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Brood comb construction by the stingless bees *Tetragonula hockingsi* and *Tetragonula carbonaria*

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Abstract *Tetragonula hockingsi* and *T. carbonaria* are two closely related species of Australian stingless bees. The primary species-specific character is the architecture of the brood comb. The brood comb of *T. hockingsi* is an open lattice comprising clumps of about ten cells that are connected by vertical pillars. In contrast, in *T. carbonaria* the brood comb is a compact spiral in which all brood cells (except on the margins) are connected by their walls to adjacent cells at the same height. We made detailed observations of the cell construction process in two colonies of each species. From these observations we formed a species-specific hypothesis about the algorithm followed by the bees during cell construction. The two algorithms allowed us to make predictions about the locations of new cells. Both *T. hockingsi* and *T. carbonaria* share a preference for constructing new brood cells in the clefts formed by two or three adjacent existing brood cells, but there are differences in detail for other components of the building process. The fundamental difference in the cell construction process of the two species is that for *T. hockingsi*, when a cluster of cells contains ten cells, the next cell added to the cluster is offset upwards by half a cell length,

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or, less often, a vertical pillar rather than a new cell is constructed. In *T. carbonaria*, cell construction is continuous at the comb margin so that there are no gaps between cells. Furthermore, it seems that *T. hockingsi* only makes use of local knowledge of the brood comb when deciding to place new brood cells, whereas *T. carbonaria* could make some building decisions based on knowledge of the total structure. We translated the species-specific algorithms into agent-based lattice swarm computer simulations of the cell construction process for the two species. These simulations produced representations of brood combs that are similar to those seen in vivo, suggesting that our biological rules are realistic.

Keywords Brood cell · Nest construction · Stigmergic algorithm

1 Introduction

The nests of social insects are often highly elaborate, complex and, to our eyes, beautiful structures. The construction of the nest involves the activities of many, sometimes thousands of individuals. For example, a particular worker honey bee's lifetime contribution to nest construction might be to work on 3–4 different cells of a comb, on different days, for a single week (Seeley 1982; Seeley and Kolmes 1991). It is thought that in many cases individual workers have no concept of what the overall nest architecture should be, or how to achieve it (Grassé 1959; Karsai 1999; Theraulaz and Bonabeau 1999; Camazine et al. 2001; Garnier et al. 2007). How then are the activities of hundreds of cell-building workers coordinated so that a symmetrical comb is constructed?

Instead of workers building to a 'blueprint' that is hardwired into their neurology, it is thought that the overall nest structure emerges from the construction rules followed by individual workers as they work on the modular units that make up the overall structure (Camazine et al. 2001). Compellingly realistic simulations of real-life nest structures can be generated using agent-based models that follow simple nest-building rules in silico (Theraulaz and Bonabeau 1995a; Karsai and Pénzes 1998, 2000). For example, paper-wasp-like combs can emerge from a simple algorithm that specifies that if two joined cells are present, the next cell is built between them, and if three joined cells are present, the next cell should be built in the cleft created by the three (Camazine et al. 2001).

Despite the pleasing similarity between in silico structures and real life combs, simulations of a comb construction process do not (and cannot) 'prove' that real-life workers use the same nest building rules as are specified in a computer algorithm (Camazine et al. 2001). Nonetheless, support for the idea that insect workers follow simple 'stigmergic' (Grassé 1959) rules to produce structures like combs would be increased if we could observe nest construction in vivo, derive the rules followed by individual workers as they build cells, make precise predictions about what the workers would do next based on our conception of the rules that they follow, and then observe the workers complete the work that we had predicted. The veracity of our hypothesis would be further improved if we could study two related species with different comb structures, discern the different rules followed by workers during the comb construction process, make testable predictions about where cells would be built based on the rules thus derived, and then produce lifelike models of the two different comb structures in silico by specifying the species-specific rules in two versions of an algorithm. This is what we have attempted to do here with two species of Australian stingless bee, *Tetragonula hockingsi* and *T. carbonaria*.

Tetragonula Moure, previously considered to be a subgenus of *Trigona* (s.l.), is a cosmopolitan genus of Asian and Australian stingless bees. In Australia, it is repre-

sented by 6 species: *T. carbonaria* Smith, *T. hockingsi* Cockerell, *T. mellipes* Friese, *T. davenporti* Franck, *T. clypearis* Friese, and *T. sapiens* Cockerell (Dollin et al. 1997; Franck et al. 2004; Rasmussen 2008). *T. carbonaria*, *T. hockingsi*, *T. mellipes*, and *T. davenporti* are collectively known as the monophyletic group 'Carbonaria' (Dollin et al. 1997; Franck et al. 2004).

Workers of the different species within the Carbonaria species group are morphologically similar, but can be readily distinguished based on DNA sequence data (Franck et al. 2004). *T. carbonaria* has the broadest distribution and is found from Sydney to Cooktown while *T. hockingsi* is distributed from Brisbane to the tip of Cape York (Dollin et al. 1997).

Stingless bees (Hymenoptera: Apidae: Meliponini) build brood cells within a nest in a space called the brood chamber. They do not reuse brood cells like many other Hymenoptera but constantly build new brood cells for the next cohort of young. These cells are destroyed after the adult bees have emerged. When the new cells are constructed at a specific place, this area is called the advancing front. The brood chamber is often surrounded by a multilayered envelope called an involucrum (Roubik 2006). Although highly eusocial, stingless bees produce brood in the manner of solitary bees, with an egg placed on top of a food mass in a sealed cell. Hence all brood cells are sealed, except for those yet to complete the provisioning and ovipositioning process (Roubik 2006). *Tetragonula carbonaria*, for example, builds approximately 5 batches of new cells each day with each batch consisting of approximately 80 new cells (Yamane et al. 1995).

Despite the morphological similarity of the workers, the nests of the various species of the Carbonaria species complex differ strongly in the morphology of their brood combs (Fig. 1, Michener 1961, Dollin et al. 1997). *T. hockingsi* and *T. davenporti* build what is probably the ancestral nest morphology: a loose aggregation of cells or cell clusters with numerous spaces between adjacent cells that are built more or less randomly with respect to the horizontal plane, and are joined by vertical wax pillars (Fig. 1(a)). In contrast, *T. carbonaria* builds combs with no spaces between the cells of the horizontal plane, in a continuous spiral (Figs. 1(b)–(d)). This difference is so striking that it remains the primary diagnostic feature for distinguishing *T. carbonaria* from the other species (Michener 1961; Dollin et al. 1997; Franck et al. 2004).

Here we present detailed observations of the comb building process of two contrasting species: the spiral comb of *T. carbonaria*, and the semi-comb of *T. hockingsi* (Fig. 1). By time-lapse photography of the comb construction process (detailed in Sect. 2), we generated a hypothesis concerning the simple rules followed by comb building workers for each species, and identified how these rules differed between the two species (summarized in Sects. 3 and 4). We then tested the ability of the rules derived from our observations to make predictions about where new cells will be constructed (see Sect. 5). In conjunction with these predictions, we further quantified the preferences of each species to build in the presence of two common configurations of existing brood cells. Finally, we incorporated our observations into realistic lattice swarm models (Theraulaz and Bonabeau 1995a, 1995b) in an attempt to reproduce the complex structures produced by the bees in real life and to explore if those structures could be reproduced using stigmergic rules. Details of our models are provided in Sect. 6 and results from our simulations appear in Sect. 7. In Sect. 8, we discuss the implications of our observations and simulation results and make some concluding remarks.

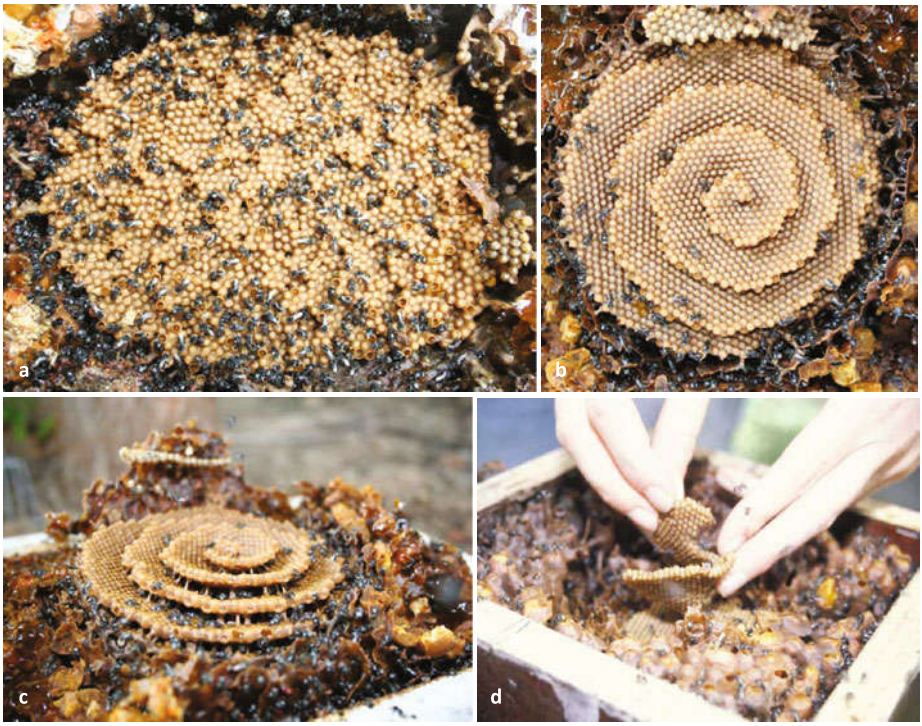


Fig. 1 Brood nest structure of the two *Tetragonula* species studied: (**a**) semi-comb structure of *T. hockingsi* (plan view); (**b**) spiral shaped brood of *T. carbonaria* (plan view); (**c**) the three dimensional structure of a *T. carbonaria* nest; (**d**) the upper portion of a *T. carbonaria* spiral stretched upwards

2 Observations on the cell construction process

Two colonies of each species, *T. carbonaria* and *T. hockingsi*, were obtained from suburban Brisbane and transferred to Sydney for observations. The colonies were housed in standard artificial nest boxes (Heard 1988; Heard and Dollin 2000) fitted with a transparent Perspex observation window. The colonies were placed in a controlled temperature room with access to the outside via plastic tubing.

Like all stingless bee species, *T. hockingsi* and *T. carbonaria* construct brood combs as part of the Provisioning and Oviposition Process, or POP. In the POP, workers first construct a new brood cell, and then provision the cell with brood food. The queen then lays in the freshly provisioned cell, and the workers then cap it. The details of the POP are species-specific, and have been described in detail for numerous species (reviewed in Drumond et al. 2000), including *T. carbonaria* (Yamane et al. 1995), but not *T. hockingsi*.

For all colonies we observed comb construction by direct observations and through video recording with a Digital Webcam Logitech 9800 Pro. Observations were made from January to February 2009 on a daily basis. We observed multiple POP batches for one hive from each species in the first month, which we used to derive the rules for brood construction. All observations were made on well established colonies.

By noting the locations of newly-constructed cells with respect to existing cells, we formed hypotheses about the cell-construction process for *T. carbonaria* and *T. hockingsi*.

In particular, we inferred the local rules used by workers concerning the locations of new cells.

After deriving the rules, we followed at least three POP batches for each of four colonies, which occur at 4 to 5 hour intervals in both species. High quality images taken before and after each POP were compared. Positions of potential sites for new cells before each POP, and where new cells were actually built after each POP, were mapped. We counted the number of potential building sites adjacent to the walls of two or three existing brood cells on a fraction of the brood comb before each POP and determined the number of these building sites that were filled after each POP. The average proportions of available two- and three-wall sites filled during each POP batch were used as the cell-building probabilities within our model.

3 The rules of construction of brood cells in *T. hockingsi*

Our observations of the building process of *T. hockingsi* are summarized below and in Fig. 2. In Fig. 2, pre-existing cells are represented by light grey cylinders and newly-constructed cells are drawn with a dark grey top. A 'layer' is a horizontal plane of clusters of cells. A 'pillar' is a vertical wax structure built to support a brood layer and provides a connector to allow movement of bees between layers. In spite of brood cells being cylindrical, bees build a new cell using sides or angles of existing cells, as if they were hexagonal.

(i) A new layer is initiated near the centre of the brood chamber and/or on the perimeter.
(ii) If cells are to be constructed on a cluster where there is only one existing cell, or a vertical pillar, a new cell is always constructed beside the existing one (Fig. 2(a)).
(iii) If on a layer there is a cluster of two adjacent cells and there are no three-cell cell-clusters present on the layer, a new cell is constructed in the cleft formed between the two adjacent cells (Fig. 2(b)).
(iv) If there are any three-cell clusters present on the layer, new cells are constructed in the clefts formed by the existing cells (Fig. 2(c)).
(v) Construction proceeds following rules (ii) to (iv) until a cluster reaches about 10 cells.
(vi) If there are two 10-cell clusters one cell diameter apart, a horizontal connection is built between the two 10-cell clusters. Immediately following construction of the connector, a new cell is constructed supported by the connector in the cleft formed by the two nearest cells (Fig. 2(d)).
(vii) When there is a cluster of approximately 10 cells, the next new cell is constructed 50 % higher than the existing layer (Fig. 2(e)). This offset cell initiates the new layer to be constructed above the existing layer. Cell construction proceeds on the, new, higher layer following rules (i) to (vii).
(viii) If a 10-cell cluster is at the edge of the brood chamber, instead of building an offset cell as in (vii) (Fig. 2(e)), a vertical pillar is constructed on top of the cell at the far edge near the chamber wall.
(ix) If there is a vertical pillar at the edge of the brood chamber the next cell is constructed adjacent to the pillar (Fig. 2(f)). Subsequent building on the new layer proceeds following rules (ii) to (vii).
(x) Cell clusters are constructed following rules (ii) to (ix) until layers on the edge of the brood comb reach the top of the chamber.

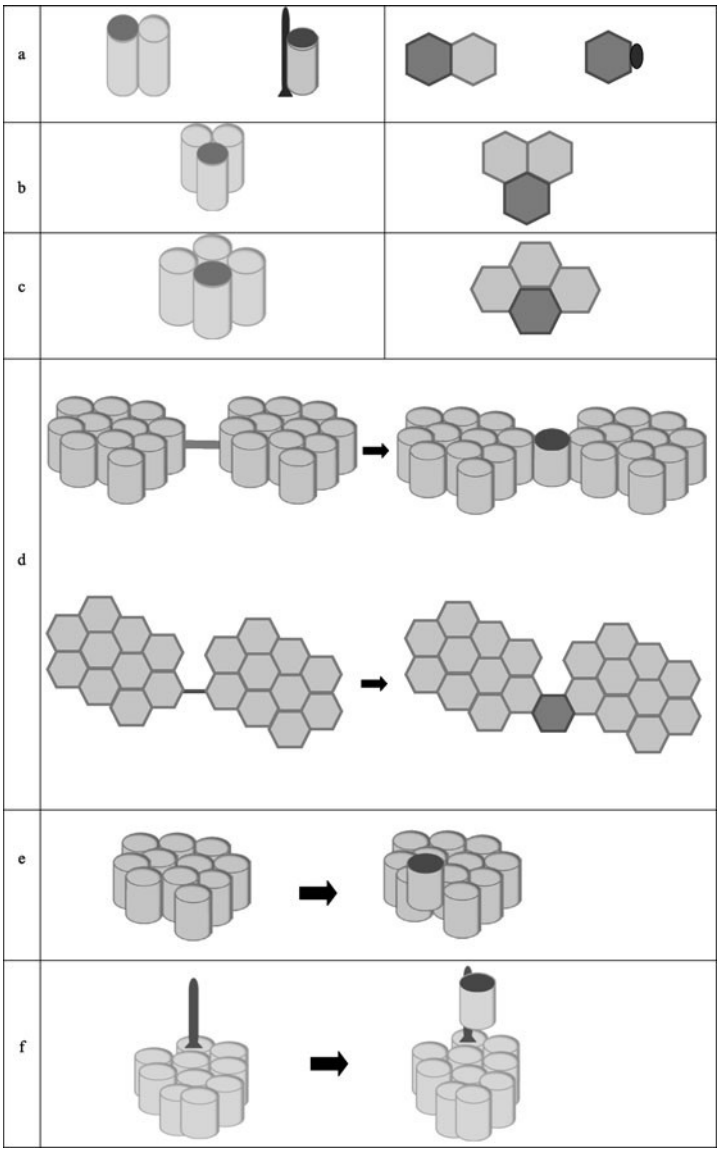


Fig. 2 Diagrams of rules derived for brood construction by *Tetragonula hockingsi*. Pre-existing cells are represented by *light grey cylinders* and newly-constructed cells are drawn with a *dark grey top*. *Hexagons* represent cells viewed from above: (**a**) new cells built beside a single cell or beside a pillar; (**b**) new cell built in the cleft formed by two pre-existing cells; (**c**) new cell built in between three pre-existing cells; (**d**) new cell attached to a connector between two groups of cells; (**e**) new cell built at a higher level in a three-wall cleft on the edge of a group of cells; (**f**) a new cell built beside a pillar previously built on top of a group of cells

4 The rules of construction of brood cells in *T. carbonaria*

Our observations of the building process of *T. carbonaria* are summarized below and in Fig. 3.

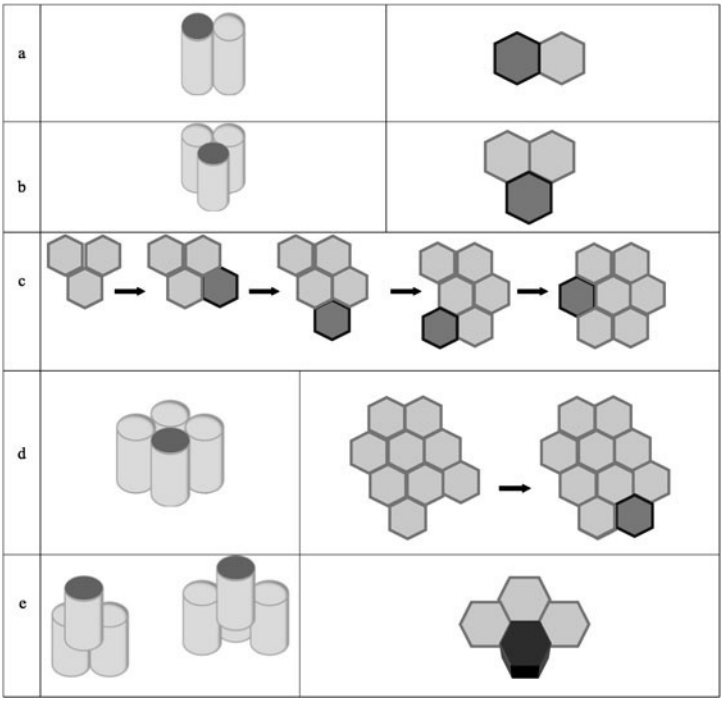


Fig. 3 Diagrams of rules derived for brood construction by *Tetragonula carbonaria*. Pre-existing cells are represented by *light grey cylinders* and newly constructed cells are drawn with a *dark grey top*. *Hexagons* represent cells viewed from above: (**a**) new cells built beside a single cell; (**b**) new cell built in the cleft of two pre-existing cells; (**c**) sequential building of new cells from a single previous cell, following the preference to build next to two pre-existing walls in (**b**); (**d**) new cell built in between three pre-existing cells; (**e**) new cell built at a higher level in two or three-wall clefts

(i) Cell construction is initiated from the centre of an existing layer.
(ii) The second cell is constructed adjacent to the existing cell (Fig. 3(a)).
(iii) The third cell is built in the cleft formed by the first two cells (Fig. 3(b)).
(iv) New cells are added in the cleft of every two cells in clockwise or anti-clockwise direction until a small layer of 7 cells is complete (Fig. 3(c)).
(v) If there are any three-cell clusters present on the layer, new cells are constructed in the clefts formed by the existing cells (Fig. 3(d)).
(vi) The subsequent cells are built in the three cell or two cell clefts formed on the perimeter of the emerging comb. The spiral shape is achieved because each cell is built slightly higher than the existing cell in either a clockwise or an anticlockwise direction.
(vii) Cell construction proceeds following rules (i) to (vi) until a layer reaches 2/3 of the chamber width. At this point a new layer is initiated by offsetting cells at the centre of the comb vertically by 50 % (Fig. 3(e)).
(viii) Cell construction stops on a layer when it reaches the chamber wall.

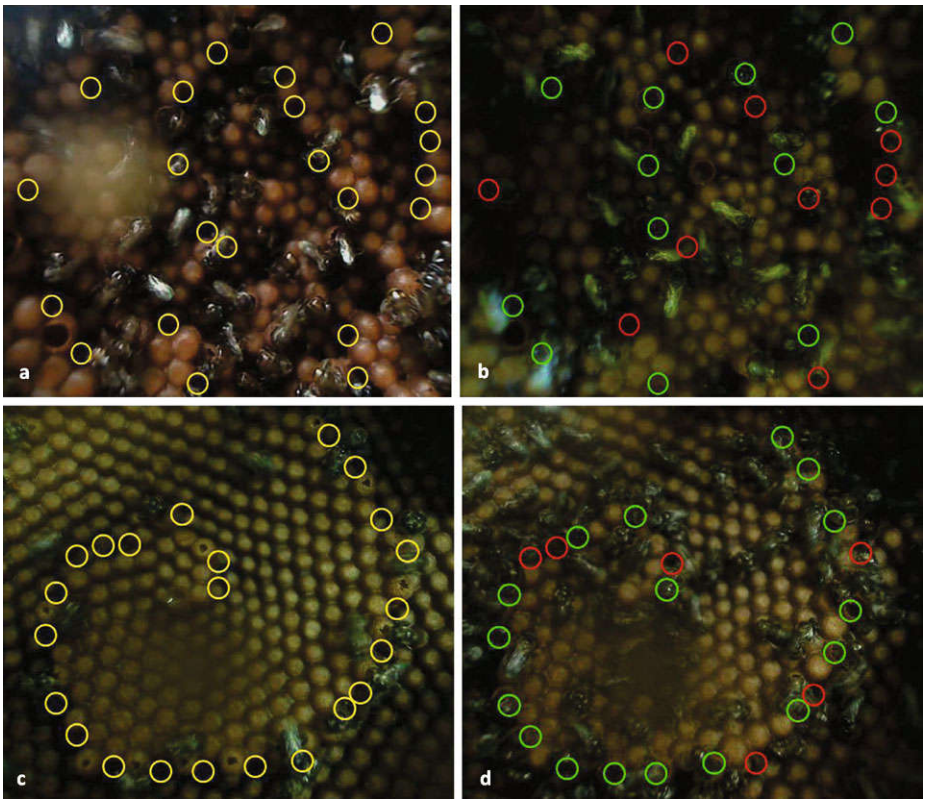


Fig. 4 Brood comb of the *Tetragonula* species studied showing the predicted sites for new cell construction in the clefts formed between existing cells (*yellow circles*), sites where cells were actually constructed (*green circles*) and the sites where we incorrectly predicted a cell would or would not appear (*red circles*) before and after the provisioning and oviposition process: (**a**) *T. hockingsi* before the POP; (**b**) *T. hockingsi* after the POP; (**c**) *T. carbonaria* before the POP; (**d**) *T. carbonaria* after the POP (Color figure online)

5 Testing the predictions of our rules

Using the hypothesized building rules derived from our observations in Sects. 3 and 4, we mapped the predicted locations of new cells on still images from video of the brood comb of two colonies from both species obtained during three inter-POP periods. We then compared our predictions against images taken after the next POP.

As an example, Fig. 4(a) shows a comb of *T. hockingsi* before a POP was initiated. The predicted locations for new cells, based on the rules above, are indicated by the yellow circles. In Fig. 4(b), we show the actual locations of newly constructed cells following the POP (green circles). Similarly, we show the predicted (Fig. 4(c)) and observed (Fig. 4(d)) locations of new cells for *T. carbonaria*. For instance, we predicted the positions of 23 new cells for *T. carbonaria* during one POP period. Of these predicted sites, the bees completed 17 during the next batch of POP (Fig. 4(d)). Thus we incorrectly predicted the location of 6 new cells. However, it is important to highlight that bees completed 20 cells after another POP batch, including many of those that we had predicted. Our overall success in predicting the sites of new cells during a single POP was 90 % for *T. carbonaria* and 65 % for *T. hockingsi*.

Table 1 The number of available and used building sites bounded by two or three existing cells

	Available		Used (*)		Proportion used	
	2 cells	3 cells	2 cells	3 cells	2 cells	3 cells
Tetragonula hockingsi						
Colony 1–POP 1	23	11	3	4	0.130	0.364
Colony 1–POP 2	38	24	6 + 2	13 + 1	0.211	0.583
Colony 1–POP 3	36	21	9	12	0.250	0.571
Colony 2–POP 1	46	19	8 + 2	11 + 5	0.217	0.842
Colony 2–POP 2	44	23	11 + 1	13 + 4	0.273	0.739
Colony 2–POP 3	53	14	9	8 + 3	0.259	0.786
				Mean	**0.223**	**0.648**
Tetragonula carbonaria						
Colony 1–POP 1	39	22	13	19 + 2	0.333	0.955
Colony 1–POP 2	41	15	11 + 1	8 + 4	0.293	0.800
Colony 1–POP 3	23	12	6	6 + 3	0.261	0.750
Colony 2–POP 1	17	23	3	22 + 1	0.118	1.000
Colony 2–POP 2	33	13	7	11	0.212	0.846
Colony 2–POP 3	28	15	9	15	0.321	1.000
				Mean	**0.256**	**0.892**

(*) numbers to the right of the plus sign indicate partially complete cells

Table 1 shows the breakdown of our observations over six POP periods for both species, listing the number of available building sites adjacent to two or three existing cells and the number of those sites subsequently built in by the end of each POP period. The mean proportion of sites bounded by two or three cells that were filled during a POP period were translated to building probabilities for use in our model (described in detail in Sect. 6.3).

6 Standard stigmergic lattice swarm model and extensions

We used the stigmergic lattice swarm model developed by Theraulaz and Bonabeau (1995a, 1995b) for simulating the building of complex nest architectures. The purpose of using a standard stigmergic lattice swarm model was twofold. First, we sought to determine if the local rules of construction that were observed for *T. hockingsi* and *T. carbonaria* were sufficient to reproduce structures through the use of simulation that were similar to real nests. Second, the results of our simulations add to observational evidence as to whether realistic nests could be constructed reliably either with or without some global knowledge of the overall structure. The building rules for *T. hockingsi* seemed to be based on purely local knowledge of small parts of the larger structure. Implicit in some of the building rules for *T. carbonaria* was apparent knowledge of the larger structure at a more global level, particularly the ability to identify the central part of the comb when building upwards.

Throughout our experimentation with the lattice swarm model, we found that our attempts to reproduce the complex architecture of a *T. carbonaria* brood comb were hampered by some of the model's restrictions, particularly on the vertical placement of brood cells. To

address this limitation, we modified the standard lattice swarm model to allow for building of brood cells at any vertical position, rather than only allowing building at a set of discrete vertical positions. The necessary modifications to the model are discussed in Sect. 6.3 and Appendix A. We adopt a modified version of the ODD protocol (Grimm et al. 2006) in the description of our implementation of the model of Theraulaz and Bonabeau (1995a, 1995b).

6.1 Model overview

Details of the lattice swarm model are complex, but the ideas behind the model are straightforward. A number of construction agents representing comb-building workers are randomly distributed throughout a three-dimensional domain. The domain comprises discrete flat horizontal layers of finite thickness. Each layer is made up of a lattice of regular hexagonal prisms; we refer to these hexagonal prisms as elements. Each agent examines its local surroundings, defined as the set of elements that share an edge with the element where an agent is currently located, including elements in the layers immediately above and below an agent. All the agents then compare their local surroundings with a list of local building rules referred to as stimuli-to-build. If the local surroundings match a stimulus-to-build identically, then an agent will construct a new cell at its current location with a given probability. Once any building action takes place, agents are randomly re-distributed throughout the domain at the beginning of the next time step before they examine their local surroundings again.

We now elaborate on our implementation of the above model.

Details of each horizontal layer of the domain were stored as regular, rectangular matrices. The numerical values of each of the elements of the matrices represented the presence or absence of building structures. Elements representing individual brood comb cells were set to 1, elements representing vertical wax pillars were set to 2, and elements representing empty space were set to 0. To construct the hexagonal geometry, where each element has 6 adjacent elements, we offset every even numbered row of the matrix, as illustrated in Fig. 5. Generally, the indices of the 6 elements adjacent to the element in row j column i were (row, column): $(j-1, i-1)$, $(j-1, i)$, $(j, i+1)$, $(j+1, i)$, $(j+1, i-1)$ and $(j, i-1)$ when j was odd, and $(j-1, i)$, $(j-1, i+1)$, $(j, i+1)$, $(j+1, i+1)$, $(j+1, i)$ and $(j, i-1)$ when j was even. There were 13 special cases where the element in row j, column i, had fewer than six nearest neighbors. These degenerate cases occurred when the element of interest was located either in one of the corners of the hexagonal array, or anywhere in the top row, or anywhere in the bottom row (different rules needed to be applied if the bottom row was oddly or evenly numbered), or in the first column (dependent on if the element was in an odd or even row) or in the last column (again dependent on if the element was in an odd or even row).

Construction agents were characterized by the row, j, column, i, and layer, z, where they were located at a particular time.

The model uses equally spaced, discrete time steps. At the beginning of each time step, all construction agents were each moved simultaneously to a random location in the domain. For *T. hockingsi* and *T. carbonaria* simulations, each of the row, column and layer coordinates that each agent was moved to were determined by selecting a uniformly distributed random number between 0.5 and $n_s + 0.5$ (where n_s was the total number of rows, columns or layers in the domain, depending on the coordinate being calculated), and then rounding the random number to the nearest integer. The random distribution of agents throughout the domain differed slightly from the standard approach used by Theraulaz and Bonabeau (1995a, 1995b), where agents were moved to

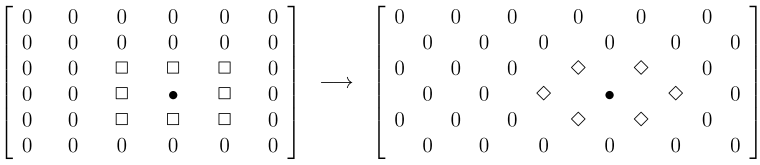


Fig. 5 A matrix can be used to store elements that are interpreted as being part of a hexagonal lattice. *In the left hand matrix*, which is drawn in the usual rectangular format, the element represented by *the filled circle* (•) has eight nearest neighbors, illustrated by *the square* (□) symbols. If even numbered rows of the matrix are treated as being offset by a half-step to the right, as *in the right hand matrix*, then the element represented by *the filled circle* only has six nearest neighbors, represented by *diamonds* (◊), which is equivalent to the cells of a hexagonal lattice. The indices of the nearest neighbors to a particular element of the hexagonal array are a function of whether the row containing the cell is odd or even numbered, as detailed in the main text

a random element adjacent to their previous location at the beginning of each time step. There is considerable time lag between the construction of sets of cells for *T. hockingsi* and *T. carbonaria* (of the order of 4 to 5 hours), and it would not be realistic for our agents to only move a very small distance over that time frame. Instead, our agents essentially sampled a random portion of the domain for potential building sites at each time step.

After all the agents had moved, they examined their local environments to determine the configuration and type of structures nearby. The local environment was defined as the set of elements that shared an edge with an agent located in row j, column i, layer z. The local environment of an agent consisted of cells in the agent's current layer (z), the layer immediately bellow the agent (layer $z-1$) and the layer immediately above the agent (layer $z+1$). Each agent would then compare its surroundings to each item on a list of stimuli-to-build. Graphical representations of the stimuli-to-build available to our agents are provided in Figs. 6 and 7. For each stimulus-to-build the focal agent is located in the central cell of layer z (marked with a cross). Empty cells are illustrated in white, cells with brood comb present are filled in gray, and cells containing components of vertical wax pillars are filled in black. Each row of the diagrams in Figs. 6 and 7 represents a different stimulus-to-build. The leftmost column uniquely identifies each stimulus for each species with a number of the form $n.m$, where n is the type of cell to be constructed at the agent's current location and m is the mth stimulus for construction of cell type n. Stimuli for building brood comb have $n=1$, stimuli for building vertical pillars have $n=2$. The numerical identifiers for each stimulus-to-build are preceded by either an h, for stimuli for *T. hockingsi*, or a c, for *T. carbonaria*. Probabilities of building in the presence of each stimulus are denoted by p_{build}. Wherever possible, these probabilities were determined empirically from our observations, or inferred using a combination of the empirically-determined probabilities and complementary observations (detailed in Sect. 6.3). Once all agents had examined their surroundings and it was determined if they were to build at their current location (row j, column i, layer z), all new cells were constructed simultaneously. The building of new cells concluded each time step.

6.2 Additional implementation details

In practice, comparisons between an agent's local environment and stimuli-to-build were made numerically rather than visually (see, for example, Pilat 2004). The first step in making

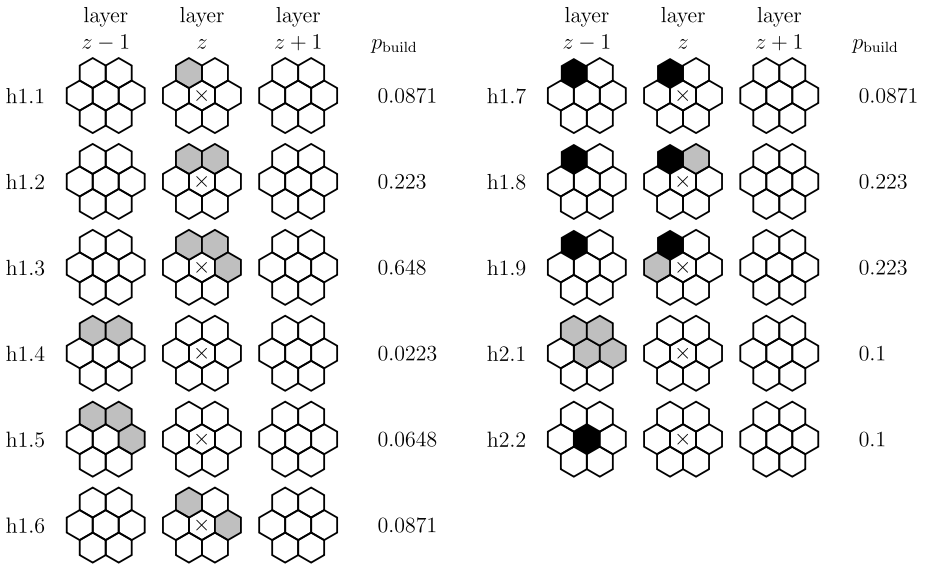


Fig. 6 Graphical representation of stimuli-to-build for *T. hockingsi*. *Each row of the diagram* corresponds to a different stimulus-to-build. *Columns*, *from left to right*, correspond to the layer below the agent ($z-1$), the layer containing the agent (z), and the layer above the agent ($z+1$). The agent is always located in the central cell of layer z. Numbering to the left of each stimulus-to-build is of the form $n.m$ where n indicates the type of block to be deposited by the agent in the central cell of layer z and m is a reference number used to identify each stimulus for each block type uniquely. $n=1$ corresponds to rules where brood cells are to be constructed. $n=2$ corresponds to construction of wax pillars. Existing brood cells are illustrated *in gray*, existing wax pillars are illustrated *in black*, and empty cells are *white*. Probabilities of depositing a new block in the presence of a stimulus-to-build are given to the right of each stimulus. The location of the agent examining its surroundings is marked with a cross. Stimuli-to-build h2.1 and h2.2 relate to the construction of wax pillars near the involucrum and are only applied within four rows or four columns of the edge of the domain

the comparison was to 'unwind' the elements surrounding an agent's location to construct a row vector representation of the local environment in a particular layer; see Fig. 8. For an agent located in layer z, row vectors representing the surrounding cells in layers $z-1$, z and $z+1$ were required. A 'surroundings' matrix was then constructed using all three row vectors, with the row vector representing layer $z-1$ becoming the first row of the matrix, the row vector representing layer z becoming the second row and the row vector representing surroundings in layer $z+1$ becoming the third row. Within our programme, stimuli-to-build were stored in an identical format to a surroundings matrix.

Our observations indicated that building preferences of the real bees were based on the number of adjacent cell walls and not on building on a particular side of existing cells. Therefore, all six rotations about the central cell of each listed building stimulus were included as stimuli-to-build.

All construction rules were applied stochastically. Whenever an agent encountered a recognized stimulus-to-build, a random number uniformly distributed between 0 and 1 would be generated. If the random number was less than the probability of building when faced with such a configuration, p_{build}, then the appropriate structure would be placed in the cell currently occupied by the agent.

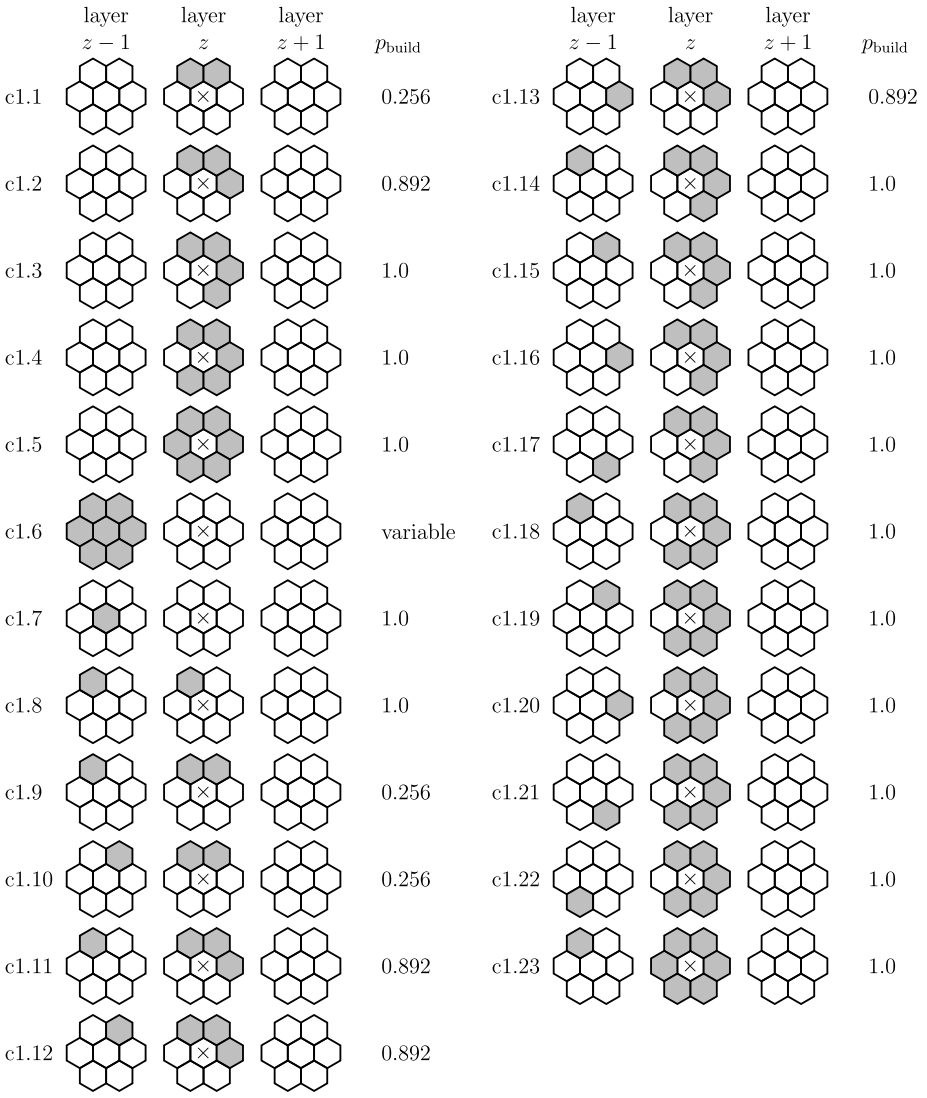


Fig. 7 Graphical representations of stimuli-to-build for *T. carbonaria* used by agents in the standard lattice swarm model. Stimulus-to-build c1.6 can only be applied in one of the central 4 cells of a given layer. Refer to Fig. 6 for further explanation of this diagram

6.3 Parameter estimation and initial conditions

T. hockingsi and *T. carbonaria* colonies consist of approximately 10,000 workers of which a small fraction are involved in cell construction. For our simulations we assumed that 2000 workers (agents) were involved in cell construction.

The standard artificial nest boxes where colonies were housed for observation had internal dimensions of approximately 150 mm × 230 mm × 200 mm. The median diameter and height of brood cells for *T. hockingsi* are 3.35 mm and 4.0 mm, respectively (Dollin

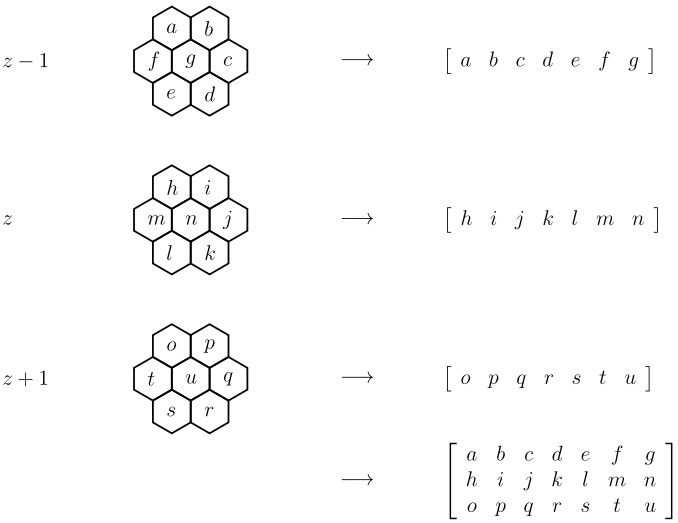


Fig. 8 The elements surrounding and including the central elements, g, n and u, in three consecutive layers, $z-1$, z and $z+1$, are re-written as row vectors. The row vectors are then combined to form a surroundings matrix. The surroundings matrix is used to compare an agent's surroundings with each stimulus-to-build, each of which is stored in the same format as the surroundings matrix

et al. 1997). The median diameter and height of brood cells for *T. carbonaria* are 2.5 mm and 3.5 mm, respectively. If we assume that a layer of cells is constructed so that cells are packed tightly in approximately the same configuration as a hexagonal lattice, then a single horizontal layer in the observation box would comprise an approximate maximum of 44×78 cells for *T. hockingsi* and 60×105 cells for *T. carbonaria*. Approximately 50 layers of *T. hockingsi* brood cells and 57 layers of *T. carbonaria* cells could be packed tightly into one of the observation boxes. Brood comb usually only covers approximately one third of the available floor space for both species (personal observations). In terms of number of cells, one third of the floor space would be covered by approximately 34×34 brood cells for *T. hockingsi* and 46×46 brood cells for *T. carbonaria*. Therefore, we chose domains of simulation of size $34 \times 34 \times 50$ elements for *T. hockingsi* and $46 \times 46 \times 57$ elements for *T. carbonaria*.

We used the observed mean probabilities of building next to two or three existing walls (see Table 1) as the basis for determining the values of p_{build} associated with each stimulus-to-build for both species. Stimuli-to-build for *T. hockingsi* and *T. carbonaria* are illustrated in Figs. 6 and 7; see Sect. 6.1 for details of the naming convention for all stimuli.

For *T. hockingsi* we set $p_{\text{build}} = 0.223$ for stimulus h1.2 (the stimulus derived from the real bees' tendency to build in the cleft of two adjacent, existing cells) and $p_{\text{build}} = 0.648$ for stimulus h1.3 (derived from the tendency to build in the cleft of three adjacent cells). *T. hockingsi* tends to build clusters of approximately ten cells. Stimuli h1.4 and h1.5 represented the starting point for new clusters of cells initiated by building upwards in the cleft formed by two or three adjacent cells, respectively. We set $p_{\text{build}} = 0.0223$ and $p_{\text{build}} = 0.0648$ for stimuli h1.4 and h1.5, respectively; these probabilities are 1/10th the probability of building in the same layer next to two or three existing brood cells. We set the probabilities of forming a connector to start a new cluster in the same layer (stimulus h1.1), connecting existing clusters (stimulus h1.6) or starting a new cluster connected to a wax pillar (stimulus h1.7)

as one tenth the sum of the probabilities of building next to either two or three existing cells (i.e. $p_{\text{build}} = 0.0871$). Stimuli h1.8 and h1.9 were an extension to the process illustrated in Fig. 2(f), where a second brood cell is placed next to a wax pillar and an existing brood cell. We set $p_{\text{build}} = 0.223$ for stimuli h1.8 and h1.9 due to their close association with stimulus h1.2. We had no quantified observational data for the frequency at which wax pillars were built on top of brood cells, so we approximated p_{build} as 0.1 for stimuli h2.1 and h2.2, close to the probabilities associated with starting a new cluster of cells. In reality, wax pillars are most commonly constructed near the involucrum (at the edges of the domain for simulation purposes), so stimuli-to-build h2.1 and h2.2 were restricted to working within four rows or columns of the edge of the domain.

For *T. carbonaria* we set $p_{\text{build}} = 0.256$ for stimulus c1.1 (the stimulus for building in a cleft formed by two adjacent existing cells) and $p_{\text{build}} = 0.892$ for stimulus c1.2 (the stimulus for building in the cleft formed by three adjacent cells). We used observation (viii) from Sect. 4 as the basis for stimuli to build upwards. First, we allowed for a central vertical connecting cell to be placed on any of the four brood cells located at the centre of a horizontal layer (stimulus c1.6). Our observations indicated that *T. carbonaria* tend to build upwards from the centre when a circular layer of cells fills approximately two thirds of the width of the domain. In our simulations, such a circular layer would comprise a little over 1000 brood cells. To match observations, we regulated the tendency to build upward by setting $p_{\text{build}} = 0$ for stimulus c1.6 initially, and then increasing p_{build} by increments of $1/1000$ for every new cell that was constructed. Each time a central connector was built using stimulus c1.6, we reset p_{build} to zero for this stimulus. Stimuli c1.7 and c1.8 relate to initiating building in the layer above the central connector following Fig. 3(a); we set $p_{\text{build}} = 1$ for both these stimuli. p_{build} was set to 0.256 for stimuli c1.9 and c1.10, and to 0.892 for stimuli c1.11, c1.12 and c1.13, which are rules for building adjacent to existing two and three cell groupings close to the central connector. During preliminary calculations, we employed stimuli-to-build based on Fig. 3(e) (and identical to stimuli h1.4 and h1.5), which reflect the tendency of *T. carbonaria* bees to build upwards as they are building outwards. We found that implementing the rules based on Fig. 3(e) resulted in structures that did not resemble *T. carbonaria* brood combs. Two of the key reasons for the discrepancy between real and simulated structures were that our agents built upwards irrespective of whether they were building towards or away from the centre of the structure, and that the large discrete jumps in building height imposed by the model did not reflect the subtle incline that *T. carbonaria* brood combs possess. We abandoned stimuli based on Fig. 3(e) when using the standard lattice swarm model, but revisited them when we modified the model to allow for continuous variation in building heights (see Appendix A). Throughout the preliminary calculations, we also tested whether or not it was necessary to confine the vertical connector to the centre of the domain; we found that it was necessary to do so as in some instances multiple connectors could be built with a gap of a single element between them, and close building of connectors would hinder building on the layer above because the local surroundings did not match a stimulus to build. Another difficulty in reproducing the brood comb of *T. carbonaria* was that we found that fissures were forming in each of the layers of the comb. We explored this problem in detail, see Appendix B, and ultimately determined that it was necessary to add some stimuli that fill in any gaps that could not be dealt with by stimuli c1.1 and c1.2. The additional gap-filling rules are listed as stimuli c1.3 to c1.5 and stimuli c1.14 to c1.23. $p_{\text{build}} = 1$ for all gap-filling stimuli. It is rare that even the early stages of fissures are evident in real *T. carbonaria* nests. Interestingly, after performing the calculations described in Appendix B, we noticed that gaps such as those dealt with by stimulus c1.3 also appear in real *T. carbonaria* combs, but they are quickly filled.

Table 2 Correspondence between the observations of Sects. 3 and 4 and stimuli-to-build that appear in Figs. 6 and 7

Species	Observation	Stimulus-to-build	Notes
T. hockingsi	(ii) (Fig. 2(a))	h1.1	
	(iii) (Fig. 2(b))	h1.2	
	(iv) (Fig. 2(c))	h1.3	
	(v)	–	Implicit in probabilities associated with starting new clusters.
	(vi) (Fig. 2(d))	h1.6	
	(vii) (Fig. 2(e))	h1.4, h1.5	
	(viii)	h2.1, h2.2	Only used within four rows or columns of the edge of the domain (near involucrum).
	(ix) (Fig. 2(f))	h1.7, h1.8, h1.9	
T. carbonaria (standard model)	(ii) (Fig. 3(a))	–	Forms part of initial condition
	(iii) (Fig. 3(b))	c1.1	
	(iv) (Fig. 3(c))	–	Implicit in stimuli c1.1 and c1.2. There is no control on building clockwise or anti-clockwise. Basis for initial condition.
	(v) (Fig. 3(d))	c1.2	
	(vi)	–	No stimulus.
	(vii) (Fig. 3(e))	–	Implicit in the variable probability associated with building upwards for c1.6. Stimuli c1.7 to c1.23 model early stages of new layer construction.
	–	c1.3, c1.4, c1.5	Rules included to fill-in gaps in the brood comb.

Table 2 summarizes the connections between the observations in Sects. 3 and 4 and the stimuli-to-build in Figs. 6 and 7 for both species.

The initial building conditions for both species had the central element in the bottom layer (layer 2 in practice) of the domain and the six elements in the bottom layer adjacent to the central element filled with brood comb initially; all other potential building sites were empty at time $t = 0$ for each simulation. This initial condition was equivalent to the early stages of a layer being formed for *T. carbonaria* (see Figs. 3(a)–(c)), or the partial completion of a cluster of cells for *T. hockingsi*.

The *T. carbonaria*-like brood comb produced by a standard lattice swarm model lacked some of the defining features of a real brood comb. These defining features included the details of the spiral and the tendency to build incrementally upwards moving away from the centre of the structure. Both of these features required more flexibility in the vertical placement of cells than is allowed by the discrete layers of a standard lattice swarm model. We extended the standard lattice swarm model to allow for building at any height within the domain to determine if we could more accurately reproduce the structure of a *T. carbonaria* nest. We also modeled the tendency of *T. carbonaria* to preferentially build upwards when

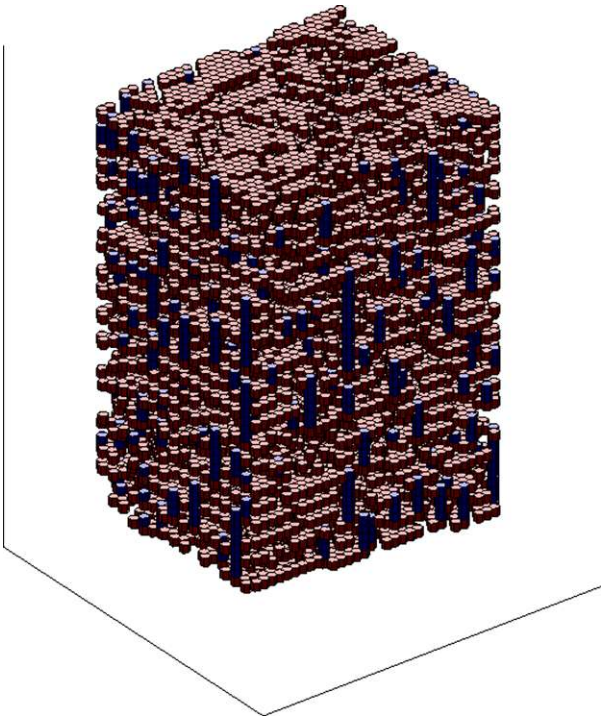


Fig. 9 Brood comb constructed by our model *T. hockingsi* agents. Brood cells are represented by *red hexagonal prisms* and wax pillars constructed near the edge of the domain are represented by *blue hexagonal prisms*. The domain of the simulation consisted of 50 horizontal layers of brood comb, each comprising 34×34 hexagonal cells. 2000 agents were involved in the construction of the brood comb. The illustrated structure comprises 13134 brood cells and 706 wax pillar components (Color figure online)

building in a particular sense (clockwise or anti-clockwise) to try the reproduce the conical-helix seen in a real *T. carbonaria* nest. Extensions to the model are detailed in Appendix A.

7 Simulation results

The stigmergic lattice swarm model was capable of producing a complex nest architecture that resembles the brood comb of *T. hockingsi*. Example output from the model is given by a three dimensional perspective plot provided in Fig. 9, and cross-sections of some of the layers of the comb are provided in Fig. 10. In both figures, brood comb cells are represented by red hexagonal prisms, and wax pillars are illustrated as blue hexagonal prisms. In Fig. 9, a light source (and shadows) have been included to better illustrate the three dimensional structure. Distinct clusters of groups of approximately ten cells are visible throughout the structure, similar to a real brood comb. At the edges of the brood comb, the structure has adopted the shape of the domain boundaries. In reality, the involucrum surrounding *T. hockingsi*'s brood comb is round, so real combs comprise circular, rather than square horizontal cross-sections. The similarities between real and simulated brood combs where only local rules for building were employed suggests that our observed building rules were realistic, and it is plausible that a *T. hockingsi* brood comb is constructed via a similar stigmergic process.

The standard lattice swarm model with the addition of the non-stigmergic building rule for the construction of a vertical connector at the centre of the domain (c1.6) was capable of constructing a brood comb that bears many of the features of a real *T. carbonaria* comb. A three dimensional plot of output from the model is provided in Fig. 11, with horizontal

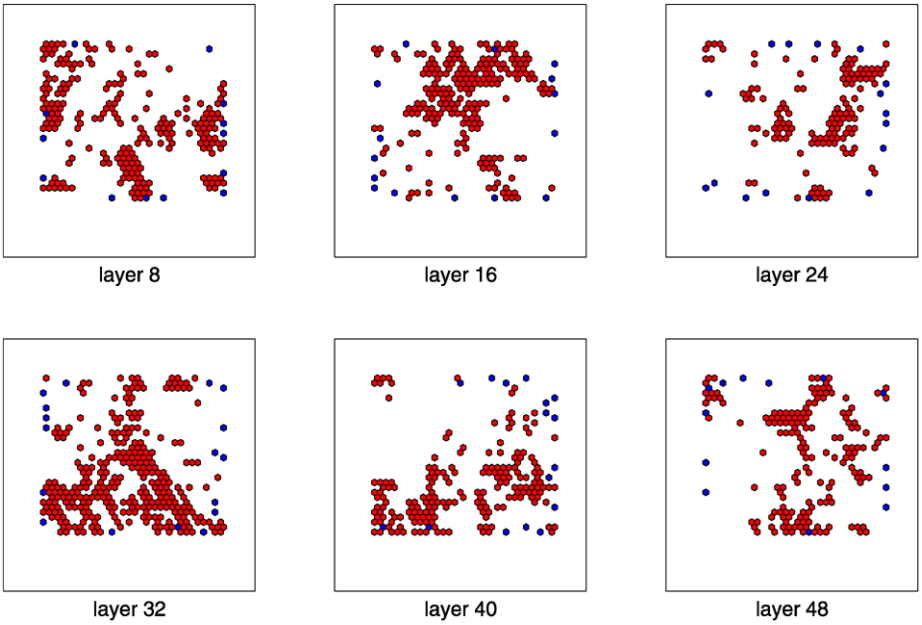
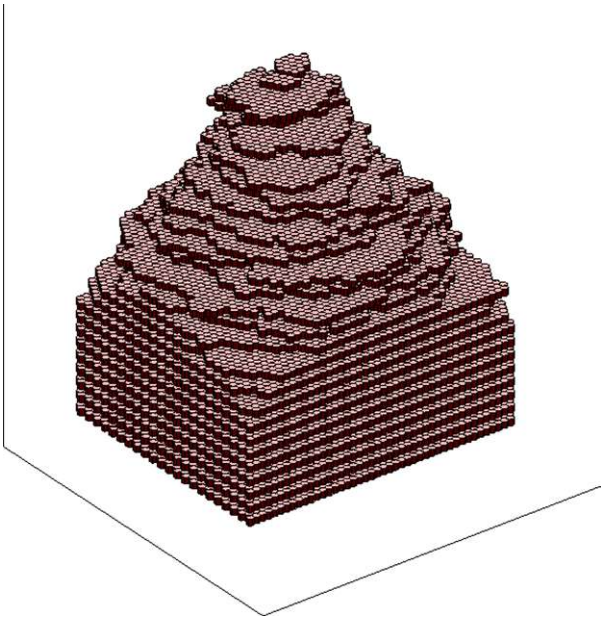


Fig. 10 Plan view of selected horizontal layers of the brood comb in Fig. 9. The pictured layers correspond to $z = 8$, 16, 24, 32, 40 and 48 (Color figure online)

Fig. 11 Brood comb constructed by our model *T. carbonaria* agents using the standard lattice swarm model. Brood cells are represented by *red hexagonal prisms*. The domain of the simulation consisted of 57 horizontal layers of brood comb, each comprising 46×46 hexagonal cells. 2000 agents were involved in the construction of the brood comb. The illustrated structure comprises 31799 brood cells



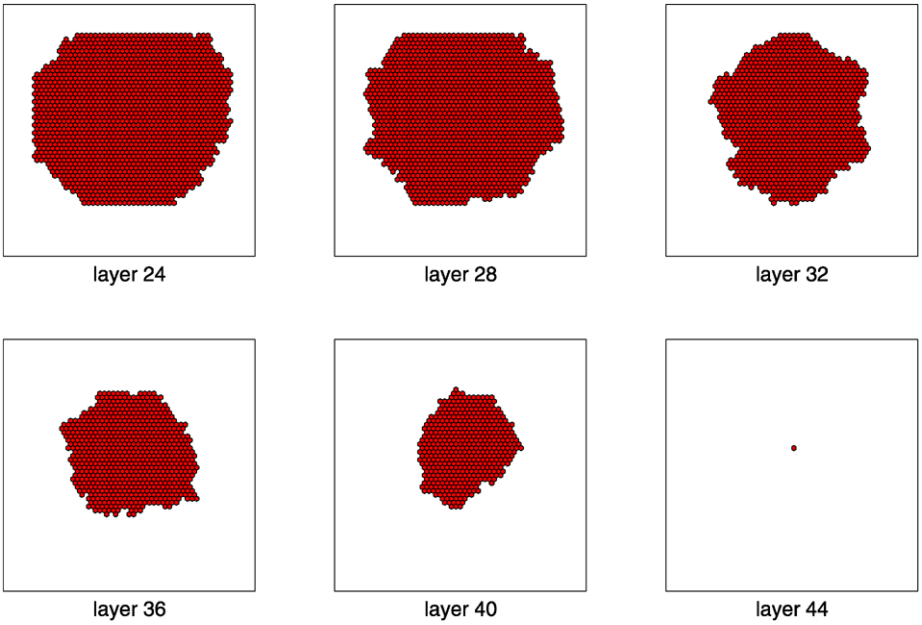


Fig. 12 Plan view of selected horizontal layers of the brood comb in Fig. 11. The pictured layers correspond to $z = 24$, 28, 32, 36, 40 and 44

cross sections of the comb provided in Fig. 12. At the upper levels of the simulated comb the circular layering that is evident in real combs is present. The squarer shape of the comb in lower layers is due to the shape of the domain's boundary.

The least convincing nest architecture came from simulations performed using the extended version of the lattice swarm model described in Appendix A, where building of cells could occur at any height. Within this model, we attempted to replicate the spiral seen in *T. carbonaria*'s brood comb by using an initial condition that would be conducive to spiral formation, and making our agents build incrementally upwards when cells were built upwards in a clockwise direction relative to the heights of existing brood cells. Figure 13 provides a plot of a structure produced by the extended lattice swarm model. The general upward curve of brood cells moving outwards from the centre of the comb that is seen in real *T. carbonaria* brood combs is evident, but there are fissures in the comb in spite of stimuli being used to fill in any gaps. The particular simulation illustrated stalled because no buildable sites could be found at the centre of the domain during the phase where cells were to be built upwards from that region. Hence, many fewer cells are present than in the figures for standard lattice swarm simulations of *T. hockingsi* and *T. carbonaria*.

8 Conclusions

Our behavioral observations allowed us to postulate a set of rules for the construction of brood combs of two closely related Australian *Tetragonula* stingless bee species. Once determined, these rules could be translated into stimuli-to-build for use in the stigmergic lattice swarm model developed by Theraulaz and Bonabeau (1995a, 1995b). The resulting simu-

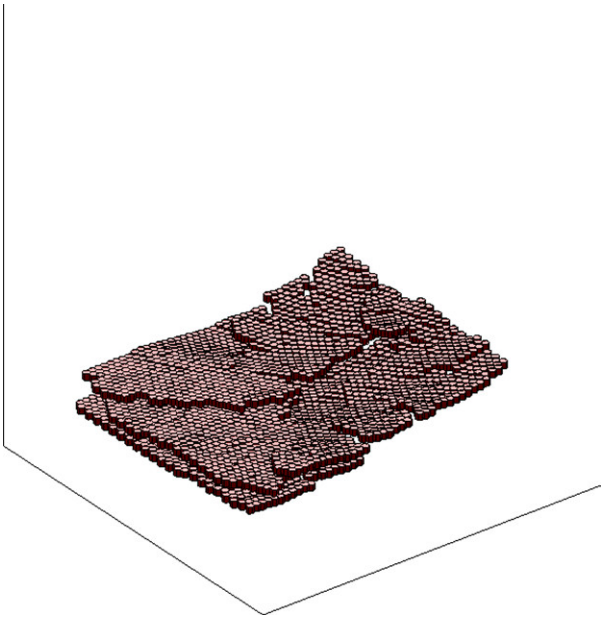


Fig. 13 Brood comb constructed by our model *T. carbonaria* agents using the extended version of the lattice swarm model that allows for greater flexibility in vertical brood cell placement. 2000 agents were involved in the construction process. The illustrated structure comprises 3185 brood cells

lations produced representations of comb structures that are similar to the morphologies of the natural combs of the two species.

Our simulations successfully generated the overall structure of a *T. hockingsi* brood nest: the resulting structure was made up of many interconnected clusters of brood comb cells—similar to those observed in nature. We had less success in reproducing a structure that resembled a *T. carbonaria* brood nest. Over short distances, the cells were connected in a continuous manner, similarly to the natural comb. At a larger scale, the simulations replicated the layered appearance of a *T. carbonaria* brood comb, although the spiral structure did not emerge. We sought to overcome some of the discrepancies between real and simulated *T. carbonaria* nests by making several extensions to the lattice swarm model. The first major extension removed the restriction that only allowed brood cells to be placed at particular vertical heights. The other major extension made agents build upwards relative to nearby cells in a clockwise direction. Even with these extensions, our simulation was unable to reproduce the *T. carbonaria* spiral, although it did generate some additional features of the natural brood comb such as the upward curving of the structure moving outwards from the centre.

Our behavioral observations show that there are two fundamental similarities in the choice of site to build a new brood cell by both *T. hockingsi* and *T. carbonaria*. These similarities are the preferences of both species to build adjacent to existing clusters of two or three brood cells. In addition to the two species of stingless bee studied here, other species such as *Polistes* wasps exhibit similar preferences when constructing new cells (Downing and Jeanne 1990; Karsai and Theraulaz 1995; Karsai and Pénzes 1996, 1998, 2000).

The details of the building processes employed by *T. hockingsi* and *T. carbonaria* differ in detail beyond the two and three-walled building site preferences. *T. hockingsi* tends to build clusters of approximately ten brood cells; often new clusters of cells are initiated by placing a new brood cell significantly higher than other cells in an existing cluster, usually of the order of half a cell height. In contrast, subtle height differences in the placement of adjacent brood cells in a *T. carbonaria* nest contribute to the brood comb's concavity. The preference

to build upwards in either a clockwise or anti-clockwise sense results in the characteristic spiral of *T. carbonaria*.

Both our observations and simulations suggest that an important difference between the cell construction processes of *T. hockingsi* and *T. carbonaria* is whether or not each species build their brood comb through stigmergy alone. *T. hockingsi* seems to rely on purely local stimuli to decide on the placement of new cells, and our simulation results suggest that a *T. hockingsi*-like brood comb can be reproduced using a stigmergic algorithm. Implicit in our observations of *T. carbonaria* is that the species could make use of some of the global properties of its brood comb to decide on cell placement. The use of global properties is evident in the tendency to start building from the centre of the domain once the brood comb fills approximately two thirds of the brood chamber's width and in the preferential construction in either a clockwise or anticlockwise direction. Following our observations and preliminary simulations, we found that the use of a non-stigmergic building rule, based around confining the placement of a central connector cell to the centre of the domain, was necessary to produce a brood comb that resembled a *T. carbonaria* nest.

It is still plausible that *T. carbonaria* relies only on local stimuli to decide on cell placement, but not in the restricted sense in which only local stimuli are applied in the standard lattice swarm model used here. For example, the centre of a layer of cells could be identified as a local minimum in cell height by bees walking across the brood comb. Bees working on cell construction might not only take into account the placement of existing cells immediately adjacent to a potential building site, but might take note of cells a little further away that could still reasonably be regarded as part of a local stimulus. The complexity of identifying building rules in reality and applying such rules within a simulation increases dramatically as a function of the number of cells considered, but it might still be tractable to extract and analyze such information. It is possible that another important consideration in constructing a *T. carbonaria* brood comb, particularly the spiral, is that the workers may explicitly choose not to build in particular locations. Such a decision not to build could be a function of the age of a cell, or a bi-product of a strong preference to build next to younger cells. The effect that cell age might have on construction work was examined in detail in the theoretical study of Karsai and Pénzes (2000) where it was found that biologically realistic cell arrangements like those made by *Polistes dominulus* could be achieved by simulation by preferentially connecting the youngest existing cell to its next youngest nearest neighbor. It should be noted that the building rules used by Karsai and Pénzes (2000) were not strictly stigmergic because they relied on evaluation and comparison of multiple potential building sites. Beyond the choice of building sites for new brood cells, future modeling work might make use of more realistic movement rules for agents. Such movement rules could include exploration of elements close to the location of each agent via a short random walk, or rules that only allow agents to 'walk' across solid surfaces, such as the involucrum, or existing brood cells.

Roubik (2006) observed that individual colonies of stingless bees from a variety of genera (*Melipona*, *Plebia*, *Plebina*, *Nannotrigona*, *Trigona* and *Tetragona*) would at different times produce brood combs that were either a series of connected, stacked, flat, circular components or a continuous spiral. It is still uncertain what triggers these changes in architecture, but possible influences include: low titers of queen pheromone due to aging, food availability, infections and changing seasons. In the case of *Tetragonula*, *T. carbonaria* and *T. hockingsi* colonies are often found in nature side by side, and the characteristic shape of each species' brood comb remains constant throughout the entire year (personal observations). This suggests that the differences in brood comb structure are likely due to genetic differences, rather than environmental influences. Given the genetic similarities between

T. hockingsi and *T. carbonaria* it is extraordinary to note that the fundamental differences in the building activity of these two species could be plausibly encoded by a single gene, or a small group of genes.

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RMB and TMS contributed equally to this work; RMB made the behavioral observations and derived the algorithms; TMS conducted the computer simulations; MRM provided assistance with technical aspects of the modeling and advice on the manuscript; TAH provided the hives and discussed behavioral data; BPO performed the literature review. RMB, TMS and BPO wrote the paper. This work was supported by an Australian Research Council grant to Madeleine Beekman and MRM. RMB was supported by an Endeavour Fellowship and a CNPq Fellowship (PDE 201470/2008-0).

Appendix A: Model extensions

Here we describe extensions to the standard lattice swarm model that allowed for cells to be built at any height within the domain, and an in-built tendency for all agents to build upwards in a clockwise or anti-clockwise direction. Implementation of these extensions required some alteration to stimuli-to-build for *T. carbonaria* and the initial building condition, which are also detailed below.

The random row and column that each agent was moved to at the beginning of each time step was calculated using the same method described in Sect. 6.1. The random height that each agent was moved to was a uniformly distributed random number between 0.5 and $n_l + 0.5$, where n_l was the vertical extent of the domain measured in cell heights. Domain dimensions used in our simulations were $46 \times 46 \times 57$ brood cells.

Each agent examined its local surroundings in turn; if an agent determined that it was at a buildable site, it constructed a new cell immediately. This is different to the standard model, where building did not take place until all agents examined their surroundings. For the purposes of comparing local surroundings with stimuli-to-build, an agent located at a vertical height of z_c identified all cells with the z coordinate of the top of each cell, z_t, in the range $z_c - h \leq z_t < z_c + h$ as belonging to layer z, where h was half the height of a brood comb cell. Similarly, existing brood cells with $z_c - 3h \leq z_t < z_c - h$ were identified as belonging to layer $z-1$, and existing brood cells with $z_c + h \leq z_t < z_c + 3h$ were identified as belonging to layer $z+1$. Existing cells were no longer recorded as part of a matrix for each horizontal layer, but rather stored in vectors identifying the row, column and the location of the top of each cell. All cells were assumed to be of the same height ($2h = 1$ cell height for our simulations). The coordinates in these vectors were used to construct a surroundings matrix for each agent.

We built in a preference for building upwards when moving clockwise relative to existing cells. To determine relative clockwise/anti-clockwise placement of cells we drew vectors from the centre of the domain to the coordinates of a focal agent, $\mathbf{f}$, and to the coordinates of the centre of adjacent existing cells, $\mathbf{b}$. We formed the vector cross product $\mathbf{b} \times \mathbf{f}$, and then examined the sign of the vertical component of the resulting vector. If the vertical component was positive then the placement of an existing cell was anti-clockwise relative to an agent's location. If the vertical component was negative then the placement of an existing cell was clockwise relative to an agent's location. The building height of a new cell was set as the maximum height of any cells anti-clockwise of an agent's location, plus a small increment of 0.1 cell heights. If there were no cells anti-clockwise of an agent, then building height was set as the minimum height of any cells that were clockwise relative to the agent.

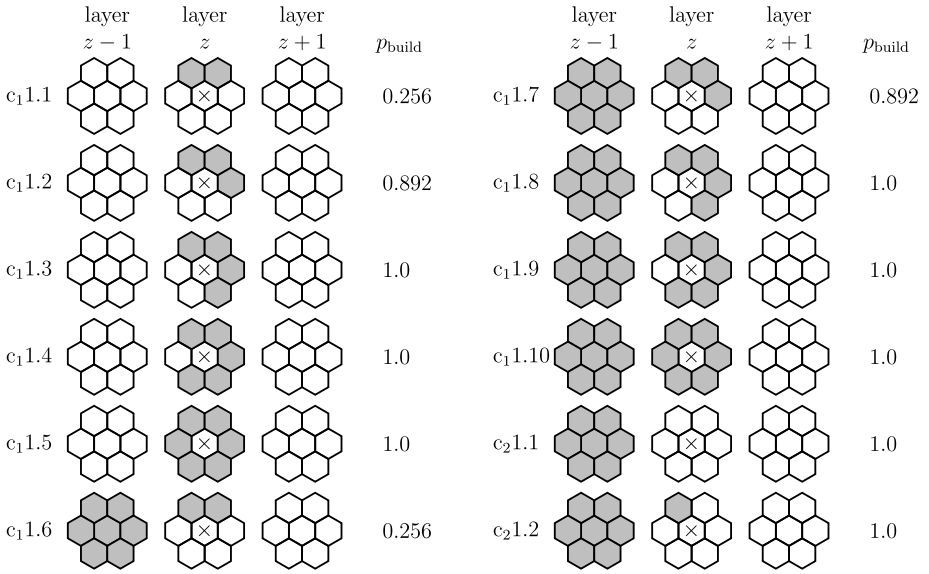

Fig. 14 Graphical representations of stimuli-to-build for *T. carbonaria* used by agents in the extended lattice swarm model. Stimuli preceded by c_1 are available to agents during stage 1 of the two alternating stages of construction. Stimuli preceded by c_2 are available during stage 2, and can only be applied in one of the central 4 cells of a horizontal cross-section of the domain. Refer to Fig. 6 for further explanation of this figure

We explicitly applied the extended lattice swarm model in two alternating stages; such a multi-stage or modular construction algorithm is referred to as a coordinated building algorithm (see Theraulaz and Bonabeau 1995b for details). Stage 1 related to the filling of a layer with 1058 brood cells (the approximate number of cells required to construct a circular region that filled two thirds of the width of the domain). Stage 2 related to building 2 cells near the centre of a layer to initiate a new layer before returning to stage 1. The stimuli-to-build for these two stages are provided in Fig. 14, and are closely related to the stimuli used for *T. carbonaria* in the standard model. We set $p_{\text{build}} = 0.256$ for stimuli $c_1 1.1$ and $c_1 1.6$ in stage 1—the stimuli for building in the cleft formed by two adjacent existing cells. Stimuli $c_1 1.6$ applied to brood cells built above (but not usually directly connected to) cells considered to be part of layer $z-1$. We set $p_{\text{build}} = 0.892$ for stimuli $c_1 1.2$ and $c_1 1.7$ in stage 1 (stimuli for building next to a cleft formed by three cells). Stimuli $c_1 1.3$ to $c_1 1.5$ and $c_1 1.8$ to $c_1 1.10$ in stage 1 were necessary gap filling rules equivalent to those used in the standard lattice swarm model. Stimuli $c_2 1.1$ and $c_2 1.2$ during stage 2 represented the tendency of *T. carbonaria* to build upwards from the centre of the domain. Building heights for the top of any cells built during stage 2 were selected as 1 cell height above the top of any cells identified as being part of layer $z-1$ by an agent. Application of both stage 2 stimuli was restricted to the centre of the domain in exactly the same way as stimulus c1.6 was restricted for the standard lattice swarm model.

Table 3 summarizes the connections between the observations in Sect. 4 and the stimuli-to-build in Fig. 14 for *T. carbonaria*.

We used a similar initial condition for building with the extended model to that used for the standard model. The central element in the bottom layer of the domain was filled with a brood comb cell. The top of this brood comb cell was located at $z = 2$. Six additional brood comb cells were connected to each of the six walls of the initial hexagonal cell. These

Table 3 Correspondence between Sect. 4 observations and stimuli-to-build in Fig. 14

Species	Observation	Stimulus-to-build	Notes
T. carbonaria (extended model)	(ii) (Fig. 3(a))	$c_2 1.2$	
	(iii) (Fig. 3(b))	$c_1 1.1$, $c_1 1.6$	
	(iv) (Fig. 3(c))	–	Basis for initial condition. Tendency to build upwards in clockwise sense is in-built.
	(v) (Fig. 3(d))	$c_1 1.2$, $c_1 1.7$	
	(vi)	–	Clockwise building increments.
	(vii) (Fig. 3(e))	$c_2 1.1$, $c_2 1.2$	Active once approximately 2/3 the width of the domain is filled.
	–	$c_1 1.3$, $c_1 1.4$, $c_1 1.5$, $c_1 1.8$, $c_1 1.9$, $c_1 1.10$	Rules included to fill-in gaps in the brood comb.

brood cells were placed with their tops at $z = 2.1$, 2.2, 2.3, 2.4, 2.5 and 2.6, respectively, arranged so that the height of each cell increased when moving clockwise around the edge of the central cell. This initial condition was intended to help facilitate the construction of the spiral shape of a *T. carbonaria*-like nest.

Appendix B: Modifications to *T. carbonaria* stimuli-to-build

As with *T. hockingsi*, *T. carbonaria* was observed to have a preference for constructing new brood cells next to the walls of pairs or trios of existing cells; see observations (iii) and (iv) in Sect. 3 and observations (iii) and (v) in Sect. 4. Such a preference for the positioning of new structures is not unique to the two *Tetragonula* species that we observed. It is also known that some species of wasp, such as those belonging to the genus *Polistes*, have the same preference (see Fig. 19.19 in Camazine et al. 2001). When only rules for building based on the presence of two or three adjacent, existing cells are applied deterministically, the agents of a stigmergic algorithm tend to produce structures that initially have holes in them that can lead to the construction of distinct, disconnected lobes; (see, for example, Fig. 12(a) in Theraulaz and Bonabeau 1999). The reason that the holes lead to the formation of lobes is that they correspond to configurations of cells that are not included on the list of stimuli-to-build. One example is an empty cell that has had four of its adjacent cells filled with brood comb; in such a case the central cell will never be filled. At best the agents can build near the unfillable hole, but the likely result is the formation of a fissure separating sections of brood comb. Holes and lobes are undesirable when trying to reproduce the well-connected geometry of a *T. carbonaria* brood comb. To limit the production of lobes, Theraulaz and Bonabeau (1999) applied their rules for construction probabilistically with the probability of building when an agent encountered two existing adjacent cells set to 0.057 and the probability of construction when an agent encountered three existing adjacent cells set to 0.55. The probabilities were derived from observations of *Polistes* wasps and the result was a much rounder grouping of cells (see Theraulaz and Bonabeau 1999, Fig. 12(b)).

Preliminary simulations suggested that even the application of building rules using the probabilities noted by Theraulaz and Bonabeau (1999) was insufficient to completely prevent the appearance of unbuildable sites, and then fissures, within our model structures. This was partially due to the horizontal extent of the structures produced by our model. The

structures illustrated in Fig. 12 of Theraulaz and Bonabeau (1999) lie on a region of approximately 20 × 20 hexagonal cells, and even at that extent, unbuildable sites are visible on the edges of the rounder structure in Fig. 12(b); for example, one unbuildable site appears near the top right hand corner where an empty cell is surrounded by four filled neighboring cells. To quantify the effectiveness of applying the probabilities of building used by Theraulaz and Bonabeau (1999) in preventing the formation of unbuildable sites within a domain we performed two sets of simulations where the only available stimuli-to-build were stimuli c1.1 and c1.2 from the *T. carbonaria* building rules. In the first set of simulations, both rules were applied with certainty (the probability of building when encountering either stimulus was set to 1). In the second set of simulations, stimulus c1.1 was applied with probability 0.057 and stimulus c1.2 was applied with probability 0.55. Each set of simulations was comprised of 1000 replicates. Simulations were performed in a domain with 20 horizontal layers and each horizontal layer was made up of 20 × 20 hexagonal cells. We used 20 agents for each simulation which were free to move anywhere in the domain, but all construction was limited to the second layer due to the initial condition where the cell in row 10, column 10, layer 2 and the six cells adjacent to that cell were filled with brood comb. Simulations were run until agents constructed 120 additional brood comb cells. After all simulations were complete we identified all empty cells in the buildable layer (layer 2). We then characterized each of the empty cells as being surrounded by zeros, as being a buildable site if an empty cell and its surrounding six cells corresponded to a stimuli-to-build, or being unbuildable if there were filled cells next to the empty cell but the entire configuration did not correspond to a stimulus-to-build. We found that the application of stimuli c1.1 and c1.2 using the probabilities derived by Theraulaz and Bonabeau (1999) was effective in reducing the number of unbuildable sites. The mean number of unbuildable sites that formed across 1000 simulations when the stimuli were applied deterministically was 120.7 with a standard deviation of 5.3. The mean number of unbuildable sites that formed across 1000 simulations when the stimuli were applied stochastically was 26.7 with a standard deviation of 4.8. However, even with the substantial reduction in the number of unbuildable sites in a domain with layers with 20 × 20 cells, the presence of even a few unbuildable sites in the smaller domain would ultimately lead to the formation of lobes in a larger structure.

Ultimately, it was necessary for us to add rules to our stimuli-to-build to allow our agents to fill in the gaps in a structure by constructing new cells when a potential building site was surrounded by 4, 5 or 6 existing cells (stimuli-to-build c1.3, c1.4 and c1.5 for *T. carbonaria* in Fig. 7).

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