in hives with small round entrances (2 cm diameter, 3.14 cm² area) exhibit tidal ventilation in which honeybees actively draw air out of the nest entrance for a while and then stop, allowing air to passively flow back into the nest. Either entrance geometry would allow for air flow in and out; however, small entrances are more likely to favour temporal modulation of flow, while large entrances are likely to favour spatial modulation. Since nest entrances in feral colonies have a range of shapes and sizes that span more than an order of magnitude, a natural question is when and how temporal modulation of in/outflow gives way to the spatial modulation of ventilation dynamics in nests with moderate to large entrances.

2. Experimental observations

To answer this question, we quantify the fanning behaviour of bees at a large nest entrance shown schematically in figure 1a. We used four Langstroth beehives (801, 20 000–40 000 bees each) with a single slit-like rectangular nest entrance (2 cm × 36 cm) that we monitored over time. In order to quantify the influence of the distribution of fanning bees along the entrance on the induced flow pattern, we counted the number of fanning bees in each of 15 bins along the entrance (see figure 1d; electronic supplementary material, Movie S3). Although there are fanning bees just inside the entrance, we counted only the visible ones, which serve as a proxy for local fanning intensity. Simultaneously, we used a VelociCalc anemometer to measure the flow speed perpendicular to the entrance at the boundaries between the bins, with flow being positive outwards, and negative inwards. Flow direction was measured by placing a wool fibre at each position; if its motion was imperceptible or non-directional, no velocity value was recorded (see electronic supplementary material, Movie S1). A

thermocouple attached to the tip of the anemometer allowed us to measure the temperature at each location, which can also be qualitatively visualized using an infrared camera (figure 1b). All measurements were carried out five times a day over the course of three consecutive days. In figure 1d, we show the density of fanning bees, air velocity and air temperature as a function of the position along the entrance for one of the hives observed (see electronic supplementary material, figures S1 and S2—for the complete dataset involving multiple bee colonies).

We observed correlated variations in density, velocity and temperature at the entrance across space and time. In contrast with the observed rapid temporal modulation of ventilation behaviour in nests with small openings [31], our observations show that for larger entrances, ventilation behaviour is spatially modulated (i.e. in/outflow separated in space) but temporally steady, at least over times when the ambient temperature was steady. This dynamic adaptation to the physiological needs of a colony demands a dynamic explanation that links the behaviour of individuals distributed at the hive entrance to the observed correlations between fanner density, air velocity, and air temperature in space and time.

3. Mathematical model

Honeybee colonies show broad inter-individual variation in the temperature thresholds that induce fanning, in part because of their high genetic diversity [18,32]. This variation can lead to emergent task allocation via the so-called task threshold model [15], which states that when the demand for a task is large, more individual bees will respond due to the broad variation in the task thresholds [32]. This variation is higher in colonies with a queen which has mated multiple times [18], and promotes the temporal stability of thermoregulation. Furthermore, honeybees that are heated in a laboratory setting are more likely to fan at a given temperature when they are in a group than when they are alone [32]; independent of group size, individuals showed broad variation in temperature thresholds. In the largest group size considered (10 individuals), the mean temperature at which bees begin to fan was near the preferred hive (i.e. brood) temperature (approx. 36°C). While there are computational fluid dynamics models of airflows within a Langstroth beehive [33], they consider flows driven by metabolic heat generated by clusters of bees within the nest (up to 0.03 m s⁻¹ at the nest entrance), and do not account for the active ventilation dynamics seen in experiments. Here, we show how a minimal model of active ventilation driven by local sensing and actuation allows us to understand how the flows driven by fanning honeybees (up to 3 m s⁻¹) are globally organized at the nest entrance.

Our minimal framework for the spatio-temporal organization of fanning starts by characterizing the local fanning response of individual bees to the local air temperature. We must also account for fluid flow which is induced by the bees and which carries the signal to which the bees are responding (i.e. heat derived from the nest). For simplicity, we consider the case when the hive and environmental temperatures are constant and focus on the dynamics of the bees at the entrance. To link bee behaviour, air temperature and airflow we need to quantify how (i) the

distribution of fanning bees, $\rho(x, t)$, (ii) the local air temperature, $T(x, t)$, and (iii) the local flow velocity, $v(x, t)$ vary with time t along the nest entrance. Because the nest entrance in this hive has a high aspect ratio (short but wide) we can model the entrance x as a one-dimensional line (figure 2a).

Consistent with the task threshold model, we assume that the probability of a bee stopping and initiating fanning behaviour is determined by the local temperature [32]. Therefore, the local density of fanning bees, $\rho(x, t)$ changes according to the equation

$$\frac{\partial \rho}{\partial t} = k_{\text{on}}(T) - k_{\text{off}}(T), \quad \rho(x, t) \in [0, \rho_{\text{max}}], \quad (3.1a)$$

where k_{on} is the rate at which bees initiate fanning behaviour, k_{off} is the rate at which they cease fanning behaviour and ρ_{max} is the maximum density achievable (given spatial constraints at the nest entrance). These rates are assumed to be sigmoidal functions of the local air temperature, i.e.

$$k_{\text{on}} = k_0 \frac{\tanh(m(T - 36^\circ\text{C})) + 1}{2} \quad (3.1b)$$

and

$$k_{\text{off}} = k_0 - k_{\text{on}}, \quad (3.1c)$$

where k_0 is an inverse time scale of the order of a few seconds, and m controls the slope of the sigmoidal function (figure 2b), and is fit to approximately reproduce the variation in observed temperature thresholds [32] (see electronic supplementary material). Although recent studies of fanning behaviour in controlled laboratory settings suggest that the thermal response thresholds for fanning are affected by group size [32], the presence/absence of larvae [34] and heating rate [35], our minimal representation of the fanning response as a switch-like behaviour allows us to focus on the interaction with airflow and temperature. We note that the parameter m is the only behavioural parameter in our model and it controls the range over which organized ventilation can occur. It is likely that natural selection has acted on the inter-individual variation in fanning thresholds to ensure efficient ventilation over the range of temperatures experienced by the bees.

To characterize the air flow, we assume that each bee generates an outward air flow with velocity v_b . Because the nest has just one opening, air that is actively drawn from the entrance must be balanced by air flowing passively into the entrance elsewhere in order to ensure conservation of mass. Flow conservation at the entrance demands that (see electronic supplementary material for a simple derivation of this relation)

$$v(x, t) = l_b v_b \left[\rho(x, t) - \frac{1}{L} \int_0^L \rho(x, t) dx \right] + D_v \frac{\partial^2 v(x, t)}{\partial x^2}, \quad (3.2)$$

where D_v is a scaled momentum diffusivity (with dimensions of squared length), L is the size of the nest entrance, l_b is a characteristic length scale derived from the fanning driven pressure gradient and fluid friction. The first two terms characterize the difference in the local density of fanning bees from the average density over the entire length of the entrance and conserve the volume of air in the hive (since the net flow rate vanishes). The last term is associated with local fluid friction and ensures that fanning behaviour not only drives local flow but also entrains the airflow laterally, and penalizes large velocity gradients, e.g.

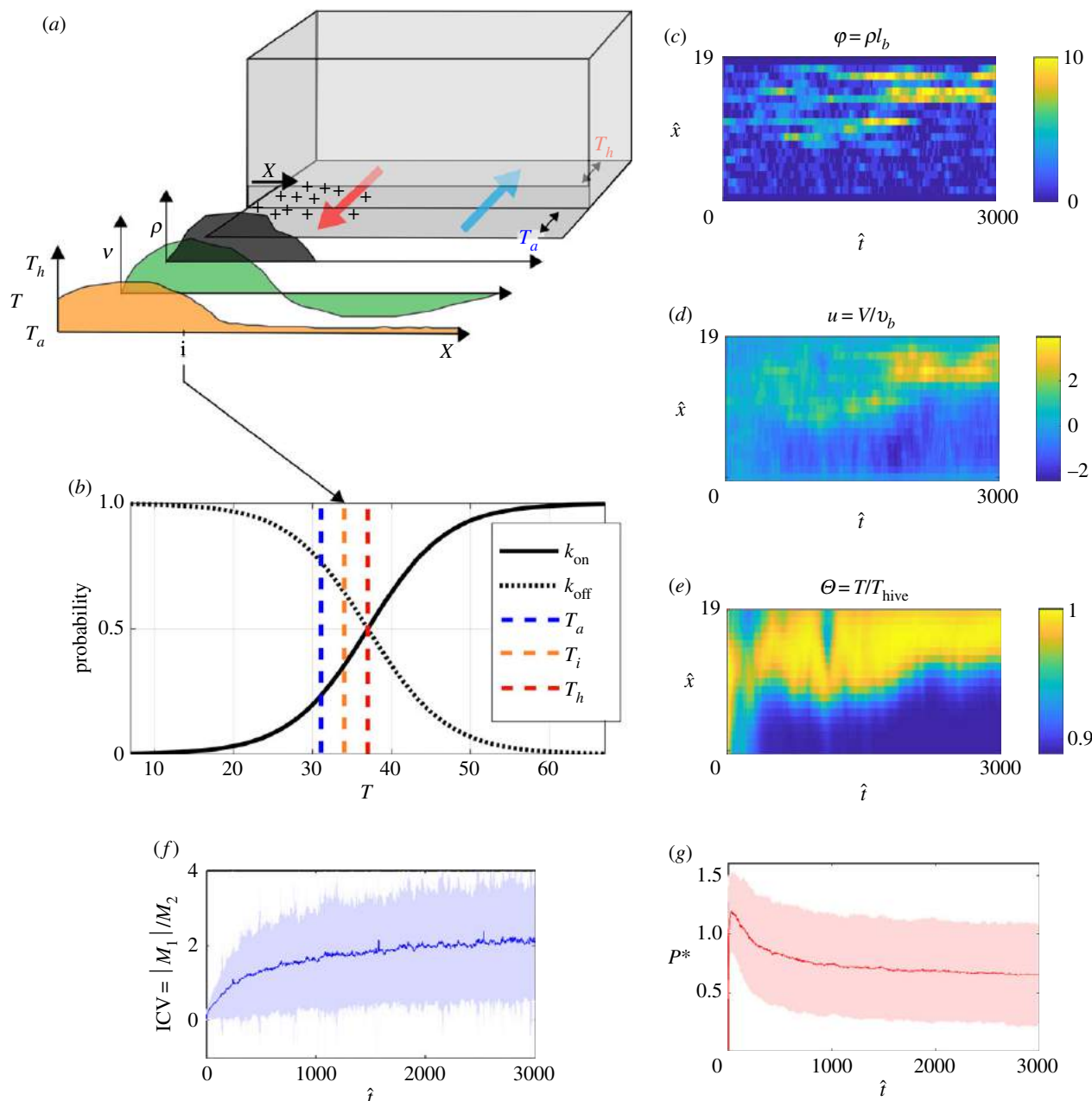


Figure 2. Theoretical model and numerical simulations. (a) The model relates the density of fanners $\rho(x, t)$, air velocity $v(x, t)$ and air temperature $T(x, t)$ as a function of location along the nest entrance x at time t . Air drawn from the entrance by the bees has a positive velocity. ‘+’ symbols denote the position of individual fanning bees. In reality bees can be positioned inside the nest entrance or outside the nest entrance. For simplicity, we consider the density of fanning bees ($\rho(x, t)$) along a line representation of the nest entrance (x). (b) The probability that a bee will begin (stop) fanning k_{on} (k_{off}) is high at high(low) temperatures and low at low(high) temperatures. (c) The density of fanning bees $\rho(x, t)$, (d) local air temperature $v(x, t)$ and (e) the local air velocity over the first 1000 steps of a representative numerical simulation, with initial conditions corresponding to a uniform fanner density, the hive temperature 36°C along the entire entrance and no initial velocity. Ambient temperature was fixed at 28°C . (f) The mean inverted coefficient of variation (ICV) is plotted for the first 3000 time steps of 1000 simulations. Error bands indicate standard deviation. High ICV indicates that fanners are highly clustered. (g) The scaled power P^* lost to friction throughout the simulation. As fanners become more clustered, the amount of fluid friction is reduced, indicating that self-organization leads to increased ventilation efficiency. Here, \hat{x} and \hat{t} are dimensionless measures of length x and time t ($\hat{x} = x/l_b$, $\hat{t} = tv_b/l_b$). (Online version in colour.)

reversals in flow direction. Together, the global inhibition from conservation of volume and lateral flow entrainment due to friction may lead to emergent spatial patterning (for a detailed description see electronic supplementary material, figure S10).

Finally, to characterize the dynamics of the local air temperature along the entrance, we assume that air temperature is governed by the local velocity and temperature difference between the entrance temperature and the upstream temperature, and can be described by a

modification of Newton’s law of cooling (neglecting complex flow dependences, see electronic supplementary material):

$$\frac{\partial T(x, t)}{\partial t} = -cv(x, t)\Delta T + D_T \frac{\partial^2 T(x, t)}{\partial x^2} \quad (3.3)$$

$$\text{and} \quad \Delta T = \begin{cases} T - T_h, & \text{if } v \geq 0 \\ T_a - T, & \text{if } v < 0, \end{cases}$$

where c is a characteristic inverse length (chosen so that Newtonian cooling due to fanning dominates lateral diffusion), T_a

and T_h are the ambient and hive temperature and D_T is the thermal diffusivity.

The variables in our model can be rescaled using the following definitions: $\hat{x} = x/l_b$, $\hat{t} = tv_b/l_b$, $u = v/v_b$, $\phi = \rho l_b$, $\Theta = T/T_h$, which leads to a dimensionless set of our original equations with four dimensionless parameters: (i) L/l_b , a dimensionless measure of the entrance length, (ii) D_v/l_b^2 , a measure of the effect of fluid friction, (iii) $D_T/v_b l_b$, a scaled thermal diffusivity (inverse Peclet number), and (iv) cl_b , a length scale associated with bee fanning. In addition, we have two parameters that characterize each of the sigmoids associated with the switching of the fanning response (see electronic supplementary material for scaled equations and boundary conditions).

To complete the formulation of the model, we need to specify boundary conditions for the temperature and velocity of the airflow. The air velocity v is assumed to be zero at the ends of the nest entrance, while the temperature was assumed to satisfy the Robin boundary condition

$$\alpha(T_0 - T_a) + (1 - \alpha)l_b \frac{\partial T}{\partial x} \Big|_{x=0} = 0, \quad (3.4)$$

where T_0 is the temperature at the boundary and α is a dimensionless parameter that we use to characterize the thermal conductivity of the boundary (i.e. the walls on either side of the entrance): $\alpha = 0$ corresponds to the a perfectly insulating boundary while $\alpha = 1$ corresponds to a perfectly conducting boundary (see electronic supplementary material, figure S5).

Together, equations (3.1)–(3.4) along with the initial and boundary conditions above form a mixed elliptic-parabolic system for the dynamics of ventilation coupled to an ordinary differential equation for the density of fanner bees. We used Matlab to solve the initial boundary value problem using a centred finite difference scheme in space and a simple Euler method in time (see electronic supplementary material and code) using the following values for the parameters: width of the nest entrance $L = 0.38$ m, wingspan of a bee $l_b = 0.02$ m, air velocity generated by an individual fanning bee $v_b = 1$ m s⁻¹ [36]. The diffusion coefficients D_v and D_T were fit to match observed behaviour ($D_v = 1 \times 10^{-3}$ m² and $D_T = 5 \times 10^{-5}$ m² s⁻¹; see electronic supplementary material, figure S3 for a sweep of these parameters). All simulations were executed with the following initial conditions: (1) fanning bee density initially given a uniform distribution with one fanning bee per bin (1 bin = l_b), (2) local air velocity was zero along the length of the entrance, (3) and the local air temperature was initially T_h .

Fanning bees initially formed multiple clusters allowing for spatial separation of inflow and outflow (figure 2c). The light (yellow) regions in figure 2c–e denote areas in which fanning bees actively draw warm airflow from the nest. The dark (blue) regions denote cooler regions where bees are not fanning and air passively enters the nest to balance the active outflow driven by fanners. Over time, several dominant clusters grew as other smaller clusters petered out (figure 2c). By $\hat{t} = 2000$ (approx. several minutes), a single dominant cluster emerged leading to one region of outflow and one or two regions of inflow. This condition appeared to be stable, however, when the simulations were run over longer times, $\hat{t} > 10^4$ (approx. several hours), the dominant cluster drifted in space. We quantified this clustering of fanning bees using the inverse of the coefficient of variation (ICV) of the density

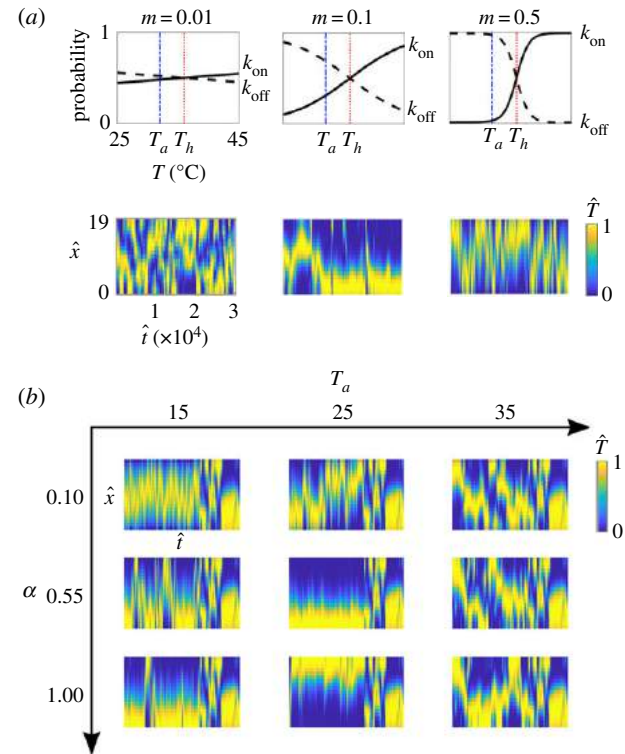


Figure 3. (a) Effect of slope of behavioural switch functions on ventilation dynamics for a fixed ambient temperature, $T_a = 32$. $k_{on}(T)$ and $k_{off}(T)$ prescribe the probability of a given bee to begin fanning or cease fanning at a given local air temperature. The slope of these functions is controlled by the parameter m . In the colourmap \hat{T} is the normalized temperature. (b) Effects of ambient temperature T_a and boundary conductivity α on ventilation dynamics. The parameter α controls the thermal conductivity of the boundaries of the nest entrance. When α is near 0, the boundary is perfectly conductive and the position of fanning bees and the warm outflow that they generate tends to be found near the centre of the nest entrance. When α is near 1, the boundary is perfectly insulated. Under this condition, the bees tend to fan more at one boundary of the nest entrance or the other. $\hat{x} \in [0, 19]$ and $\hat{t} \in [0, 3 \times 10^4]$. (Online version in colour.)

of fanning bees, i.e. $ICV = |M_1|/M_2$, where M_i is the i th moment of the density. If ICV is large, the bees are highly clustered. We also quantified the amount of power lost to fluid friction using the dimensionless parameter $P^* = \int (\partial u / \partial \hat{x})^2 d\hat{x}$. As shown in figure 2f, 2g, clustering of fanners was inversely related to the amount of fluid friction in the system, suggesting that self-organization leads to more efficient ventilation by reducing friction (or shear) at the nest entrance.

To explore the role of m , the parameter which controls the variation in the temperature threshold associated with the behavioural switch functions k_{on} and k_{off} , we carried out representative simulations for various values of m and a fixed ambient temperature, $T_a = 32^\circ\text{C}$. In figure 3a, we see that when m is extremely low ($m = 0.01$), fanning behaviour is weakly coupled to temperature and no distinct fanning group forms. Temperature is normalized at each time step, $\hat{T} = (T - T_{min}) / (T_{max} - T_{min})$. When m is extremely high ($m = 0.5$), fanning behaviour occurs only over a narrow range of temperatures. At moderate m ($m = 0.1$), a stable fanning group forms over a broad range of temperatures, except when $T \approx T_h$ (i.e. $\Delta T < 2$). We used this value for all subsequent figures as it best fits data on the diversity of fanning temperature thresholds reported in the literature [18,32].

To explore the effect of boundary insulation, we used different values of $\alpha = 0.1, 0.55, 1$ and ambient temperatures

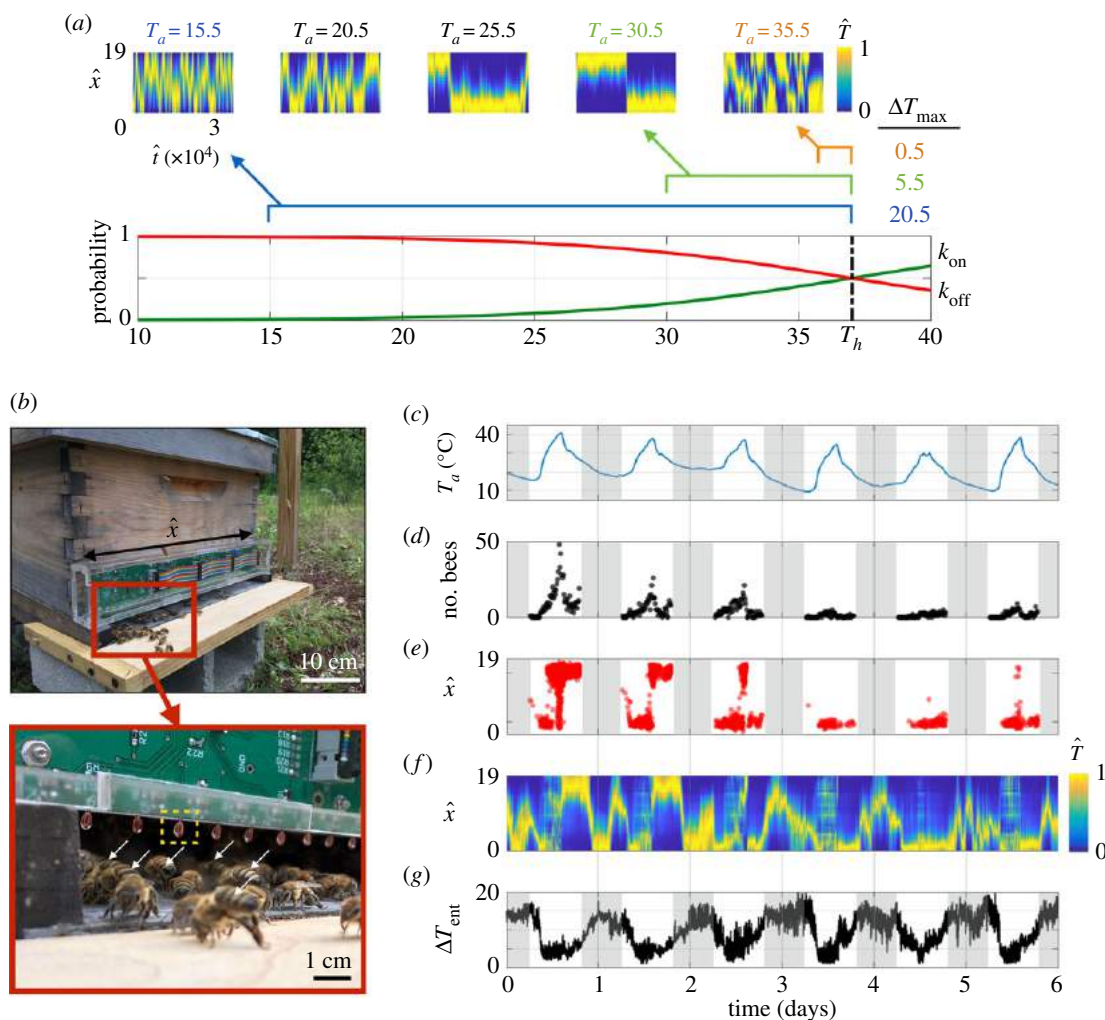


Figure 4. Predicted and observed ventilation dynamics over long time scales. (a) Numerical simulations predict that the position of the fanning group will drift over long time scales (30 000 time steps, $T_h = 36^\circ\text{C}$, $D_v = 1 \times 10^{-3}$, $D_t = 5 \times 10^{-5}$, $m = 0.1$, $c = 0.05$, $\alpha = 0.25$). At low temperatures ($T_a = 15 - 20^\circ\text{C}$), the fanners tend to occupy the centre of the nest entrance and drift in space. At higher temperatures ($T_a = 25.5 - 30.8^\circ\text{C}$), the fanning group clings to the boundary of the nest entrance. When the ambient temperature approaches hive temperature ($T_a = 36^\circ\text{C}$), no singular, persistent fanning group emerges. (b) The temperature sensors along the entrance allow a true measure of air temperature in the flow stream. Fanning bees are indicated with white arrows and one of the temperature sensors is highlighted with a yellow box. (c) The diurnal oscillations in ambient temperature. (d) Total fanning bee number over time—grey regions indicate dark hours when it was difficult to record fanning behaviour directly. Within a day, fanning intensity tracked the diurnal oscillation in T_a . Across days, the number of fanning bees visible outside the nest entrance varied with daily temperature. (e) The position of the fanning bees indicates that single fanning group forms except when T_a is very close to T_h . During warm hours the fanning group tends to cling to the boundaries of the nest entrance. (f) The local air temperature shows that the position of the fanners is associated with warm, outflowing air. The position of the fanning group (and outflow) tends to drift during the night when T_a is low. The entrance temperature has been normalized ($\hat{T} \in [0,1]$). (g) The range of local air temperatures measured at any instant in time ($\Delta T_{ent} = T_{max} - T_{min}$) is also reported. (Online version in colour.)

$T_a = 15, 25, 35^\circ\text{C}$ (figure 3b). When $\alpha \ll 1$, corresponding to a strongly conducting boundary, the fanning group is more likely to occupy the centre of the nest entrance. This occurs because heat is being continually lost to the environment through the boundary (if $T_a < T_h$) and the warmest region of the entrance where bees are most likely to fan is the centre of the entrance. When $\alpha \approx 1$, the system loses no heat through the boundary. Therefore, when the fanning group is positioned near the boundary, heat diffuses towards the opposite side of the entrance (where inflow is occurring) but not through the boundary. This condition is relatively stable and the fanning bees are more likely to continue fanning near the boundary than they are to drift away from the boundary. Varying T_a changes the range of temperatures over which the behavioural switch function can act and therefore has a dramatic effect not only on the number of bees fanning and the maximum flow speeds but also on the spatial organization.

In figure 4a, we see that when $T_a < T_h$ ($\Delta T \geq 10^\circ\text{C}$), the cluster drifted relatively freely. However, at higher T_a the cluster tended to cling to the boundaries of the entrance with occasional spontaneous switching from side to side. At intermediate ΔT the fanning group/outflow is attracted to the boundaries because they are partially insulating. The simulations in figure 4a ($T_a = 25.5, 30.5$) show that the fanning group/outflow occasionally becomes detached from the boundary and can switch to the opposite boundary. This transition is due to the stochastic nature of k_{on} and k_{off} , and is consistent with occasional experimental observations as well (see figure 4f at $t = 0.95$ days). Varying the slope m of k_{on} and k_{off} or the thermal conductivity of the boundary α both influence the likelihood that the fanning group/outflow will detach from the boundary at a given ΔT . As T_a approached T_h ($\Delta T \leq 2^\circ\text{C}$), the dominant cluster broke up to form multiple ephemeral clusters (figure 4a).

Our model demonstrates that the interaction between fanning bees and the flow field in which they are embedded allows for emergent clustering of fanning bees and ultimately leads to ordered, efficient airflow through the nest entrance without a leader or central coordination. An explicit prediction of the model is that the dominant cluster should drift in space over long time scales and that this drift is qualitatively different at various temperatures.

4. Long-term observations of ventilation dynamics

In order to test these theoretical predictions, we developed a method to continuously monitor the position of fanning bees at the nest entrance and the resultant flow pattern in the field under naturally varying conditions over many days. In the absence of our ability to continuously measure air velocity simultaneously at many positions within a cluttered and dynamic environment, we used temperature as a proxy for flow direction at the nest entrance (figure 1d). We placed custom 32-sensor arrays above the nest entrances (1.8 cm × 37 cm) of three additional Langstroth beehives enabling us to sample local air temperature with high spatial and temporal resolution (1.17 cm sensor spacing, 10 s sampling intervals, figure 3b). Short videos were taken of the entrance of one of these hives every 10 min during daylight hours and the position of visible fanning bees was recorded (see electronic supplementary material, Movie S2–S3).

The ambient temperature oscillated according to a 24 h diurnal cycle (figure 4c) with variation in minimum and maximum daily temperatures throughout the observation period. The total number of fanning bees visible at the nest entrance tracked these oscillations and fanning intensity was higher on warmer days (figure 4d). The position of fanning bees during warm daylight hours revealed that the fanners tend to form well-defined clusters which tend to cling to the boundaries of the nest entrance (figure 4e). On warmer days, the ambient temperature would approach the nest temperature at midday and the fanning group would break up into multiple, less-defined clusters. When the ambient temperature fell again, a single cluster would again emerge. For the hive depicted in figure 4 (Hive 1), the dominant fanning group often occupied the east side of the entrance during the morning and the west side of the entrance during the afternoon. This suggests that under some conditions, solar radiation may impose an environmental asymmetry that can bias the position of the fanners. This was not the case for Hives 2 and 3, suggesting that this is not the only factor determining the position of the fanners. The air temperature profile along the nest entrance reflected the distribution of fanning bees. In figure 4f, we normalize the air temperature so that ($\hat{T} \in [0,1]$) at each time step so that the entire dataset can be represented in a single heat map; without normalization, the diurnal oscillations in T_a would dominate the heat map. Removing these externally imposed oscillations allows us to focus on the temporal changes in spatial patterning. For comparison the difference between the minimum and maximum temperature at the nest entrance ($\Delta T_{\text{ent}} = T_{\text{max}} - T_{\text{min}}$) is also plotted in figure 3g. We see that the position of the dominant fanning group as indicated by the warm, outflowing air tended to drift away from the boundaries during the night when ambient temperatures were low, as predicted by the model.

The nuances of the ventilation behaviour are inevitably affected by the particular environmental conditions experienced by a colony, and yet the qualitative predictions made by our model are born out in the observed behaviour in naturally fluctuating conditions. When T_a is lower than T_h a single cluster of fanners forms and tends to drift in space. As T_a increases the cluster tends to fix to a boundary. Which boundary the cluster fixes to may be biased by asymmetries in the environment. Finally, as T_a approaches T_h , the cluster breaks up into multiple or less defined clusters. Our observations are in agreement with theoretical predictions and suggest that collective nest ventilation is not just a product of the bee behaviour, but arises from the local flow-mediated interactions between individual bees and of the resultant hive-scale fluid dynamics.

5. Conclusion

There are two behavioural components of this process that are critical to self-organized ventilation. First, the bees must (and do) fan air out of rather than into the nest entrance. This allows the bees to sense the upstream nest temperature. If the bees fanned into the nest entrance, they would have no information about the state of the hive. Interestingly, another cavity nesting honeybee species, *Apis cerana*, fans into the nest entrance [37]. This species likely uses an alternative strategy to the one described here or occupies nests with a small nest entrance in which spatial organization is not required [31]. Second, the switch function that determines the probability at which a bee will fan at a given temperature has likely been tuned through natural selection. If the slope of this function is too shallow, fanning behaviour is weakly coupled to temperature and no organization will emerge (see electronic supplementary material, figure S5A,E). If the slope is too steep, fanning behaviour can occur only over a small range of temperatures (see electronic supplementary material, figure S5C,G). Indeed, it is known that colonies with high genetic diversity have more variation in individual temperature thresholds for fanning and are able to achieve a more stable hive temperature through time [18]. Our theory suggests that this diversity is also critical to the stability of spatial patterning of fanning behaviour which is required for efficient ventilation.

Our study demonstrates how harnessing the dynamics of the physical environment allows for large-scale organization of a physiological process. This differs from classical stigmergy, which facilitates coordination by integrating spatial information over longer time scales.

Honeybees sense local air temperature (which is coupled to speed and direction of airflow) and drive airflow when temperatures are high. Because the individuals are embedded in a common flow-field, their behaviour is influenced by non-local interactions mediated by flow. The self-organization of fanners into groups which efficiently partition inflow and outflow, reduce friction and avoid antagonistic fanning behaviour is ultimately the result of flow-mediated information processing that integrates locally sourced information over large spatial scales even in the absence of direct interaction between neighbouring individuals. This ability to manipulate existing physical processes locally to create self-organized behaviour on large scales may be a pervasive strategy in the evolution of complex systems.

Data accessibility. Data included in this manuscript are available upon reasonable request. Links to simulation code are included in the electronic supplementary material.

Authors' contributions. J.M.P. and L.M. conceived and designed the study, created the mathematical model and wrote the manuscript. J.M.P. conducted the field measurements and analysed the data. J.M.P. performed the simulations of the mathematical model with significant help and contributions from O.P. L.M. supervised the project. All authors contributed to revisions and gave final approval for publication.

Competing interests. We declare we have no competing interests.

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Supplementary Information for "Collective ventilation in honeybee nests"

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A. Supplementary Movies

1. *SI Movie 1*

Manual measurements of flow direction, flow speed, air temperature and fanner distribution. This video demonstrates how the data reported in Fig. 1D, Fig. S8, and Fig. S9 were collected.

2. *SI Movie 2*

Thermistors suspended in airflow and undisturbed by fanning bees.

3. *SI Movie 3*

Manual digitization of fanner position at nest entrance during long-term monitoring.

4. *SI Movie 4*

Continuous monitoring of ambient temperature, fanner distribution and temperature profile at nest entrance. This movie is an animation of data reported in Fig. 3C-G.

5. *SI Movie 5*

Simulation: Self-organization of fanning groups ($T_a = 32^\circ\text{C}$, $\Delta T_{max} = 4$). This animation tracks fanner density, velocity and temperature during the first 3000 time steps of a simulation in order to highlight the self-organization of a clustered distribution of fanners from an initially uniform distribution. This simulation has the same ambient temperature as those in Fig. 2D-E. Parameters values reported in Table S1.

6. *SI Movie 6*

Simulation: Spatio-temporal dynamics of ventilation at $T_a = 15.5^\circ\text{C}$, $\Delta T_{max} = 20.5$. This animation complements Fig. 3A1. Parameters values reported in Table S1.

7. *SI Movie 7*

Simulation: Spatio-temporal dynamics of ventilation at $T_a = 30.5^\circ\text{C}$, $\Delta T_{max} = 5.5$. This animation complements Fig. 3A4. Parameters values reported in Table S1.

8. *SI Movie 8*

Simulation: Spatio-temporal dynamics of ventilation at $T_a = 35.6^\circ\text{C}$, $\Delta T_{max} = 0.5$. This animation complements Fig. 3A5. Parameters values reported in Table S1.

B. Study Site

All hives observed were located at Concord Field Station, Harvard University, Bedford, Massachusetts.

C. Study Organisms

All colonies were originally started from packages derived from Rossman Apiaries in Georgia. The colonies were started with an Italian queen.

D. Manual measurements

Fig. S1 and Fig. S2 contain the results of manual measurements of fanner distribution, air velocity and temperature at the nest entrance of 4 hives from 07/21/2015 to 07/23/2015. These data complement Fig. 1.

E. Numerical simulations

The MATLAB code used to generate the data in all figures presented in this paper is available on GITHUB (<https://github.com/jacobmpeters/honeybeeVentilationModel.git>).

1. *Parameter choices*

Our simulations tracked the change of local density (ρ), local temperature (T) and local velocity (v) at every position along the nest entrance over each iteration (time). These values were held in three arrays of length L/l_b . L was fixed at 38cm, the approximate width of the nest entrance in the experimental setup and l_b was set to 2cm, the approximate wingspan of a fanning bee. We chose to fix T_h to 36 °C which is the temperature at which honeybees are known to regulate their core nest temperature⁴. Ambient temperature was fixed throughout each simulation, but was varied across simulations to explore the effects of varying ΔT . D_v and D_T for Fig. 2 and 3 were 1×10^{-4} and 4×10^{-5} , respectively. These choices were used to fit the simulations to the observed behavior. We explore the effect of these diffusion coefficients on the model's behavior in **Fig. S3**.

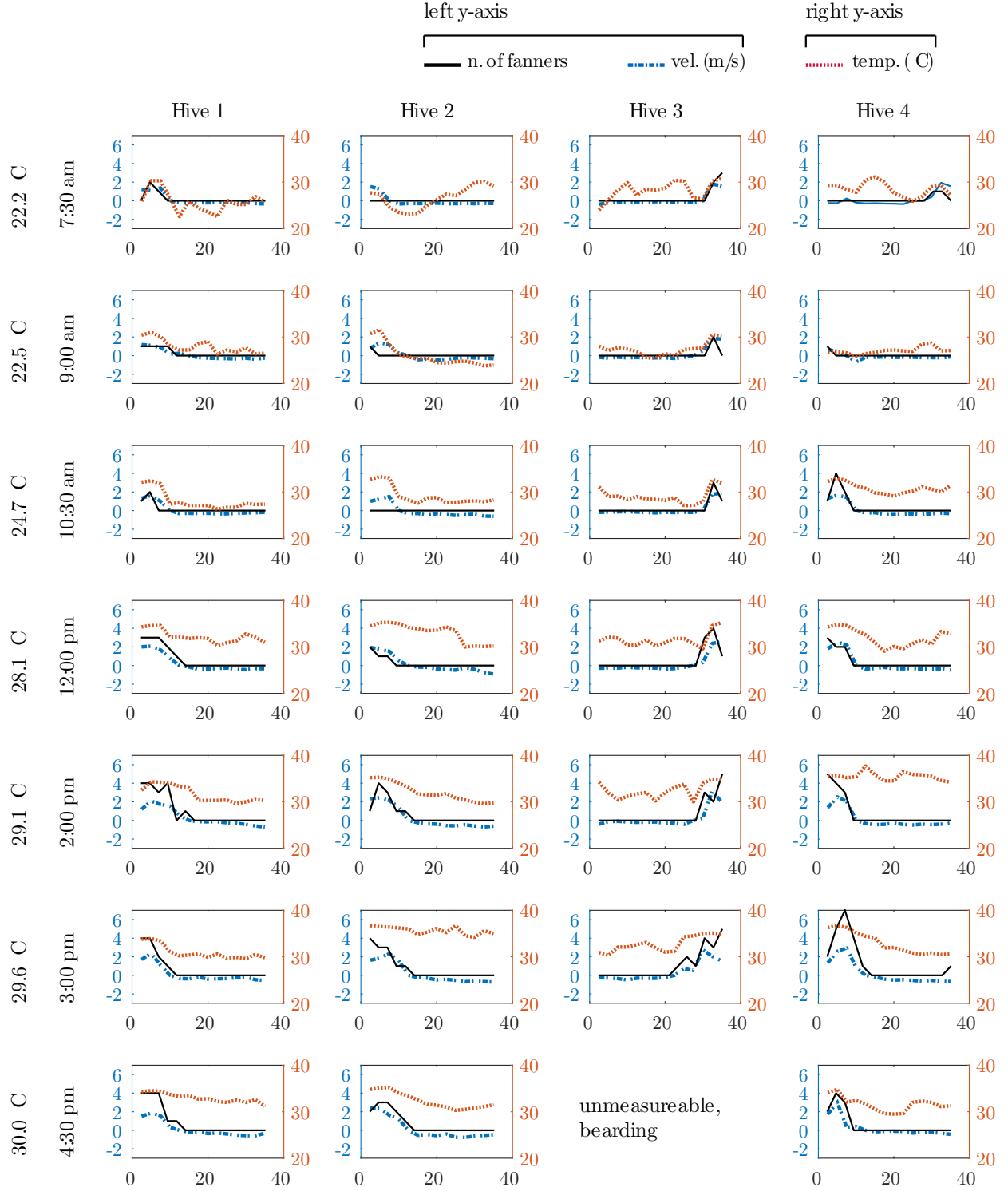


FIG. S1. Fanning activity, air velocity and air temperature as measured along the nest entrance (x-axis, cm). Measurements were made from 4 hives at 7 times throughout the day (07/21/2015). The density of fanning bees, air velocity and air temperature were spatially coupled.

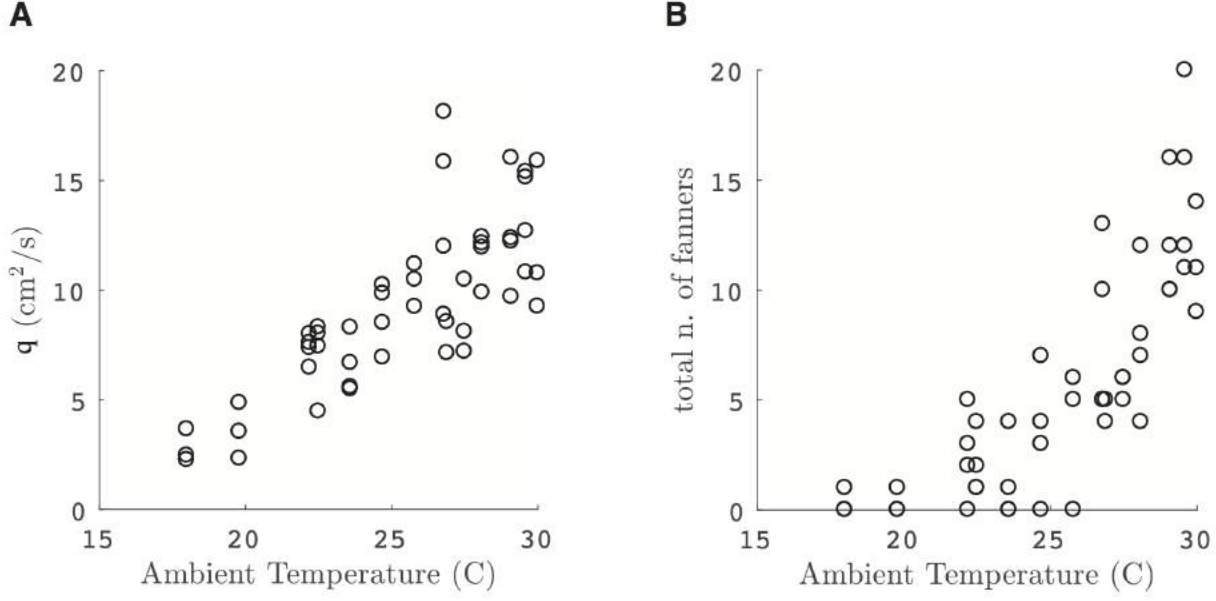


FIG. S2. The relationship between ventilation behavior and ambient temperature according to manual measurements made from 4 colonies from 07/21/2015 to 07/23/2015. (A) Flux of air at the nest entrance ($q = \frac{\int |v| dx}{2}$). Note that because our measurements were sampled from a 1D space, we report flow rate in cm^2/s rather than cm^3/s . (B) Total number of fanners visible at the nest entrance as a function of ambient temperature.

In the continuous form of the model, k_{on} and k_{off} relate the rate at which bees begin to fan and cease fanning to the local air temperature. In the context of the simulations, these values describe the probability that a bee will fan or cease fanning at a given temperature and are governed by the following equations: $k_{\text{on}} = k_0 \frac{\tanh(m*(T-36))+1}{2}$ and $k_{\text{off}} = k_0 - k_{\text{on}}$. The parameter m controls the slope of this sinusoidal function. Cook et al. 2013 report the distribution of temperature thresholds above bees will fan when heated in groups of 1, 3 and 10 bees over a range of temperatures². They found that the distribution of temperatures at which individuals are induced to fan is dependent on group size. For the purposes of our study we assumed that the distribution associated with groups of 10 bees was most similar to that which would be found at the hive entrance. We used $m = 0.1$ because it approximately replicates this distribution. This value also adequately reproduced the same dynamics that we observed at the nest entrance. See SI Fig. S4 to see the effects of m on ventilation dynamics.

2. *Implementation*

We used a finite difference scheme to solve the differential equations. All simulations began with the following initial conditions: T was set to 36°C across the entire entrance, ρ was a uniform distribution (essentially 1 bee per bin), and v was an array of zeros. At each time step we randomly select one bin of size l_b and allow ρ at this bin to evolve according to probability functions k_{on} and k_{off} . ρ can change only discretely in multiples of one bee/ l_b . We chose to allow ρ to change at one position per time step to mimic the discrete decisions made by bees. Equations 2 and 3 were then solved to update the velocity and temperature arrays given the new density array. These steps were then repeated in subsequent loops, each time randomly choosing a position to update.

3. *Boundary conditions*

Bees were not allowed to fan at the boundaries, so $\rho = 0$ at $x = 1$ at $x = L/l_b$. Velocity at the boundaries was also fixed at 0 to enforce the nonslip condition with the walls of the nest entrance. Finally, the diffusion of heat along x requires a boundary condition that accounts for the thermal conductivity of the boundaries (the walls of the nest entrance), which depends on the thickness and material properties. We implemented a Robin Boundary Condition in which the conductivity of the boundary is controlled by the parameter α . When $\alpha \approx 0$, the wall of the nest entrance behaves as a perfect conductor. When $\alpha = 1$, the wall behaves as a perfect insulator. See SI Fig. S5 to see the effect of this parameter choice on ventilation dynamics.

F. *Mechanisms of self-organization*

Our basic model is derived from the equations of mass and momentum conservation of air flow, recognizing that this flow is driven by bee fanning. We denote the direction parallel to the hive entrance using a coordinate x , and the direction perpendicular to the hive entrance by y , the fluid velocity components in the two direction by $u(x, y, t), v(x, y, t)$ respectively, and the temperature by $T(x, y, t)$. Since there are no flows in the x direction, and no variations in the temperature and flow velocity in the y direction, we have $u = 0, v = v(x, t), T = T(x, t)$. Then, momentum balance in the y direction reads $\rho_f(\partial v/\partial t + v\partial v/\partial y) =$

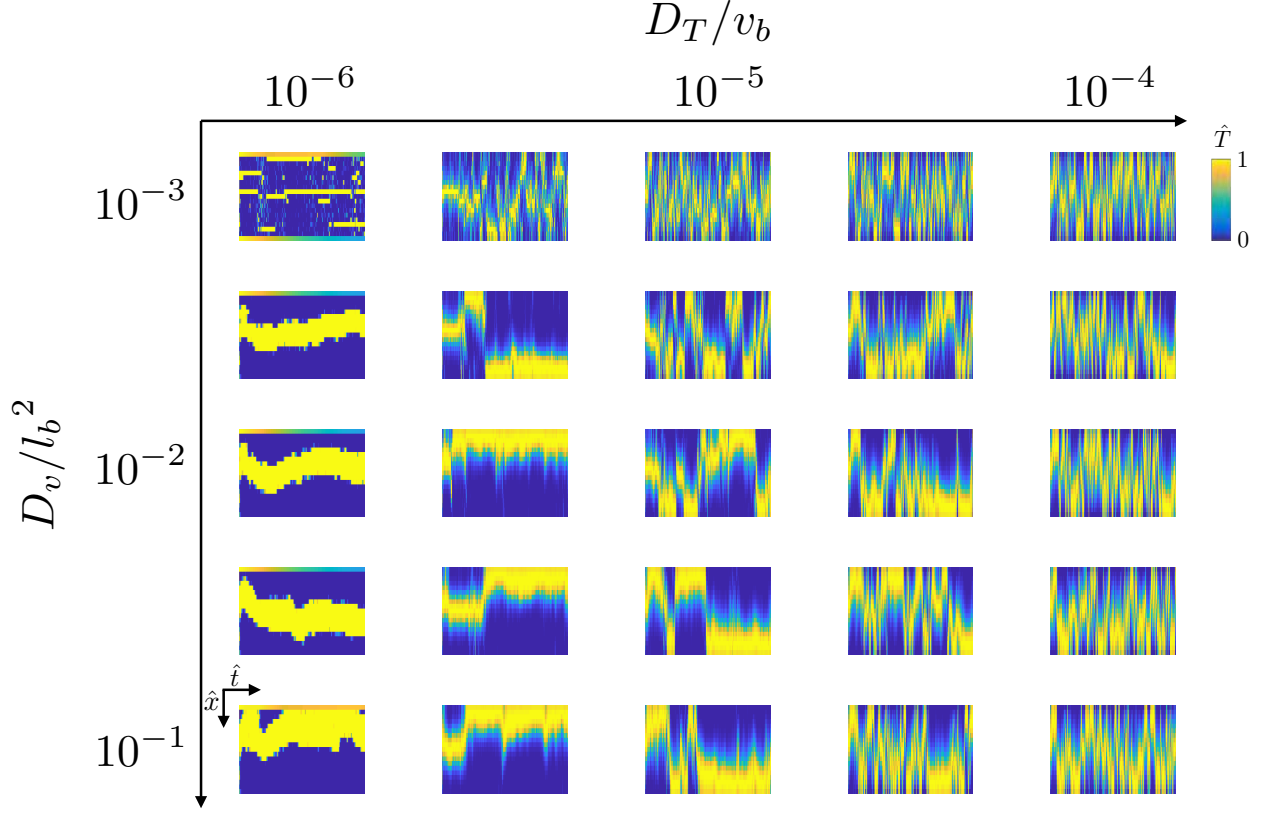


FIG. S3. Effects of diffusion coefficients, D_V and D_T , on ventilation dynamics. At low D_V and D_T , there is minimal shear imposed by velocity gradients (effective diffusion of velocity) and minimal diffusion of heat through x . In this condition, the positive feedback between fanning behavior, air velocity and temperature occurs only locally and there is not short-range attraction between fanning groups. This leads to the formation of many small fanning groups. As D_V and D_T increase, positive feedback occurs in both space and time. This leads to fewer, larger fanning groups. $\hat{x} \in [0, 19]$ and $\hat{t} \in [0, 2 \times 10^4]$.

$-\partial p/\partial y + f + \mu \partial^2 v/\partial x^2$, where ρ_f is the fluid density, and f is the body force that consists of the fluid friction with the floor of the hive entrance, i.e. $f = -\zeta v$, where ζ is the friction factor. If the flow reaches steady state relatively quickly compared to any changes in the environment associated with diurnal variations, momentum balance reduces to a simple equation that now reads $-\zeta v + \mu \partial v/\partial x^2 - \partial p/\partial y = 0$. Since the pressure gradient is predominantly an active one generated by the bees over their length, a simple expression suggests that $\partial p/\partial y \sim \rho \rho_f v_b^2$ in the active region where ρ is the linear density of fanning bees, and v_b is the constant flow velocity generated by a bee. In the passive region, the pressure gradient is reversed by an amount that is dictated by mass balance. Indeed, integrating the

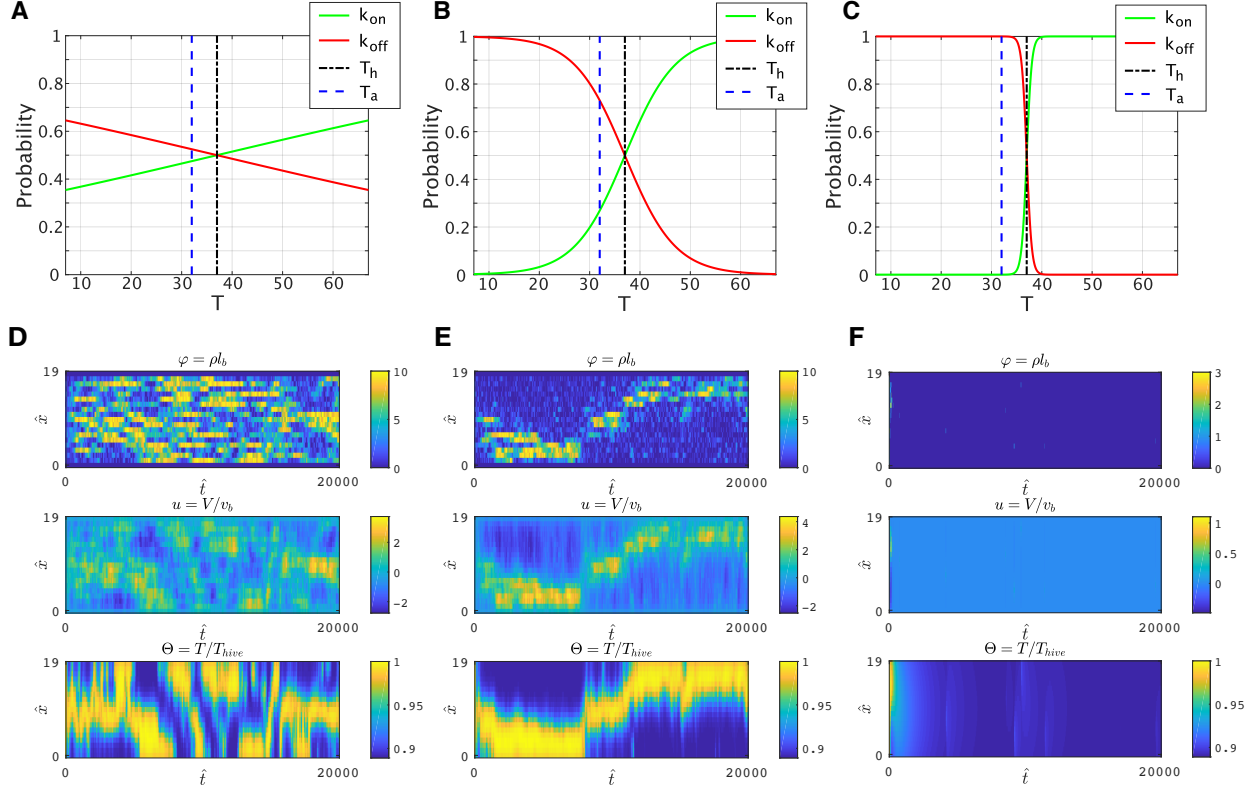


FIG. S4. Effect of slope of behavioral switch functions on ventilation dynamics. K_{on} and K_{off} prescribe the probability of a given bee to begin fanning or cease fanning at a given local air temperature. The slope of these functions is controlled by the parameter m . (A,E) When m is extremely low ($m = 0.01$), fanning behavior is weakly coupled to temperature and no distinct fanning group forms. This leads to high fluid friction and poor ventilation efficiency. (C,E) When m is extremely high ($m = 1$), fanning behavior will occur only over a narrow range of temperatures. (B,F) At moderate m ($m = 0.1$), ventilation can occur over a broad range of temperatures and a stable fanning group will form, except when T is very close to $T_{\text{hive}} (\Delta T < 2)$. Because the slope of these switch functions is the only behavioral parameter in our model—the others pertaining only to the properties of the physical environment—it is likely that natural selection has acted on this parameter to ensure efficient ventilation. We selected $m = 0.1$ for our simulations because it most adequately fits data on the diversity of fanning temperature thresholds reported in the literature^{1,2}. $\hat{x} \in [0, 19]$ and $\hat{t} \in [0, 2 \times 10^4]$.

equation for mass balance over the length of the hive entrance L , we must have $\int_0^L v dx = 0$ for global mass balance (assuming that the dominant flow into the hive occurs only at the entrance). Then final equation for fluid flow at the entrance then reads

$$\zeta v = \rho_f v_b^2 \left[\rho(x, t) - \frac{1}{L} \int_0^L \rho(x, t) dx \right] + \mu \frac{\partial^2 v(x, t)}{\partial x^2}. \quad (\text{S1})$$

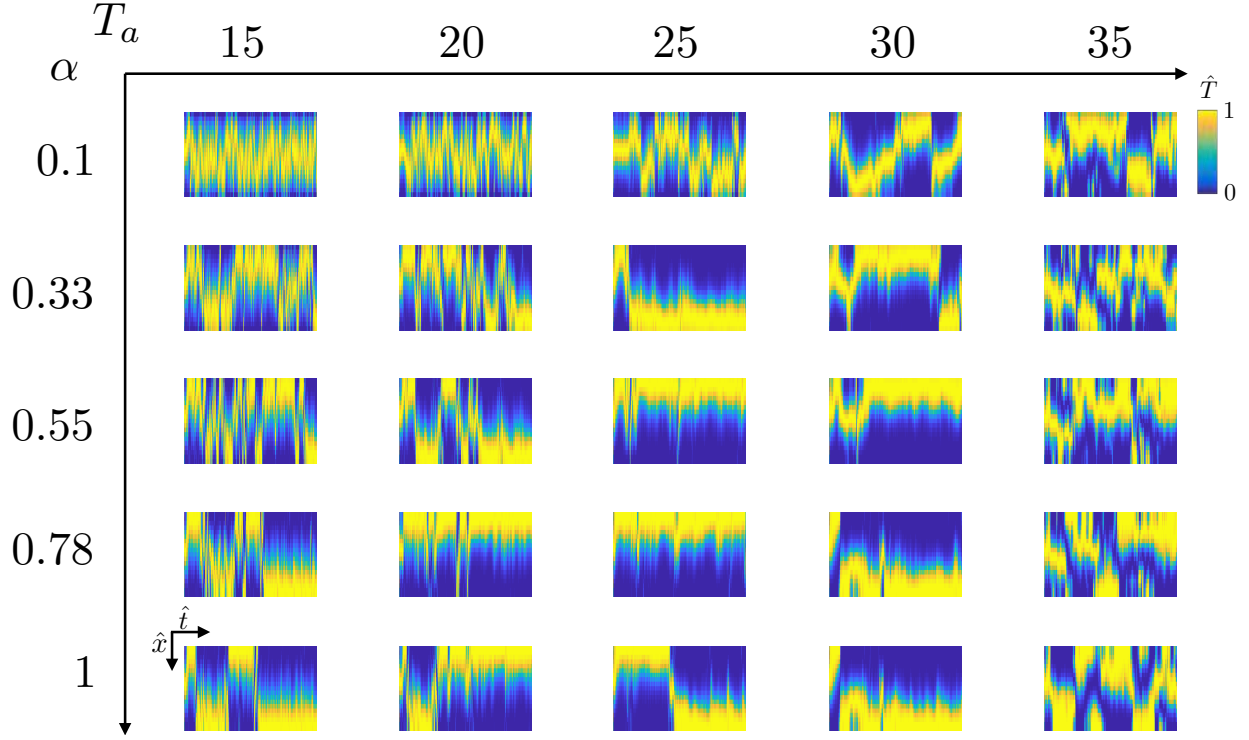


FIG. S5. Effects of ambient temperature and boundary conductivity on ventilation dynamics. The parameter α controls the thermal conductivity of the boundaries of the nest entrance. When α is near 0, the boundary is perfectly conductive. When α is 1, the boundary is a perfect insulator. When α is small, the fanning group is more likely to occupy the center of the nest entrance. This occurs because heat is being continually lost to the environment through the boundary (if $T_a < T_h$) and the warmest region of the entrance where bees are most likely to fan is the center of the entrance. When α is high, the system loses no heat through the boundary. Therefore, when the fanning group is positioned at **or** near the boundary, heat diffuses toward the opposite side of the entrance (where inflow is occurring) but not through the boundary. This condition is relatively stable and the fanning bees are more likely to continue fanning near the boundary than they are away from the boundary. $\hat{x} \in [0, 19]$ and $\hat{t} \in [0, 2 \times 10^4]$.

Dividing both sides by ζ and defining a characteristic length scale $l_b = \rho_f v_b / \zeta$ and a scaled momentum diffusivity (with dimensions of the inverse length squared), $D_v = \mu / \zeta$, we obtain Eq. (2) in the main text.

For heat balance at the hive entrance, we may write an equation that accounts for advection, diffusion and sources as $\partial T / \partial t + u \partial T / \partial x + v \partial T / \partial y = D(\partial^2 T / \partial x^2 + \partial^2 T / \partial y^2) + q$. Again, with the assumptions of variations only in x and $u = 0$, along with a simple cooling law that assumes $q = -cv\Delta T$, i.e. the cooling rate is linearly proportional to the temperature difference and the fluid velocity (neglecting any complex dependence on the Nusselt

number), we find that the resulting equation for heat balance at the entrance reads

$$\frac{\partial T(x, t)}{\partial t} = -cv(x, t)\Delta T + D_T \frac{\partial^2 T(x, t)}{\partial x^2} \quad (\text{S2})$$

If we use the dimensionless variables defined by $\hat{x} = x/l_b$, $\hat{t} = tv_b/l_b$, $u = v/v_b$, $\phi = \rho l_b$, $\Theta = T/T_a$, we are led to a dimensionless set of our original equations with four dimensionless parameters, given by:

$$u = \left[\phi - \frac{l_b}{L} \int_0^{L/l_b} \phi d\hat{x} \right] + \frac{D_v}{l_b^2} \frac{\partial^2 u}{\partial \hat{x}^2}. \quad (\text{S3})$$

$$\frac{\partial \Theta}{\partial \hat{t}} = -cl_b u \Delta \Theta + \frac{D_T}{v_b l_b} \frac{\partial^2 \Theta}{\partial \hat{x}^2} \quad (\text{S4})$$

In Fig. S6, we elaborate on the succinct mathematical description indicated in Eqn S1 that describes the dynamics of airflow in and out of the nest entrance. The first term (A) denotes the outward airflow due to the actively fanning bees. However, since the nest volume is fixed, this outflow must be balanced by inflow elsewhere. This simple consequence of fluid conservation demands the presence of the second term (B), which serves as an inhibitor of flow (as it reverses the flow direction). Finally, the last term (C) characterizes the effect of flow entrainment due to the shear induced by motion in and out of the nest; the net effect is that of penalizing large velocity gradients. The accompanying figures show how a population of active fanners leads to a local actively driven outflow, that via conservation of fluid demands passive inflow in those regions where there are no active fanners. The resulting increase in fluid friction due to shear gradients in these regions causes additional entrainment of flow from the nest. This leads to the bees there sensing the nest temperature, driving local recruitment of bees and creating a positive feedback that drives the clusters to coarsen into a single one when the temperature difference between the nest and the environment is large. The different schematics 1,2,3, show how fluid flow can serve as both activator and inhibitor depending on the spatial heterogeneity of the initial density of fanning bees.

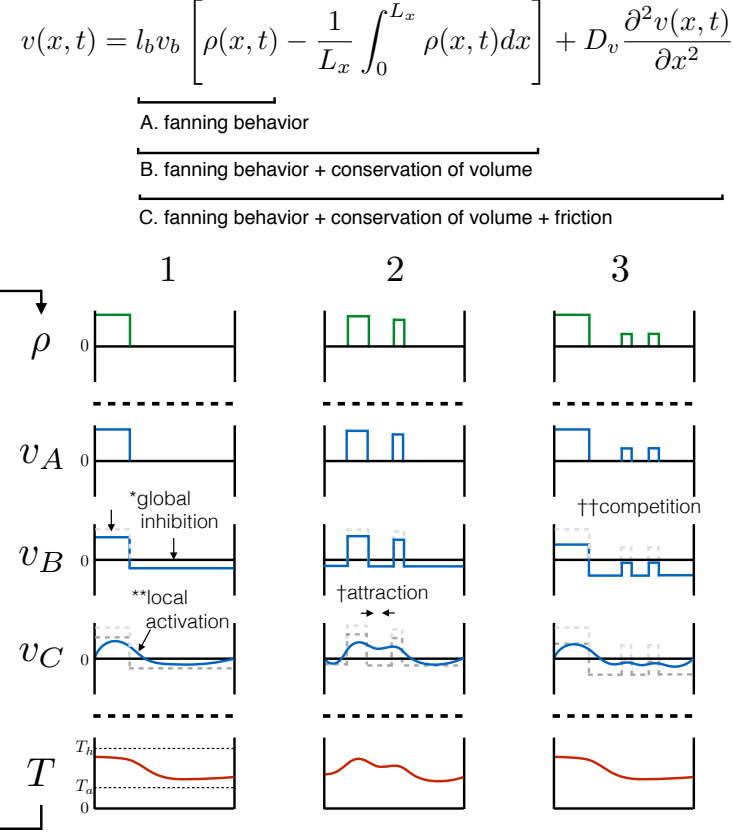


FIG. S6. A schematic illustrating the mechanisms of self-organization which emerge from the model. Equation 2 is broken down into components: (A) the direct result of fanning behavior, (B) conservation of volume, and (C) friction (or effective diffusion of velocity). Below, the following variables are plotted: the distribution of fanners (ρ), velocity calculated considering only fanning behavior (v_A), velocity calculated considering fanning and conservation (v_B), velocity considering fanning, conservation and friction (v_C), and the temperature profile (T). Scenario 1 is a simple example which illustrates how conservation of volume contributes to global inhibition of fanning behavior (*) and friction (as well as the diffusion of heat) contribute to local activation (**). That is, bees are more likely to fan adjacent to other fanning bees due to friction and diffusion. Scenario 2 illustrates a case in which this friction/diffusion drives attraction between adjacent fanning groups (†). Fanners are more likely to fan between fanning groups as a result of friction/diffusion. Finally, Scenario 3 illustrates the potential for conservation of volume to act as a global inhibitor which ultimately drives competition between fanning groups (††). Large fanning groups are more likely to grow and smaller groups are likely to shrink and disappear due to this competition.

G. Long-term hive monitoring

Thermistors were uniformly distributed along the nest entrance ((1.8 x 37cm), leading to a 1.17cm spacing between thermistors. The thermistors were suspended from rigid lead

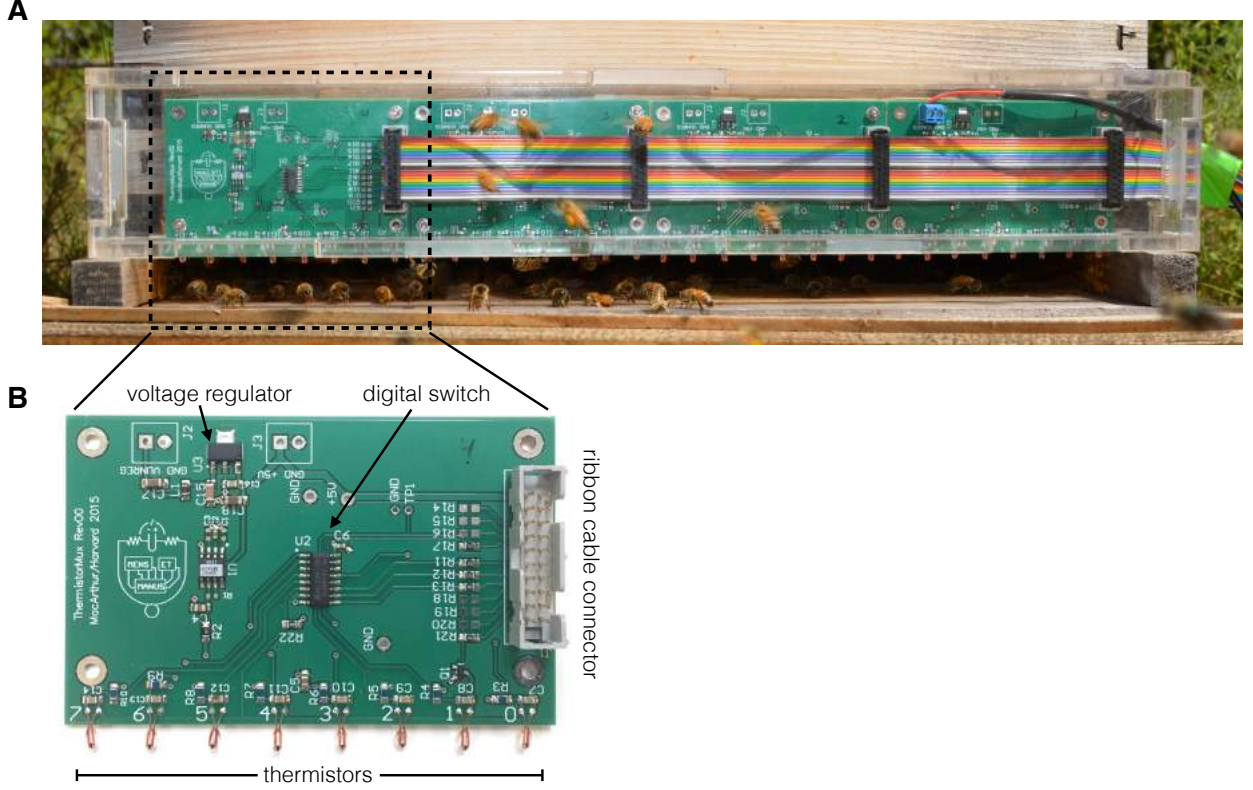


FIG. S7. Custom sensor array. A) The ThermistorMUX circuit installed at the nest entrance. B) One of four PCB modules.

TABLE S1. Dimensionless parameters and constants. Values reported here were used in simulations unless otherwise specified in the figure captions. $L = 0.38m$, $l_b = 0.02m$, $v_b = 1m/s$, $c = 0.05/m$, $D_T = 5 \times 10^{-5}m^2/s$, $D_v = 1 \times 10^{-3}m^2$.

Parameter	Description	Value
L/l_b	scaled entrance length	19
D_v/l_b^2	scaled fluid friction	2.5
$D_T/v_b l_b$	scaled thermal diffusivity	2.5×10^{-3}
cl_b	scaled fanning length	1×10^{-3}
m	behavioral switch response	$0.1/^\circ C$
α	scaled boundary conductivity	0.25

wires so that the bead of the thermistor was isolated from the circuit board and suspended in the airflow generated by the bees. The thermistors were occasionally contacted by the wings of fanning bees but they were typically not directly touching the bodies of the bees (see Fig. S8A and SI Movie 2). A Logitech c920 web cam was mounted approximately 3 ft above the nest entrance pointing down such that an orthogonal view of the "porch" was

visible. Four-second videos of fanning activity were collected every 5 minutes from 9/16/15 to 9/24/15. Temperature measurements from each of the 32 thermistors was acquired every 5 seconds over this period. An additional Parallax SHT11 digital temperature sensor was placed nearby in the shade in order to measure the ambient temperature. This protocol was repeated for two additional hives from 7/7/2016 to 7/19/2016 (Fig. S8 for complete dataset). The position of all fanning bees visible on the outside of the nest entrance during the videos taken during daylight hours were digitized by mouse click using a custom MATLAB program (See SI Movie 3). Fanning activity also occurs just inside the entrance of the hive, however these bees were not visible in our videos and are not represented in our data. We assume that analyzing the position and number of fanning bees visible in the videos is sufficient to capture the phenomena that we are interested in.

The sensor array used in this study was designed by Jim MacArthur to continuously measure air temperature at the nest entrance with high spatial and temporal resolution. The sensor array consists of four PCB modules bearing 8 thermistors each (Fig. S7). The circuit board is covered with an acrylic case. During data collection an opaque covering was used to prevent radiative heating from the sun. The thermistors were suspended in the flow stream in order to acquire an accurate air temperature without directly contacting the bees (See SI Movie 3). Each PCB module has a voltage regulator to ensure a consistent reference voltage. A digital switch allows a single digital signal to switch between each of the 8 thermistors which are read through a common analog pin. When a given thermistor is not being read, it is not receiving current, preventing self-heating. Each of modules has a ribbon cable connector allowing them to interface with the Arduino. The Arduino was programed using the Arduino IDE to select and read each thermistor in sequence. Data was transfered to a MATLAB program using a USB-Serial connection. Schematics, drawings, and code required to reproduce this setup are available on GITHUB ([ENTER STABLE LINK HERE](#)).

H. In large colonies CO_2 and temperature at the nest entrance are coupled in space but are decoupled in time

Heat is thought to be the primary cue that induces the fanning response in honeybees. However, Seeley (1974) observed that a small colony (approximately 10,000 bees) experi-

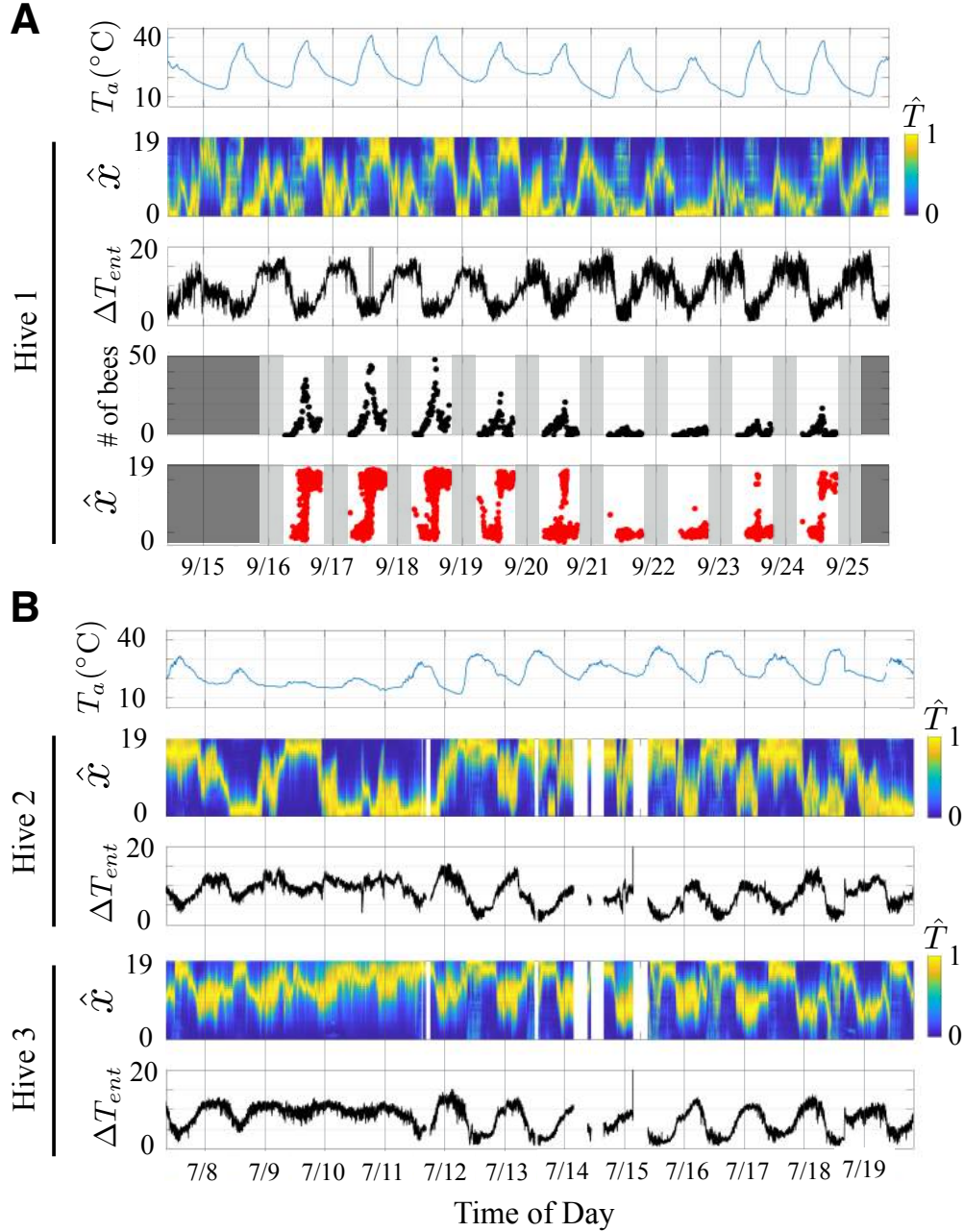


FIG. S8. Complete dataset of fanning behavior at nest entrance of three colonies in response to ambient temperature oscillations. A1) Ambient temperature, T_a , oscillations measured in the apiary from 9/14/2015 to 9/25/2015. A2) Normalized entrance temperature, $\hat{T} \in [0, 1]$, as measured by 32 thermistors distributed across the nest entrance. A3) The differential, ΔT_{ent} , between the maximal (outflow) and minimal (inflow) temperature readings measured at the nest entrance at a given time. A4) The number of fanners visible at the nest entrance over time. Dark gray regions indicate times when video data was not available. Light gray regions indicate times when it was too dark to collect accurate data. A5) The position of fanning bees along the nest entrance. B1) Ambient temperature, T_a , oscillations measured in the apiary from 7/7/2016 to 7/19/2016. B2-5) Entrance temperature data for Hive 2 and Hive 3.

enced dramatic spikes in CO_2 concentrations which were abated by a proportional fanning response by the colony³. Over a 52 hours of CO_2 measurements from the brood nest of a small (10,000 bees) and large colony (35,000 bees), Seeley reported that the large colony had a lower mean CO_2 concentration (0.44%) than did the small colony (0.78%). In addition, the larger colony showed much less variation in CO_2 concentration (0.16%) than did the small colony (0.34%). Seeley suggested that this better homeostasis in CO_2 concentration in the large colony was likely due to near continuous thermoregulatory ventilation rather than fanning in response to CO_2 .

In our model, we assumed that the fanning response at the nest entrance would primarily track the local air temperature given because we were using large, mature colonies. We tested this assumption by measuring both CO_2 and temperature at the nest entrance of Hive 3. Because CO_2 sensors are larger and much more expensive than thermistors, we were not able to make a high resolution sensor array as we did for the temperature measurements. Instead, we partitioned the nest entrance into two discrete regions by placing a 15cm wooden partition in the center of the nest entrance to block airflow in this region (Fig. S9A). This allowed use to study the spatial dynamics of the fanning group while using only two CO_2 sensors. The bees established an outflow region on the left of the partition allowing air to passively move into the hive on the right side. This segregation of inflow and outflow emerged from the behavior of the bees and the physical constraints imposed by the partition (Fig. S9B). This configuration persisted for the three day period over which data was collected.

As expected, temperature and CO_2 were coupled in space—outflowing air was enriched in both CO_2 and heat relative to inflowing air (Fig. S9C). However, the temperature and CO_2 concentration of outflow were decoupled in time. The temperature of outflowing air tracked the ambient temperature. During the heat of the day when thermoregulatory ventilation was peak, CO_2 was at a minimum. When thermoregulatory fanning decreased during the the night, CO_2 was maximal. There are two possible explanations for this: 1) the number and density of bees in the nest at night is higher during the night resulting in higher CO_2 production, and 2) as the thermoregulatory fanning response decreases at night, CO_2 is evacuated at a lower rate. It seems likely that both mechanisms contribute. We also noticed an interesting dip in the CO_2 concentration at around 6am which was reproducible across days that we cannot yet explain.

These measurements bolster our assumption that temperature is the dominant cue in-

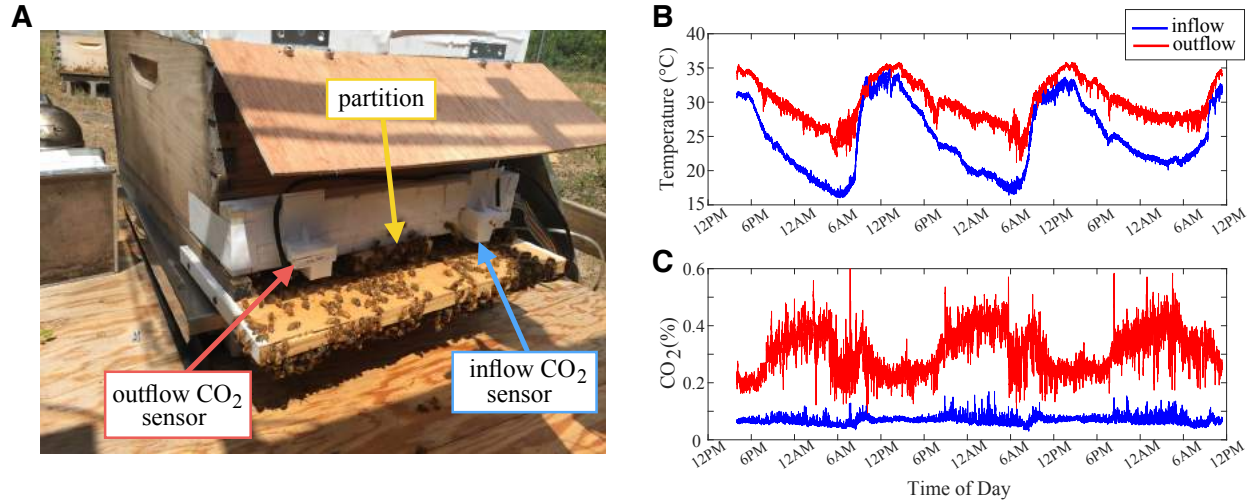


FIG. S9. A) Setup for acquiring CO₂ concentration data. B) Temperature of outflowing air was consistently higher than inflowing air, but varied with the ambient temperature. C) Similarly, CO₂ was higher in outflow than in inflow. However, CO₂ was decoupled from temperature, reaching a minimum during the heat of the day and a maximum at night.

ducing the fanning response in large, mature colonies. A probability function for the CO₂-induced fanning response could be added to our model once it is resolved by future experimental work, but it is unlikely to qualitatively change the dynamics of the model because CO₂ and temperature are spatially coupled at the nest entrance.

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