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Phil. Trans. R. Soc. Lond. B 1998 **353**, 1561-1576
doi: 10.1098/rstb.1998.0310

THE ROYAL SOCIETY

A model for the emergence of pillars, walls and royal chambers in termite nests

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A simple model of the emergence of pillars in termite nests by Deneubourg is modified to include several additional features that break the homogeneity of the original model: (i) a convection air stream that drives molecules of pheromone along a given direction; (ii) a net flux of individuals in a specific direction; (iii) a well-defined self-maintained pheromone trail; and (iv) a pheromonal template representing the effect of the presence of a queen that continuously emits pheromone. It is shown that, under certain conditions, pillars are transformed into walls or galleries or chambers, and that this transformation may not be driven by any change in the termites' behaviour. Because the same type of response at the individual level can generate different patterns under different conditions, and because previous construction modifies current building conditions, we hypothesize that nest complexity can result from the unfolding of a morphogenetic process that progressively generates a diversity of history-dependent structures.

Keywords: termites; nest construction; self-organization; template; morphogenesis

1. INTRODUCTION

'The first detailed account of termites was given to the Royal Society of London in 1781 by Henry Smeathman who had returned from a voyage to Guinea. It was said that his paper was received with some scepticism, which is scarcely surprising, for he described small insects that could build towers standing well above the height of a man.' (Howse 1970.)

In social insects, and particularly in termites, there may be several orders of magnitude of difference between the size of an individual and the size of a nest built by the colony: for instance, the ratio (nest size)–(individual size) may reach 10^4 to 10^5 in some termite species (30 m diameter mounds have been observed in *Macrotermes bellicosus* (Grassé 1984), whereas individuals are at most a few millimetres long). In this respect, termites are among the most impressive builders in nature (Smeathman 1781): only man has been able to attain such ratios. Furthermore, nest structures found in termites often combine a high degree of regularity (for example, nests of the termite *Apicotermes*) with a large diversity of subunits that allow complex regulatory mechanisms to be implemented (see, for example, Grassé (1984) and Lüscher (1961)). The building activities of termites can even transform landscapes over large scales and, for example, lead to the formation of regular band structures, or to the emergence of regularly spaced domes distributed over several square kilometres (Grassé 1984). Among the most impressive structures are those produced by African termites of the subfamily Macrotermitinae: the fungus growers. A mature nest of a *Macrotermes* species usually has six main types of structure in each mound.

1. Roughly cone shaped outer walls, which can be up to 60 cm thick. These protective outer walls often have conspicuous ribs containing ventilation ducts which run from the base of the mound towards its summit (see figure 1*a*). The walls protect the colony from both the climate and predators (such as aardvarks and army ants).
2. Brood chambers within the central 'hive' area. They have a laminar structure and contain the nurseries where the young termites are raised. The hive consists of thin horizontal lamellae supported by pillars.
3. A base plate with (in some cases) spiral cooling vents. Collins (1979) discovered that, in some colonies of this species, the base plate is equipped with vanes, presumably to promote cooling (Bristow & Holt 1987). Collins (1979, p. 243) provides the following description of these structures: 'in plan view, the plate is circular, up to 3.5 m across, and supported by a solid pillar approximately one-quarter of the width of the plate. Very small cones protruding from the underside of the

Received 14 April 1997 *Accepted* 10 June 1997

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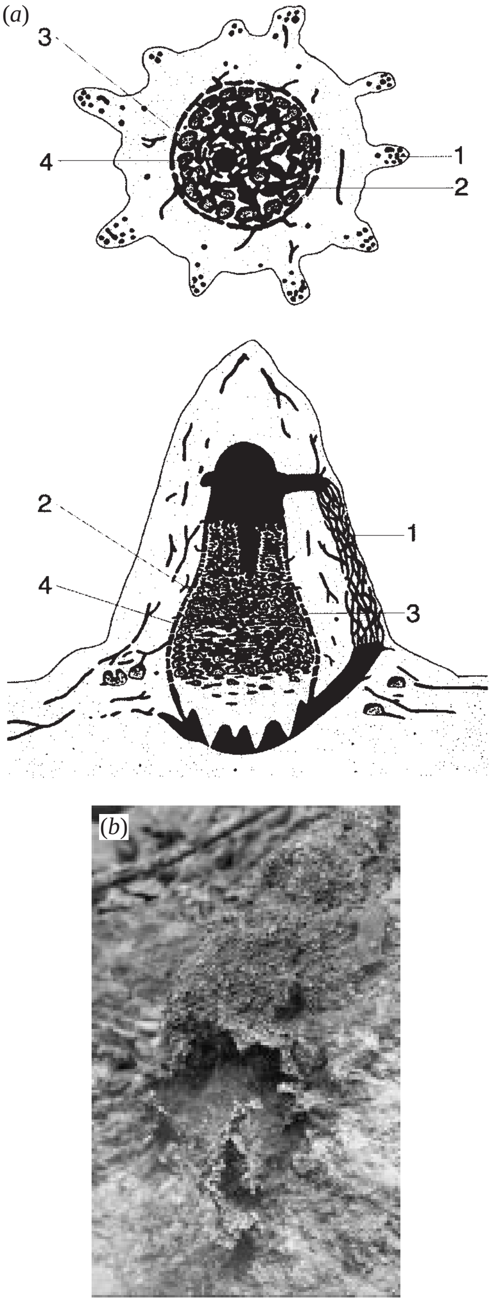

Figure 1. (*a*) Cross-section of a *Macrotermes* mound (after Lüscher 1961): (1) walls containing ventilation ducts; (2) brood chambers; (3) base plate; (4) royal chamber. (*b*) Covered gallery leading to a foraging site (*Macrotermes muelleri*) (after Grassé 1984).

> plate fit into cavities on the pillar surface, but plate and pillar are not physically bonded, the plate merely resting on the pillar surface. The underside of the base-plate bears a remarkable series of clay vanes . . . encircling the plate in a series of spirals. Three or four complete turns of the spiral are common before a break occurs and a new spiral begins. The vane is stalactitic in cross-section, up to 2.5 cm thick at its attachment, 1 mm thick and very fragile at the irregularly wavy fine edge. The vanes are generally coated with a white layer of mineral salts, increasing with age of mound.'

4. A royal chamber, which is a thick-walled protective bunker only slightly larger than its largest occupant, the queen, with a few minute holes in its walls through which workers can pass. It tends to be located in the best-protected central part of the nest, often immediately below ground level beneath the hive. This chamber is a very important part of the nest, as it's where eggs are produced by the queen. The king remains in the chamber with the queen, and copulation takes place regularly (this is necessary because, for example, a queen of *Macrotermes natalensis* can produce 36 000 eggs per day (Grassé 1984)).
5. Fungus gardens, draped around the hive and consisting of special galleries or combs that lie between the inner hive and the outer walls. *Macrotermes* rely on their fungus gardens for much of their nutritional supplies.
6. Peripheral galleries constructed both above and below ground which connect the mound to its foraging sites (see figure 1*b*; Grassé 1984).

In such a structure, air ventilation is important and the air conditioning system of a *Macrotermes natalensis* mound works in the following way. The outer walls of many mounds are heavily fluted with substantial 'ribs' running in fairly straight lines from the base of the walls towards their summit. The ribs house part of a system of air ducts. Near the top of the nest, six to 12 radial canals, the thickness of a person's arm, pass one each into the top of the ribs and, as they descend, divide into smaller branches 2–3 cm in diameter. More or less at ground level, these branches reunite to form once again larger ducts 10–15 cm in diameter which open below the nursery area in the cellar region. The microclimatic measurements that Lüscher (1956, 1961) took at various points in this system demonstrate air circulation driven by convection currents. The activity of the termites and fermentation in their fungus gardens, in the central area, warms the air and raises its carbon dioxide content. The air rises to the upper air space (the attic) and is then forced out by the slight excess pressure generated through the radial ducts which are very close to the surface of the ribs. These fluted ribs act as lungs: carbon dioxide diffuses out, and oxygen diffuses in, through the thin walls of the ribs. The ducted air is cooled in the same process and sinks to the cellar which has the lowest temperature and the lowest concentration of carbon dioxide. The termite mound is able to exchange gases through parts of its walls without opening up holes through which enemies could enter.

As air circulation seems so important, it is not surprising that certain termites use their tactile senses to detect minute air movements. There is evidence that individuals can detect air movements one-thousandth the amplitude of those present in a closed room (Howse 1966). Bruinsma (1979) showed that air streams can affect building behaviour and help to close holes in the walls of the nest.

These observations raise the key questions of how a collection of individual termites working both literally and figuratively in the dark can build a mound of such astonishing size and complexity. Obviously, one should not seek the origin of nest complexity in the ability of individual termites to process a large quantity of information, but rather in the multitude of stimulus-responses resulting from the relatively simple behaviours of interacting termites, but virtually nothing is known about the exact nature of these elementary stimulus-response steps and how they must be connected in space and time, neither experimentally nor theoretically. Understanding that simple interactions among termites, and between termites and their environment, may be sufficient to produce complex structures is useful but one must go beyond this mere assertion to actually show how such structures as termite nests are built. Attempts in this direction are in fact rare: Grassé's stigmergy (Grassé 1959, 1984), Bruinsma's experimental work (Bruinsma 1979), and Deneubourg's theoretical model (Deneubourg 1977) of the initiation of pillars, are, to the best of our knowledge, the only works that deal seriously with the logic of construction in termites.

Our aim in this paper is to extend Deneubourg's model (inspired by Keller-Segel's (1971) model of chemotactic pattern formation in bacteria) to include the effects of heterogeneities or asymmetric fluxes (air stream, flux of individuals, trail, chemical template). These are small theoretical additions to the model, but they have some profound consequences: (i) most can be related to experimental results (Bruinsma 1979); and (ii) they will show that one single type of individual behaviour can lead to the formation of different structures, depending on environmental conditions.

Point (ii) may seem trivial to anyone with a mathematical background. Mathematically, it is well known that different initial conditions or spatial geometries can lead to widely different patterns in reaction–diffusion models. This recognition, however, is not trivial within an ethological context, as it shows that there is no need to invoke individual complexity (that is, the ability of an individual to modulate his behaviour according to numerous stimuli and to process large amounts of information) to explain changes in behaviour occurring in response to changes in environmental conditions. Our approach follows from this recognition and shows that instead of being completely coded, one way or another, in individual behaviour, the modified structure may result, at least in part, from exogeneous physical constraints.

Such constraints are due to heterogeneities in the environment, or to specific chemical or physical properties of the building material and of the signals and cues used during the building process under given climatic conditions. These constraints often have nonlinear effects which may result in important differences in the final structure. Furthermore, because previous construction may influence building stimuli, building responses (and behaviour itself) can be affected to produce new structures, leading to the complex heterogeneous structures mentioned in the first paragraph.

The building activity of social insects has been the focus of many empirical studies (Hansell 1984), in ants (e.g. Hölldobler & Wilson 1990), bees (e.g. Darchen 1959), wasps (Jeanne 1975; Downing & Jeanne 1988, 1990; Wenzel 1991; Karsai & Theraulaz 1995), and termites (Grassé 1959, 1984; Bruinsma 1979), but very few models of collective building behaviour are available in the literature (Gallais-Hammono & Chauvin 1972; Sudd 1975; Deneubourg 1977; Belic *et al.* 1986; Skarka *et al.* 1990; Franks *et al.* 1992; Karsai & Penzes 1993; Theraulaz & Bonabeau 1995), perhaps because nests of social insects seem too complex to model. Yet, some previous models have been insightful in showing how concepts borrowed from self-organization may apply to the description of building behaviour (Deneubourg 1977; Belic *et al.* 1986; Skarka *et al.* 1990; Deneubourg & Franks 1995; Franks & Deneubourg 1998). We will attempt to show that simple extensions of such models can, in certain cases, explain a lot of the complexity of real nests, without requiring concomitant complexity at the individual level.

2. EXPERIMENTAL BASIS

As mentioned earlier, few works have been devoted to the dynamics of building in termites. Most of our knowledge results from Bruinsma's (1979) PhD dissertation. He studied the building behaviour of *Macrotermes subhyalinus* termites taken from mounds near Kajiado, Kenya. The experiments involved observing groups of workers of different sizes around a queen. Individual termites pick up a piece of soil near the queen, transport the pellet to the site of deposition (at a distance of about 2–5 cm from the queen) where they deposit and cement the pellet. This leads to the construction of pillars or columns, that are lengthened until they reach a height of 0.5–0.8 cm, when workers start to build lamellae which are extended and connected to one another to form a roof over the queen. Interpillar spaces are also filled with pellets to produce walls. At the group level, one of the most noticeable dynamic effects during the construction process is that the rate of building increases very rapidly, especially in large groups. Furthermore, the per capita rate of building increases disproportionately with the number of builders. For example, after 60 min, in a group of 20 workers there were about 0.2 depositions per worker on average, whereas after a similar interval, a group of 80 workers makes about 2.5 depositions per worker, on average (see figure 2*a*) (the saturation in this increase observed beyond 80 workers certainly means that the intrinsic maximum rate of building per worker has been reached). This 'snowball effect', and the influence of group size, are typical of systems involving positive feedback and correspond to the observation by Grassé (1984, p. 523) that a critical number of workers is required to obtain a coherent structure. Figure 2*b* shows the mean number of depositions (during 10 min) per worker added 50 min after the beginning of Bruinsma's experiment, where worker groups of different sizes were put in the experimental arena with the queen: we see that the number of depositions per added worker increases significantly with the number, N, of workers already present from $t=0$ to $t=50$ min ($N=10, 20, 40, 80, 160, 320$).

Bruinsma (1979) provides evidence for three positive feedback mechanisms in the termite *Macrotermes subhyalinus*: the first two involve a cement pheromone and spatial heterogeneities, which can work as sources of short-range positive feedback, the third is a long-range positive feedback resulting from the trail pheromone.

1. After picking up a soil pellet, each worker tends to perform a walk before depositing its building material (at the beginning of the process, this walk looks random, but trail laying and trail following eventually

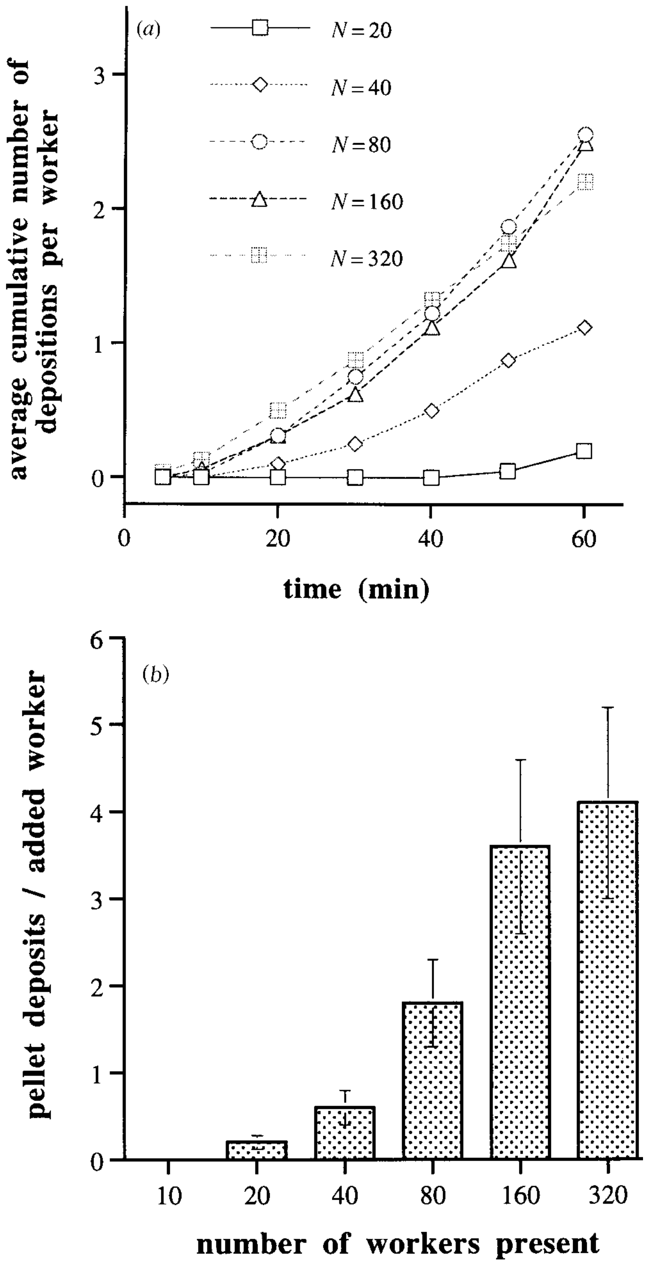

Figure 2. (*a*) Mean number (average over six to ten experiments; error bars not shown) of depositions per worker during 60 min for groups of different sizes (20, 40, 80, 320) (after Bruinsma (1979), pp. 14 and 36). (*b*) Mean number of depositions per worker introduced 50 min after the beginning of Bruinsma's (1979) experiment, where worker groups of different sizes (10, 20, 40, 80, 160, 320) were put in the experimental arena with the queen. The measures were taken in the 10 min following introduction. Error bars result from 30 replicates of the experiment (after Bruinsma (1979), p. 37).

generate walks directly to deposition sites). During this procedure, the worker turns the soil pellet into a paste by continuously kneading the pellet with its mandibles and adding an oral secretion. Bruinsma (1979) was able to show that this secretion contains an attractive cement pheromone that helps to coordinate building. The cement pheromone loses it biological activity within a few minutes of deposition. The cement pheromone: (i) orients workers from a distance of 1–2 cm toward a deposition site; (ii) induces pellet picking-up behaviour in this area; and (iii) induces deposition of pellets on other recently deposited pellets.

2. Spatial heterogeneities, such as small obstacles, also attract workers within a small radius and stimulate them to deposit along the heterogeneity.
3. The trail pheromone plays two roles in the building activity: (i) the trail is a source of long-range positive feedback (more and more workers can be recruited by such trails to building sites and such workers add to the trails, making them more and more attractive (Stuart 1967)); and (ii) it plays a role in the shaping of the galleries which are built above and along the trail.

We mentioned previously that the cement pheromone can attract workers in a zone with a radius of 1–2 cm. This is sufficient to induce a regular distribution of pellet deposits. Indeed Bruinsma (1979) showed that workers unable to lay trail are able to concentrate their activity at certain sites (and are therefore attracted by cement pheromone toward these sites). In summary, workers of the species *Macrotermes* use soil pellets impregnated with pheromone to build pillars. There are two successive phases which take place. First, the non-coordinated phase is characterized by a random deposition of pellets. This phase lasts until one of the deposits reaches a critical size. Then, the coordination phase starts if the group of builders is sufficiently large: pillars or strips emerge. The existence of an initial deposit of soil pellets stimulates workers to accumulate more material through a positive feedback mechanism, because the accumulation of material reinforces the attractivity of deposits through the diffusing pheromone emitted by the pellets. This autocatalytic, 'snowball effect' leads to the coordinated phase. If the number of builders is too small, the pheromone disappears between two successive passages by workers, and the amplification mechanism cannot work; only the non-coordinated phase is observed.

The physogastric queen of *Macrotermes subhyalinus* emits a pheromone that diffuses and creates a pheromonal template in the form of a decreasing gradient around her (figure 3*a*). Bruinsma (1979) has shown that a concentration window exists, or a threshold, that controls the workers' building activities: a worker deposits a soil pellet if the concentration of pheromone is within this window or exceeds the threshold. Otherwise, they do not deposit any pellet or may even destroy existing walls. If one places a freshly killed physogastric queen in various positions, walls are built at a more or less constant distance from the queen's body (figure 3*b*,*c*), following its contours, while a wax dummy of the queen does not stimulate construction. (The distance at which the cell is built around a dead queen is, however, slightly smaller than around a live queen: Bruinsma (1979) suggested that this could be owing to the fact that air puffs, emitted by a live queen from her spiracles, affect the transport properties of the medium in which pheromones diffuse.)

In this description, we have focused on the main organizing role played by the queen's building pheromone which creates a chemical template. For simplicity we will not consider tactile stimuli and other pheromones, such as cement and trail pheromones, which facilitate the

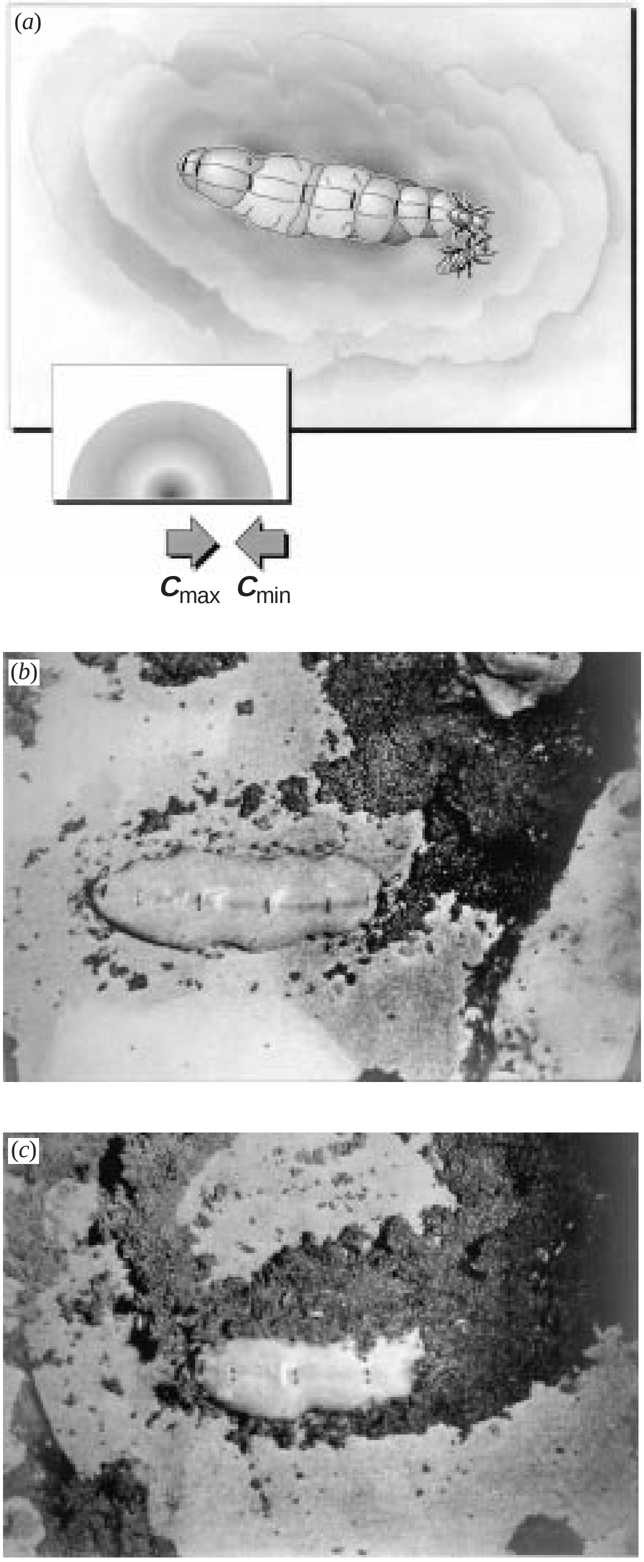

Figure 3. (*a*) Sketch of pheromonal template, representing the physogastric queen and the king. Different pheromone concentrations are represented by different grey levels. ($C_{\min}$, $C_{\max}$) is the concentration window within which depositions are most likely to occur. (*b*) Chamber being built around the queen (after Grassé (1984), p. 536), 1 h 18 min after the colony has been placed in a Petri dish and provided with soil pellets. The queen was 9 cm long, the Petri dish 25 cm in diameter and 4 cm high. A total of 1200 individuals were present in the Petri dish. (*c*) Same as *b* (after Grassé (1984), p. 540), 5 h 15 min after placement in the Petri dish.

recruitment, coordination and orientation of individual workers, and which determine the detailed shape of the reconstructed chamber.

Further evidence for the effect of the pheromone emitted by the queen comes from Bruinsma's (1979) study of the effect of a laminar air flow of low velocity (maximum relevant speed about 1 cm s^{-1} at 0.5 cm above soil level—which is about the maximum height for a worker's antennae) along the queen's body axis. Such an air flow influenced the initiation of walls around the queen, and particularly on the distance between the queen and deposition sites. Bruinsma observed a reduction in the mean distance at which soil pellets were deposited: while the average distance for the first 20 deposits was about 2 cm from the queen (in the direction orthogonal to the queen's body axis) in the absence of air flow, it was about 1.5 cm from the queen with the air flow. Other experiments indicate the primary role played by the pheromone produced and released by the queen. Hence, the experiment involving a slow air flow suggests that pheromone is convected along the air current away from the queen in a direction orthogonal to the air stream (it would have been interesting to measure the distance between the queen and the deposits along the air flow), leading to a smaller pheromonal template around the queen. As a corollary, it does not seem necessary to invoke a modification of the workers' behaviour to explain this modification in the size of the royal cell: the modified dynamics of the pheromone should be sufficient. We will show that a similar conclusion accounts for a transformation of pillars into walls as an air current is added. Although individual behaviour can in principle be modified by the air flow, and this is not absurd given the extreme sensitivity of termites to air movements, it becomes clear that a single behaviour pattern can lead to several types of structures in different environmental conditions.

3. MODEL

(a) *Basic model*

A simple model, introduced by Deneubourg (1977), shows how the different parameters characterizing the random walk of the termites, the attractivity of the cement pheromone, the diffusion of the pheromone, and so on, determine the regular distance between pillars. Let $H(r,t)$ be the concentration, at location r and time t, of the cement pheromone that is emitted into air by the deposited material and diffuses freely in air. Equation (1) describes the dynamics of H:

$$\delta_t H = k_2 P - k_4 H + D_H \nabla^2 H, \tag{1}$$

where k_2 is the amount of pheromone emitted per unit of deposited material per unit time, the total production being the product $k_2 P$, with P representing the amount of deposited material that is still active. $-k_4 H$ represents pheromone decay and $D_H \nabla^2 H$ accounts for pheromone diffusion, with D_H being the (constant) diffusion coefficient. In equation (1) and in the rest of the paper, δ_t denotes derivatives with respect to time, ∇ denotes the Nabla (or gradient) operator in space, and ∇^2 denotes the Laplacian operator in space.

To take account of the attractiveness of the cement pheromone, the dynamics of the loaded termites (the density of which is denoted by C) has to be described. We assume that the pathway of a termite results from the addition of two processes: random walk and response to the pheromone gradient (chemotactic behaviour). The simplest model of chemotactic behaviour assumes that the response is proportional to the gradient: the greater the gradient, the more the termites are attracted. Steeper gradients attract termites towards peaks of concentration, which correspond to zones where a lot of material has been deposited. The equation then reads:

$$\delta_t C = \Phi - k_1 C + D_C \nabla^2 C - \gamma \nabla (C \nabla H). \qquad (2)$$

In equation (2), it has been assumed that $\gamma\nabla(C\nabla H)$ describes the attractiveness of the pheromone gradient, γ denotes the intrinsic strength of this attractiveness (γ is assumed to be positive: this corresponds to a case in which regions of higher H concentration are indeed attractive): for the same value of the gradient, the greater γ, the greater the attractiveness. There is also a random component in individual motion, described by $D_C\nabla^2 C$, where D_C is the 'diffusion' constant of termites. It is further assumed that there is a spatially and temporally constant flow Φ of loaded termites into the system (that is, the flux of insects bringing new building material into the modelled zone), and that the rate of unloading per termite per unit time is a constant k_1. Finally, equation (3) describes the dynamics of the active material P: the amount of material P deposited per unit of time is equal to k_1C, and the rate of disappearance of P is k_2P, the total production of pheromone emitted in space per unit of time (it is assumed the the cement pheromone contained in pellets dissociates from the pellets and can then diffuse freely in air).

$$\delta_t P = k_1 C - k_2 P. \qquad (3)$$

When material is dropped, cement pheromone is emitted and diffuses, thereby attracting more termites to drop material at the site of origin of the pheromone. This accumulation of material induces a stronger and stronger emission of pheromone which attracts more and more termites. This positive feedback at different sites in the building area gives rise to competition between different pillars which are close to one another. This leads to an 'inhibition' of pillar formation in the immediate neighbourhood of a pillar and also facilitates the emergence of another pillar further away. The by-product of this amplification and competition is a regular distribution of the pillars in space, without any explicit coding of the inter-pillar distance. Note that the present model, being based on partial differential equations, is completely deterministic and therefore leads to a perfectly regular spatial distribution of pillars, whereas in reality, this regularity is observed on average: fluctuations in individual behaviours, if they are appropriately taken into account, can easily account for this statistical regularity.

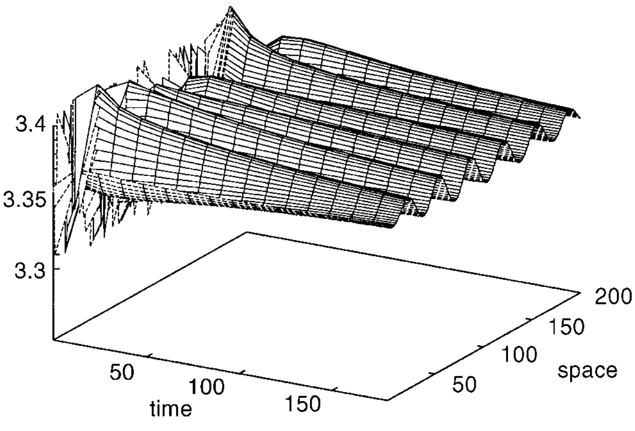

Figure 4. Temporal dynamics of P for a 1D system and $k_1=k_2=k_4=0.8888$, $D_C=0.01$, $D_H=0.000625$, $\Phi=3$, $\gamma=0.004629$. In all the numerical simulations, the temporal step is $t=0.0003$, the spatial step is $r=0.01$. Initial conditions: random for $P(r,0)$ (all wavelengths are present in the initial spatial distribution of P), and $C(r,0) = H(r,0)=0$.

As previously mentioned, this mechanism of attractiveness does not always lead, however, to the emergence of regularly spaced pillars, and quantitative conditions are required to produce such a pattern: when the density of termites or the rate of deposition is too low, the development of pillars is difficult or even impossible, and only a spatially homogeneous stationary state is observed. In this homogeneous stationary state (C_0, H_0, P_0), both spatial and temporal derivatives are equal to 0, so that:

$$C_0 = \Phi / k_1, \qquad (4a)$$

$$H_0 = \Phi / k_4, \qquad (4b)$$

$$P_0 = \Phi / k_2. \qquad (4c)$$

Deneubourg (1977) studied the conditions under which a diffusive instability could occur (see Appendix A). He did a classical linear stability analysis (Murray 1989), studying how a small perturbation of the form $e^{\omega t}e^{ikx}$ on top of the homogeneous stationary state could evolve into a spatially heterogeneous stationary state. The condition for the growth of perturbations is $Re(\omega)\geqslant 0$, which is usually satisfied for some values of the spatial wavenumber k within a certain range of the parameters governing the nonlinear terms of the equations. The relation $\omega(k)$ is called the dispersion relation, and depends on the values of the parameters. For values of k such that $Re(\omega(k))\geqslant 0$, a perturbation of that particular wavelength can grow in principle, but generally, the diffusive instability will have the wavenumber k for which $Re(\omega(k))$ is maximal (because the instability grows faster at this wavenumber). The relevant parameter here is the chemotactic parameter γ. Deneubourg (1977) showed that there exists a value

$$\gamma_c = ((k_4 D_C)^{1/2} + (k_1 D_H)^{1/2})^2 / \Phi, \qquad (5)$$

of γ such that no perturbation can grow for $\gamma < \gamma_C$. For $\gamma = \gamma_C$, there exists a wavenumber $k_C = (k_1 k_4 / D_C D_H)^{1/4}$ for which $\omega(k_C)=0$, whereas $\omega(k)<0$ for any other k: a perturbation with $k=k_C$ at $\gamma=\gamma_C$ is marginal. Deneubourg (1977) studied numerically the dynamics of a one-dimensional (1D) system with a value of γ close to the marginal value γ_C, and found that the system converges to a spatially periodic state (figure 4). The same observation is true for a 2D system (figure 5*a*,*b*). For $\gamma > \gamma_C$ and k in the appropriate range ($Re(\omega(k))>0$), the

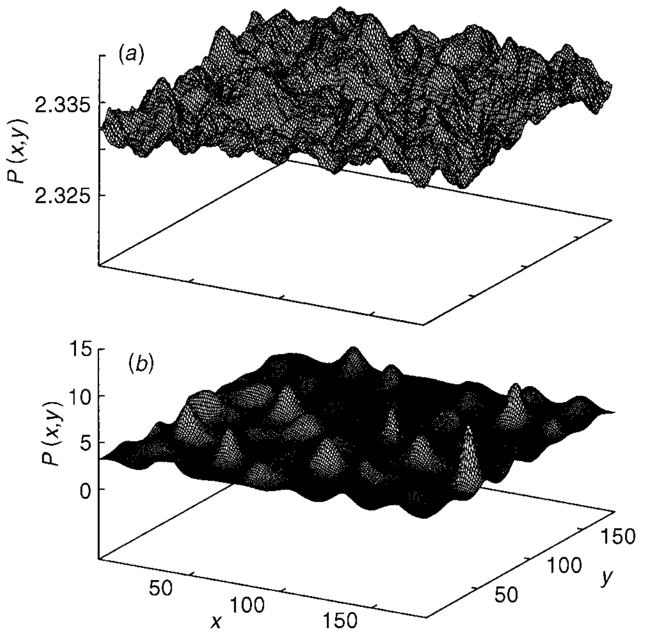

Figure 5. (*a*) Spatial distribution of *P* for a 2D system (180 × 180) and $k_1=k_2=k_4=0.8888$, $D_C=0.01$, $D_H=0.000625$, $\Phi=3$, $\gamma=0.004629$, $t=4$. (*b*) Same as in *a*, at $t=100$. Note that the distribution of pillars is only statistically regular, because of the random initial distribution of *P*. The initially fastest-growing modes do not necessarily continue to be dominant after some time, as structures can emerge locally and modify the physics of the system.

system would evolve to a spatially periodic state of diverging amplitude (that is, the size of the observed peaks diverges because $Re(\omega(k))>0$). Remember, however, that this model, as a model of the building behaviour of termites, is valid only over short time periods, as is the linear stability analysis: in particular, the dominant modes over short time periods may coexist with other modes after some time as local finite-amplitude effects start to play a role. This is why figure 5*b* shows only a statistically periodic distribution of *P*. Finally, let us briefly remark that the condition $\gamma>\gamma_C$ for the existence of coherent structures can be expressed as $\Phi>((k_4D_C)^{1/2}+(k_1D_H)^{1/2})^2/\gamma$ which is a condition of minimal flux given γ: this corresponds to the empirical observation that a minimal number of individuals is required to produce a pattern of pillars (Grassé 1984).

(b) *Addition of an air stream*

It is now interesting to examine the influence of an air stream on the previously obtained patterns, by assuming that the only effect of such an air stream is on the propagation of the pheromone (that induces chemotaxis) in equation (2). The addition of a convective term due to the air stream results in directed pheromonal diffusion along the air stream. We ignore any direct modification of the termites' behaviours due to the air stream. Can the modification in the dynamics of pheromone diffusion generate new structures, even though individuals (in the model) do not perceive the air stream and do not modify their behaviours accordingly? Under this hypothesis, equation (1) becomes:

$$\delta_t H = k_2P - k_4H + D + H\nabla^2 + u\nabla H, \qquad (6)$$

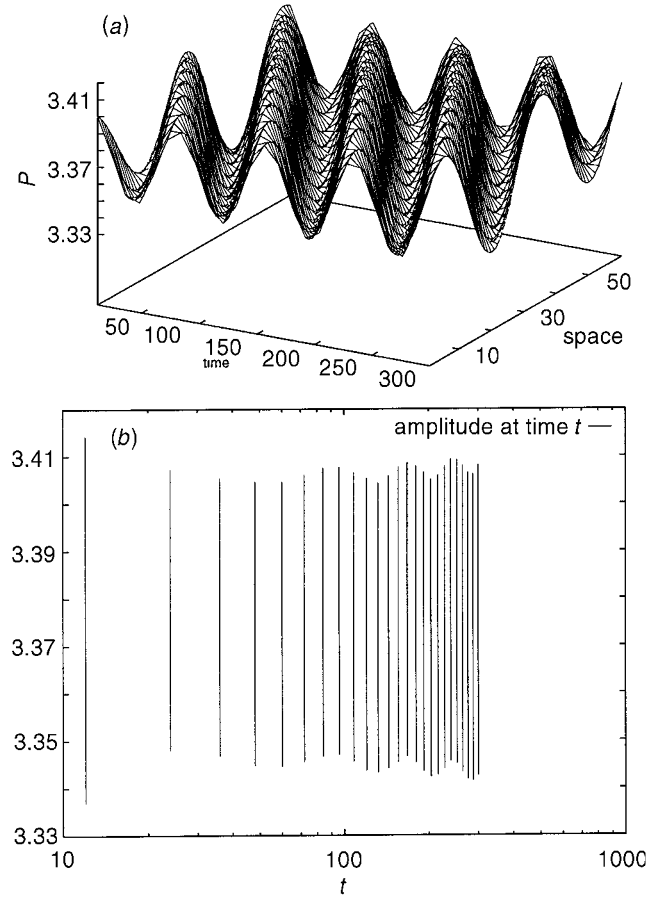

Figure 6. (*a*) Temporal dynamics of *P* for a 1D system and $k_1=k_2=k_4=0.8888$, $D_C=0.01$, $D_H=0.000625$, $\Phi=3$, $\gamma=0.004829$, wind along the *x* direction with $u=0.01$. (*b*) Temporal dynamics of the amplitude for the same system as in *a*.

where *u* denotes the velocity of pheromone transport due to the wind. Equation (2), reflecting workers' behaviours, remains unchanged. The stationary homogeneous state is identical to the previous one (C_0, H_0, P_0), but the linear stability analysis performed in the absence of wind becomes intractable when the convective term is added. A numerical procedure has been used to determine the dispersion relation for various values of *u* and γ. The inclusion of pheromone transport along the air stream introduces an imaginary term in the characteristic equation, and all $\omega(k)$ have a non-zero imaginary part provided $u\neq0$. This means that the system oscillates in time as well as in space, or more definitely that pillars are continuously shifted. Let us assume that $\gamma>\gamma_C$. In the case of a 1D system, the addition of the air stream basically leads to two regimes.

1. The periodic pattern of peaks is maintained when $u<u_C$ (that is, there still exists a wavenumber *k* such that $Re(\omega(k)\geqslant0)$, but is transported along the air stream because $\forall k$, $Im(\omega(k))\neq0$. If $\max(Re(\omega(k)))=0$, the system reaches a marginal state (that is, which does not diverge) that is periodic in both space and time.
2. The pattern disappears and is replaced by a homogeneous stationary state for $u>u_C$ (that is, the effect of *u* is to impose $\forall k$, $Re(\omega(k))<0$).

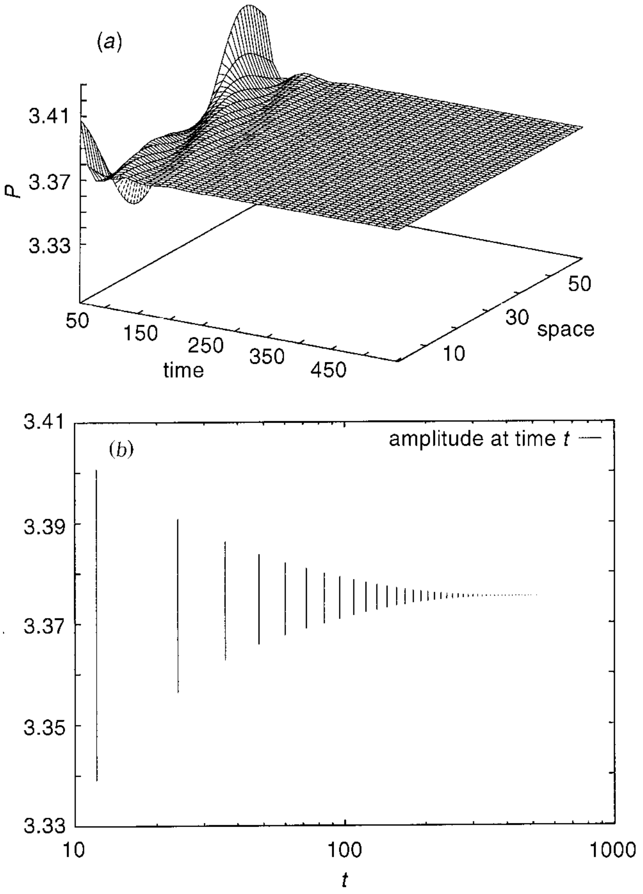

Figure 7. (a) Temporal dynamics of P for a 1D system and $k_1=k_2=k_4=0.8888$, $D_C=0.01$, $D_H=0.000625$, $\Phi=3$, $\gamma=0.004629$, wind along the x direction with $u=0.1$. (b) Temporal dynamics of the amplitude for the same system as in a.

For $\gamma < \gamma_C$, no pattern will emerge, because $u_C \rightarrow 0$ when $\gamma \rightarrow \gamma_C$. Figure 6$a$ shows the temporal dynamics of a system for which $\gamma > \gamma_C$ and $u < u_C$, so that a periodic pattern of pillars emerges, grows (and should slowly diverge because γ is greater than but close to γ_C), and is transported along the air stream. Figure 6b shows the dynamics of pillar amplitude (maximum height − minimum height): the maintenance of the pillar system can be clearly seen. By contrast, for $u > u_C$ and the same values for all other parameters, the pattern of pillars completely disappears, as can be seen on figure 7a,b.

In 2D, the situation is slightly different. An additional regime can be observed for intermediate wind forces (and of course $\gamma > \gamma_C$): periodic patterns of active material in both the x and y directions may be replaced by patterns which are periodic in the direction orthogonal to the wind and approximately constant along the direction of the wind. In other words, pillars observed in the absence of wind can be replaced in the presence of wind by walls (figure 8).

(c) *Effects of an asymmetric flux of individuals*

Another, equally interesting, possibility is to assume that termites, rather than pheromone, are 'convected' along some specific direction. This assumption corresponds to any asymmetric flux of individuals resulting from a variety of factors such as pheromone trails or air

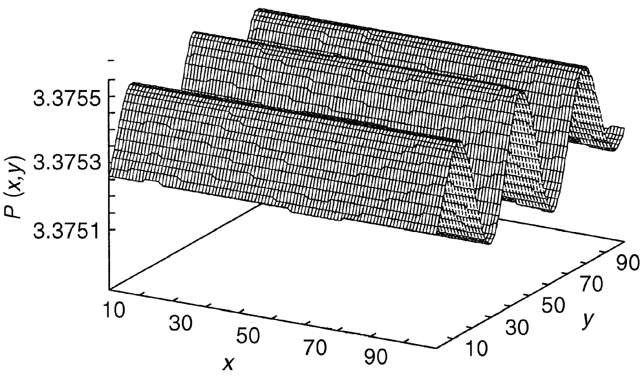

Figure 8. Spatial distribution of P at $t=100$ for a 2D system and $k_1=k_2=k_4=0.8888$, $D_C=0.01$, $D_H=0.000625$, $\Phi=3$, $\gamma=0.004629$, wind along the x direction with $u=0.01$.

streams, humidity or temperature gradients, or simply the various activities of the termites, and so on. In this latter case, we are studying the effect of a simple response of the termites to the perturbation, whereas we had neglected this response to concentrate on pheromone transport in the previous model. The simplest way of taking account of this phenomenon is to include a term $v\nabla C$ in equation (2), where v is the velocity of the termites:

$$\delta_t C = \Phi - k_1 C + D_C \nabla^2 C - \gamma \nabla (C \nabla H) + v \nabla C. \tag{7}$$

In 1D, the situation is very similar to the one observed in the presence of an air stream, although the mechanisms are very different. Figure 9 shows the dynamics of a 1D structure. In particular, for sufficiently small values of v, pillars are transported along the flux of individuals. Figure 10a,b shows the dynamics of a 2D structure, where walls appear, but not as regular as in the case where the cement pheromone is assumed to be transported along the air stream.

(d) *Effects of a pheromone trail*

Let us now assume that there is a well-defined self-maintained pheromone trail crossing the 2D system. Let $T(r,t)$ be the amount of trail pheromone at r, at time t. The simplest way of studying the effect of T is to assume that T is constant in time, and let us also assume for completeness that

$$T(x,y) = T(y) = \mathrm{e}^{-((y-y_0)/\lambda_y)^2}, \tag{8}$$

where λ_y is a constant that characterizes the width of the trail (set to 5 in the following examples). The same chemotactic term as the one used to describe the attractive effect of cement pheromone can be used here, so that the full equation reads:

$$\delta_t C = \Phi - k_1 C + D_C \nabla^2 C - \gamma \nabla (C \nabla H) - v \nabla (C \nabla T), \tag{9}$$

where v is now the force of attraction of the trail. The two chemotactic terms in equation (9) will lead to the desposition of most of the building material along the trail in the absence of any other mechanism: in effect, the trail is present at $t=0$, whereas $H(r,t)=0$ everywhere, which implies $\nabla H = 0$, so that the only effective chemotactic

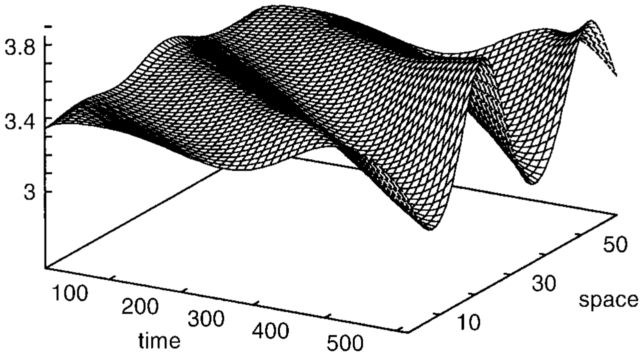

Figure 9. Temporal dynamics of P for a 1D system and $k_1=k_2=k_4=0.8888$, $D_C=0.01$, $D_H=0.000625$, $\Phi=3$, $\gamma=0.004829$, individual motion along the $-x$ direction with $v=0.01$.

effect at short times is due to the trail. Individuals are therefore attracted to the trail, and because there is a fixed probability of depositing per individual per unit time (k_1), pellets are deposited on, or in the vicinity of, the trail, creating a second chemotactic field, relying on cement pheromone, that also attracts individuals towards the trail. Almost all the pellets eventually end up on or close to the trail. Bruinsma (1979) has shown that there must be a mechanism that inhibits the deposit of pellets when the concentration of trail pheromone exceeds some threshold: such a mechanism would certainly be biologically plausible because trails should not be blocked. We have included such a mechanism by modifying equations (3) and (9) as follows:

$$\delta_t C = \Phi - F(r)k_1C + D_C\nabla^2C - \gamma\nabla(C\nabla H) - v\nabla(C\nabla T), \tag{10}$$

$$\delta_t P = F(r)k_1C - k_2P, \tag{11}$$

where $F(r)$ represents an inhibitory mechanism that prevents pellet deposits on the trail. In the present case, as $0 \leqslant T \leqslant 1$, we have chosen $F(r)=1-T(r)$. Figure 11*a* represents the function F simulating the inhibitory effect of a trail, when T is given by equation (8). Figure 11*b* represents the distribution of termites for $v=0.03$ at $t=100$: it can be seen that, because of the chemotactic attraction of the trail, a higher density of termites is observed on the trail. Figure 11*c* shows a 2D structure obtained with this mechanism: walls are formed along, and on both sides of, the trail. This is very similar to the covered runways observed in some species of termites (Bruinsma 1979; Grassé 1984). Such covered runways are important to protect the termites from the hot and dry external climate. Termites harvest grasses by foraging under cover through their immense ramifying system of peripheral corridors and arcades to harvesting sites where they cut grass and other vegetable matter, which is carried back to the nest through the protective galleries, to be used as a compost for the fungus garden. Of course, the galleries we find in the model are not covered, as this is not permitted by the model. If termites were allowed to walk on pillars or walls, the same mechanism would lead to the formation of arches or roofs for galleries (lines of isoconcentration of the 3D pheromonal template due to the trail have, indeed, the shape of an arch). Finally, figure 11*d* shows the distribution of pheromone: the pheromone being emitted by soil pellets, its concentration is highest along the gallery.

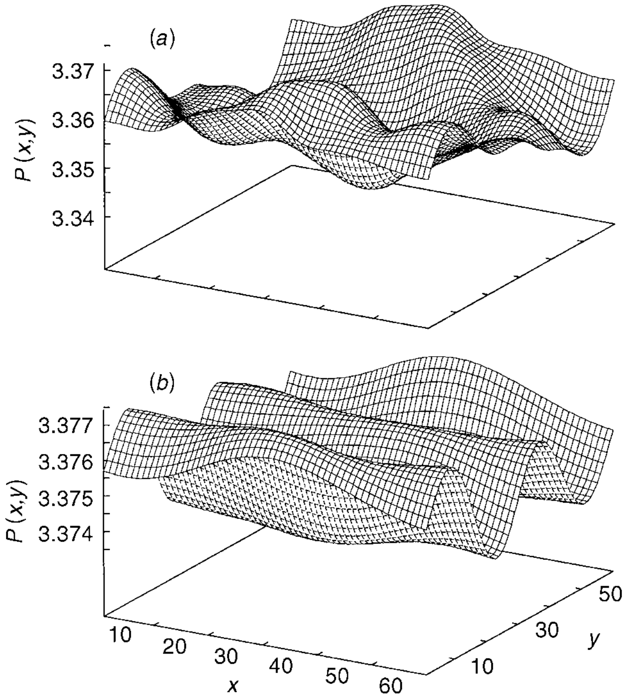

Figure 10. (a) Spatial distribution of P, at $t=0.5$, for a 2D system and $k_1=k_2=k_4=0.8888$, $D_C=0.01$, $D_H=0.000625$, $\Phi=3$, $\gamma=0.004829$, individual motion along the $-x$ direction with $v=0.01$. (b) Same as a, at $t=100$.

Here, the force of attraction, v, plays the role of a bifurcation parameter: walls can appear along the trail only if $v > v_C$. If v is too small, the attraction of the trail is not sufficient to induce the construction of walls: the inhibition function makes deposits uniformly likely away from the trail. Figure 12*a*–*c* show the same situations as figure 11*b*–*d*, but with $v=0.01$: this value of v is obviously smaller than v_C.

By continuously removing the substrate over which galleries were constructed, so that pheromone evaporation would be greatly enhanced, Bruinsma (1979) showed that the size of a gallery is owing in part to the intensity of the trail it covers, because it decreases significantly in this experiment. This provides a regulatory mechanism for gallery size as a function of traffic, because the more termites using the trail, the higher the density of pheromone and the larger the gallery.

It is rather straightforward to obtain chambers with the same chemotactic-trail-following mechanism if one assumes that chambers naturally emerge where trails intersect: this is a reasonable assumption because the local concentration of pheromone in the vicinity of a crossroad is higher (as is the traffic) so that the inhibition function has a round shape around the crossroad. For example, one can assume that $T(x,y) = \min\left(1, \mathrm{e}^{-((x-x_0)\lambda_x)^2} + \mathrm{e}^{-((y-y_0)/\lambda_y)^2}\right)$. Figure 13*a* shows the simulated inhibition function (or rather $1-F(r)$ for ease of visualization) resulting from the intersection of two pheromone trails ($\gamma_x=\gamma_y=10$, $x_0=y_0=30$), and figure 13*b* shows the spatial distribution of P after 100 time units: as

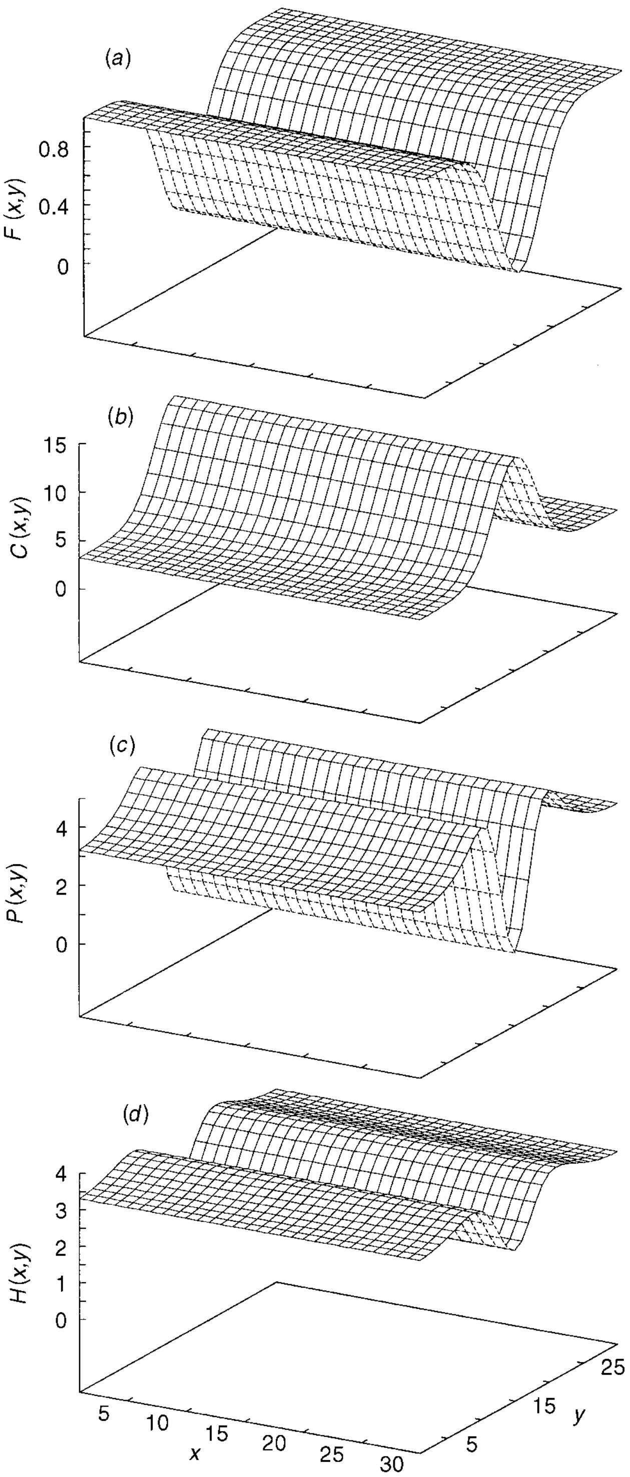

Figure 11. (*a*) Spatial inhibition function resulting from the trail along the x direction located in the middle of the system. $T(x,y)=T(y)=y_0=15$, $\gamma_y=5$, $F(x,y)=1-T(x,y)$. (*b*) Spatial distribution of C at $t=100$ for a 2D system and $k_1=k_2=k_4=0.8888$, $D_C=0.01$, $D_H=0.000625$, $\Phi=3$, $\gamma=0.004629$, added chemotactic motion toward the trail represented in *a*, with $v=0.03$. The highest density of individuals is on the trail. (*c*) Spatial distribution of P at $t=100$ for the same system as in *b*. A gallery runs along the simulated trail. (*d*) Spatial distribution of H at $t=100$ for the same system as in *b*. The pheromone being emitted by soil pellets (P), its concentration is highest along the gallery.

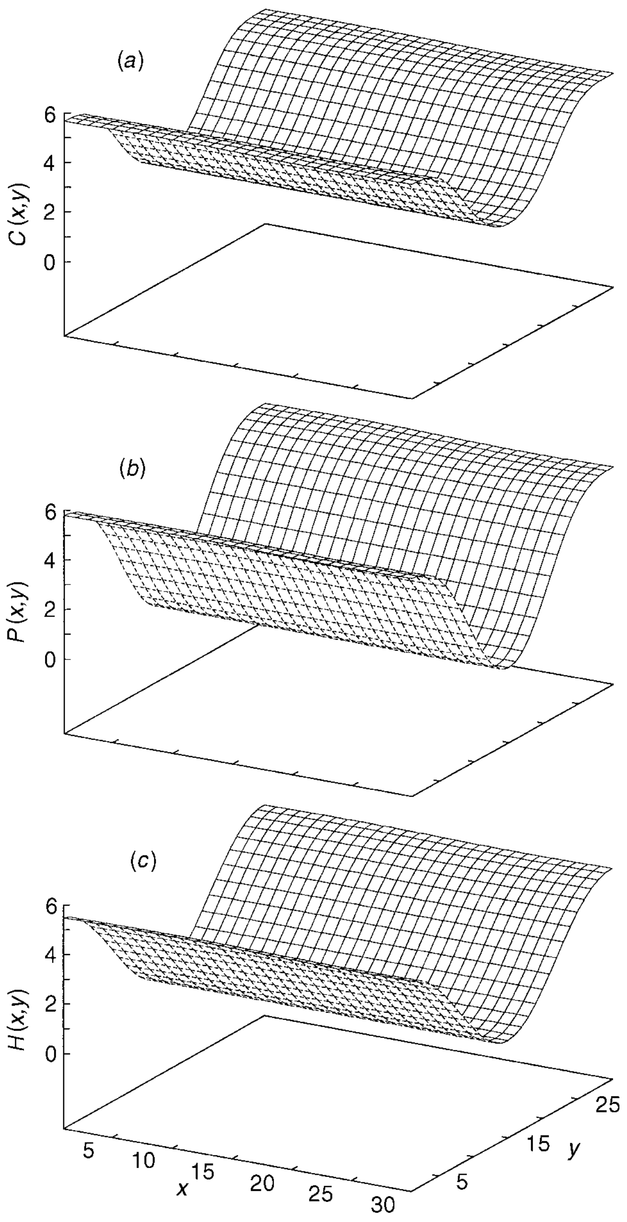

Figure 12. (*a*) Same as figure 11*b*, but with $v=0.001$. Here, the attraction of the trail is not sufficient to induce the construction of walls along it: the inhibition function makes deposits uniformly likely away from the trail. (*b*) Same as figure 11*c*, but with $v=0.001$. (*c*) Same as figure 11*d*, but with $v=0.001$.

expected, walls run along the trails and a chamber emerges at the intersection of the trails.

(e) ***Effects of a pheromonal template***

Let us end this section with a straightforward modification of the previous trail model. Consider that the trail is now replaced by the queen, who continuously emits some pheromone, as has been shown by Bruinsma (1979). The royal chamber is not a particularly complex structure, but is essential for the life and growth of the colony. Let us assume that the 'geometric centre' of the queen is located at (x_0, y_0), and that the shape of the queen is roughly elliptic with the principal axis along the x direction, so that the pheromone template she creates by emitting pheromone is given by

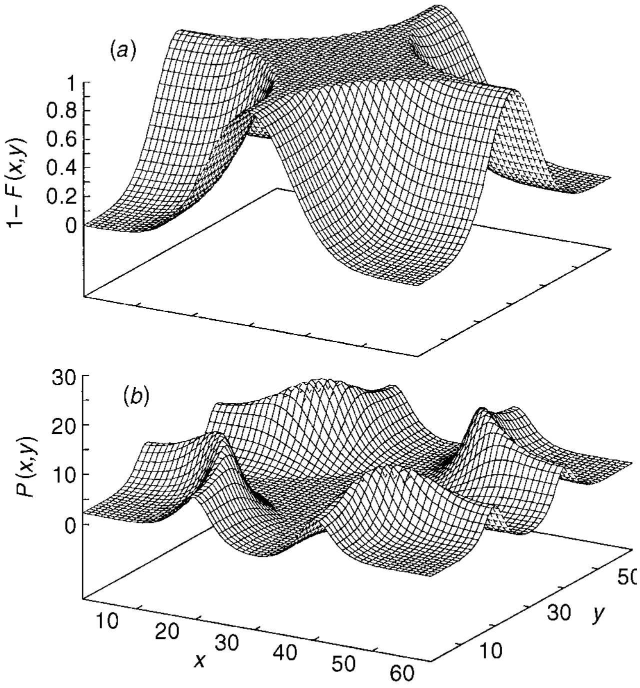

Figure 13. (*a*) Trail function simulating an intersection of two trails. $T(x,y) = \min(1, e^{((x-x_0)/\lambda_x)^2} + e^{-((y-y_0)\lambda_y)^2})$, $\lambda_x = \lambda_y = 10$, $x_0 = y_0 = 30$. (*b*) Spatial distribution of P at $t=100$ for a 2D system and $k_1=k_2=k_4=0.8888$, $D_C=0.01$, $D_H=0.000625$, $\Phi=3$, $\gamma=0.004629$, added chemotactic motion toward the trail $T(x,y)$ represented in *a* with $v=0.02$.

$$T(x,y) = e^{-[((x-x_0)\lambda_x)^2+((y-y_0)\lambda_y)^2]}, \tag{12}$$

where γ_x and γ_y are characteristic distances for the decay of the pheromonal pattern, that can be assumed to be proportional to the size of the queen in the x and y directions (the distance between the queen's body and the walls constructed around her is of the order of a few centimetres). Here again, one should use a function $F(r) = 1 - T(r)$ to prevent deposits occurring when pheromone intensity is too large: this is precisely the definition of a template, which organizes the building activity at a constant distance from the queen (figure 14*a* shows an example of a function F simulating a pheromonal template). The present mechanism for the construction of the royal chamber relies on a combination of template (represented by equation (12)) and self-organization (the positive feedback of pillar construction, mediated by workers, leads to an amplification of certain deposits): this combination is certainly very general, as templates, be they chemical or simply physical (obstacles, environmental heterogeneities, and so on) are not rare. We believe that this type of combination can produce a great diversity of structures, because the colony is able to 'take advantage' of virtually any kind of heterogeneity.

Bruinsma's (1979) description of this phenomenon is slightly more complicated than we have assumed. He showed, in effect, that workers are indeed first attracted toward the queen, that they pick up a pellet close to the queen (most pellets are picked up within 0.5 cm from the queen), and then (after some time) move away from the queen until they deposit a pellet. In the model, we have assumed that individuals do not exhibit this 'double motion', first toward the queen and then away from the queen. But, as a first approximation, the model describes similar dynamics, because individuals move towards the queen and deposit their pellet as soon as they find a suitable site. Figure 14*b* shows that a chamber can form around the queen, following the pheromonal template.

As a further indication of the relevance of the model, we have given a different shape to the template to emulate Bruinsma's (1979) experiment in which a freshly killed queen was presented in various positions (see figure 14*c* for the corresponding simulated template): figure 14*d* shows that, here again, walls are built around the modified pheromonal template. Note that walls built close to the interior angle of the queen's body are particularly amplified: this is due to crowding which is more likely to occur at that location because of the geometrical constraints imposed by the queen's chemical template. The larger amplification of walls in this zone is a prediction of the model, as is the fact that, because the very same geometrical constraints apply to pheromone diffusion, a high pheromone concentration is expected in this zone, leading to a chemical template slightly further away from the queen. Note that, as in the case of chemotactic motion towards a trail, the value of v (the force of attraction of the queen pheromone) must be greater than some value v_C, otherwise the chamber cannot be constructed.

To emulate further Bruinsma's (1979) experiments, we have added a small convective term to mimic the application of a small air flow, the effect of which is to drive molecules of both cement and queen pheromones along the stream. In addition to equation (6) that describes how the cement pheromone is affected by the air stream, we must provide a description of the queen pheromone's dynamics. Because we assumed that the queen pheromone formed a stationary, self-sustained template, the effect of a constant air stream is to transform this template into another stationary, self-sustained template. The procedure we used to determine the transformed template was the following: the transformed template was approximated by first creating the unperturbed template defined by equation (12) and by then applying to this template the convection equation $\delta_t T = u_T \nabla T$, where u_T is the convection rate of the queen pheromone. This equation was applied for a small amount of time τ:τ is a direct consequence of the time-scale of template regeneration. Although we do not know the value of this time-scale, we do know that it exists. It is really the combination of u_T and τ that determines whether or not there still is a (transformed) queen's chemical template after application of the air stream, or if it completely disappears because convection drives molecules at a higher rate than they are produced. Here, we chose to set $\tau=0.01$ and study the effects of varying u_T. We observe (figure 14*e*), as expected, that the chamber is smaller on the axis orthogonal to the direction of the air flow (that is, on the 'left' and on the 'right' of the queen) because of pheromone convection, whereas the template is elongated in the direction of the air flow, leading to walls built closer to the queen at one end (where the air flow comes from) and further away from the queen at the other end. Note that our model, in addition to replicating Bruinsma's observations, gives a strong clue in favour of the queen template hypothesis, as

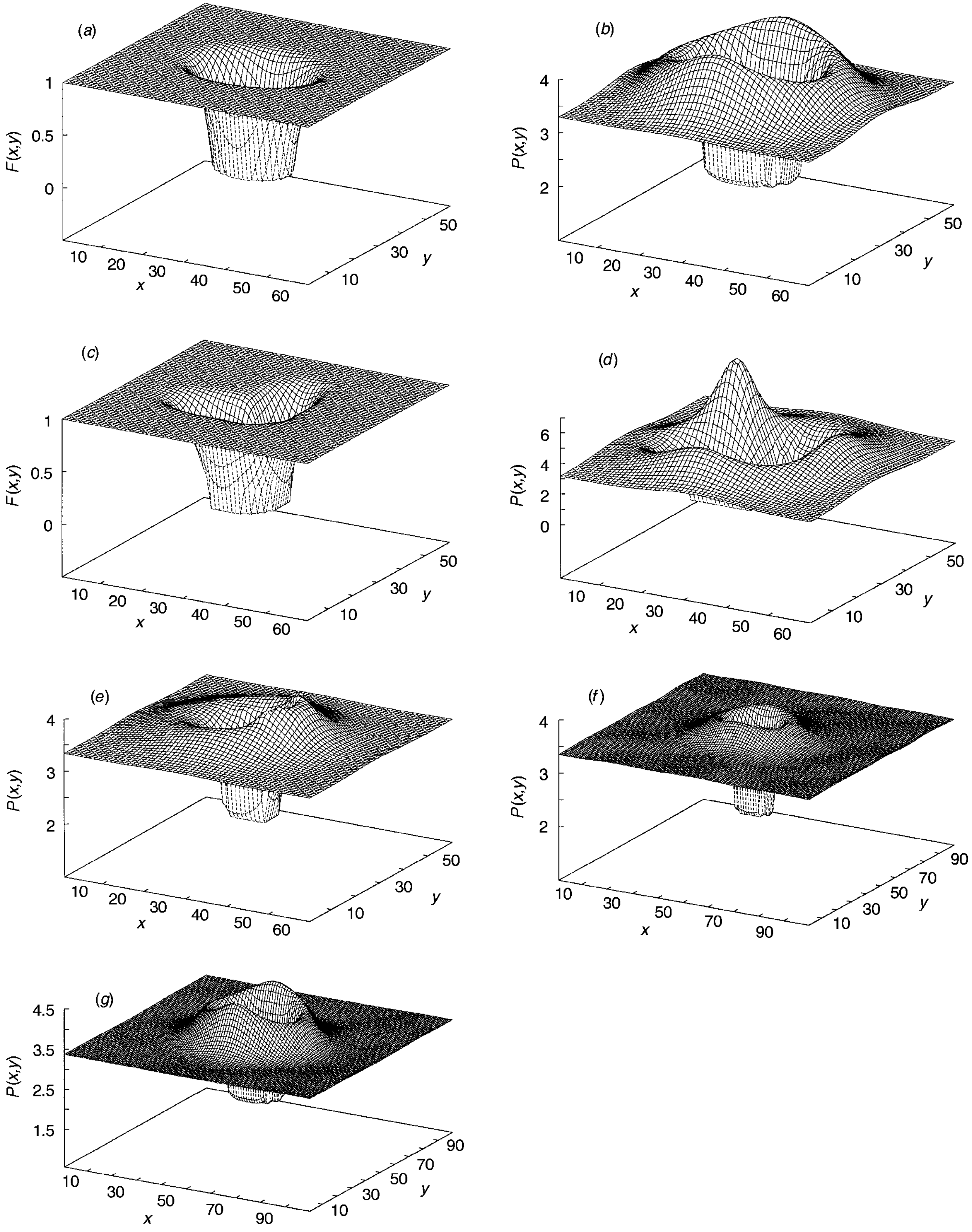

Figure 14. (*a*) Simulated pheromonal template created by the queen $T(x,y) = \mathrm{e}^{-[((x-x_0)/\lambda_x)^2+((y-y_0)/\lambda_y)^2]}$, $\lambda_x = 7$, $\lambda_y = 5$, $x_0 = y_0 = 30$, $F(x,y) = 1 - T(x,y)$. (*b*) Spatial distribution of P at $t=100$ for a 2D system and $k_1 = k_2 = k_4 = 0.8888$, $D_C = 0.01$, $D_H = 0.000625$, $\Phi = 3$, $\gamma = 0.004629$, added chemotactic motion toward the pheromonal template represented in *a* with $v = 0.02$. A chamber forms around the simulated template. (*c*) Simulated pheromonal template of a displaced queen. (*d*) Same as *b* with chemotactic motion toward the pheromonal template represented in *c*. (*e*) Same as *b* with an air stream along the $-x$ direction ($u = 0.1$). (*f*) Same as *b* embedded in a 100 × 100 grid. (*g*) Chamber ($t = 150$) obtained after perturbation of the system represented in (*f*). For $t \leqslant 50$, $\lambda_x = 5$ and $\lambda_y = 4$, and for $t > 50$, $\lambda_x = 7$ and $\lambda_y = 5$.

it allows us to test this hypothesis with 'artificial termites', the behaviour of which is not directly affected by an air stream, and to show that a modified royal chamber can be constructed in the presence of the air stream without any change in the termites behaviour.

Finally, we have studied the response of the system to a relevant perturbation: queen growth. A queen of *Macrotermes* can increase her length from 35 mm to 140 mm and multiply her mass by 125 as a result of hypertrophy of the abdomen (Bouillon 1958). The royal chamber has to grow to accomodate the growing physogastric queen. This can be modelled by increasing λ_x and λ_y. The system should be able to respond to this perturbation by increasing the size of the chamber. We find that this is indeed the case if the increase of λ_x and λ_y is sufficient. Figure 14*f* shows the stationary shape of the chamber at an early stage of queen growth ($\lambda_x=5$ and $\lambda_y=4$), whereas figure 14*f* shows the stationary shape of the chamber at a significantly later stage ($\lambda_x=7$ and $\lambda_y=5$): it can be seen that the size of the chamber has been adapted to the increasing size of the physogastric queen with exactly the same behaviour from the workers.

4. DISCUSSION

(a) *Limitations of the model*

The same basic model that has been used throughout this paper has some limitations that are important to outline.

1. It is a deterministic model describing average quantities, which necessarily smoothes out fluctuations; randomness appears only in initial distributions of individuals.
2. Given its formulation in partial differential equations, the model cannot accurately describe individual behaviour.
3. It does not take account of the physical constraints that emerge as construction proceeds: for example, workers should not be allowed to walk through walls or pillars, nor should air flow through physical obstacles.
4. The model describes the temporal dynamics of active material and neglects the accumulation of inactive material, which becomes more important as time proceeds.
5. It is a model of the initiation of architectural patterns, and its temporal domain of validity is therefore restricted. Over longer time periods, other mechanisms take over: for example, in the construction of the royal chamber, workers stand directly on the queen to build the roof of the chamber, so that the queen's body serves directly as a physical template. Despite these limitations, however, the model gives qualitative information which over short time-scales should be reliable. Furthermore, it is certainly the most parsimonious type of model given the scarcity of experimental data.

(b) *Consequences of the model*

(i) *Structure modifications without behavioural changes*

The versions of the model that involve either an air stream or a flux of individuals suggest that it is not necessary to invoke different behaviours to explain the emergence of different structures in different situations: an air stream or an asymmetric flux of individuals can lead to different structures. From the viewpoint of nonlinear science, this result is certainly not new, as it can be related to results obtained for reaction–diffusion systems supplemented by a convective term (Zhang 1993). But it is an interesting result in the context of the study of behaviour, at either colonial or ecological scales. In the model with wind, the convective term affects only pheromone transport, and this transport by itself does not affect the other ingredients of the dynamics. Furthermore, it has been assumed that the results of the building activities do not influence any of the mechanisms involved in the dynamics: in particular, the motion of carrying termites is the result of a random walk combined with a chemotactic attraction which is only controlled by pheromone fields (pheromone transport can, of course, be affected as well by the emerging structures, which act as barriers against pheromone diffusion or convection). We have assumed that other factors could be neglected, or that experiments can be done that drastically reduce heterogeneities. We have assumed that individual behaviours were not influenced by the convective term: this choice may seem rather odd as it is known that termites are highly sensitive even to extremely small air streams. But in any case, the structures that are generated are different despite the fact that individual responses are identical.

We have argued that it is important to understand how architectural patterns can be modified in modified environmental conditions without invoking any qualitative modification in the behaviours of individual termites. But, if this is an essential step, hypothesizing that individual behaviours are not modified is not always relevant. It is worthwhile to distinguish three ways new patterns can be produced: (i) from a modification of the physics of the problem even though this does not lead to any behavioural change (as in the present model); (ii) from a modification in the physics of the problem which leads to new behavioural responses (this implies that different responses to different specific stimuli are coded behaviourally); and (iii) from a modification of the physics of the system, resulting from the actions of individuals, which may or may not affect individual behaviours. In the previous cases, the various fluxes or gradients involved in the problem were assumed to be independent of individual activities. However, in some cases, fluxes or gradients can appear as the result of the action of individuals, and these fluxes or gradients have in turn an effect on individual behaviours. For instance, the pillars that emerge from the building actions of individuals create a spatial heterogeneity which modifies both fluxes of termites and of pheromone.

(ii) *A digression to Mima-like mounds*

The scope of the previous paragraph's discussion is not limited to termites, or even to animal behaviour. It is interesting to make a connection here with another phenomenon: the occurrence of large zones of regularly spaced mounds, called Mima-like mounds (Lovegrove & Siegfried 1989; Lovegrove 1991). Although the exact origin of Mima-like mounds is not precisely known (and may vary from one site to another), the prevailing theory is that they result from the tunnelling activity of pocket gophers, mole rats (Cox 1990*a*; Cox & Hunt 1990*a*,*b*), and/or to termites (Darlington 1985; Lovegrove & Siegfried 1989). An intriguing property of fields of Mima-like mounds can be understood with a generalization of our asymmetry-based model: mounds observed on gentle slopes (on the Columbian Plateau in north-central Oregon) transform into stripes as slope steepness increases (Cox 1990*b*). More precisely, mounds decrease in size, exhibit increasing asymmetry and downslope elongation, and become connected into lines orientated in the direction of the slope (Cox 1990*b*). The interplay between building behaviours, competition between neighbouring colonies, and environmental characteristics can generate regularly spaced mounds, as our basic model (equations (1), (2) and (3)) generates regularly spaced pillars. A slope introduces an asymmetry which can influence animal movements (and therefore active soil translocation) or directly the motion of physical items, such as water, stones or pieces of soil (passive soil translocation). According to our modified model, when an asymmetry is superimposed on top of the basic model, well-separated mounds should transform into lines of mounds along the slope, just as pillars transform into walls along the direction of the asymmetry. Furthermore, if water flows downslope and meets obstacles (mounds), the lateral deviation of water may prevent further development of mounds in directions orthogonal to the slope. This 'lateral inhibition' can then favour the development of other colonies further away on the orthogonal axis. This redistribution of individuals certainly influences, in turn, the types of global patterns they can generate.

(iii) *Heterogeneities and asymmetries, either self-created or imposed by the environment, can lead to highly complex emerging supertemplates*

Another viewpoint comes from recognizing that we have studied how various types of heterogeneities (or anisotropies, or asymmetries) affect the outcome of an originally homogeneous (or isotropic, or symmetric) model.

1. Environmental heterogeneities, such as wind, temperature and humidity gradients, obstacles, and so on. Gravity can also play the role of an isotropy-breaking field, as proprioceptors (position receptors) situated at the joints, sometimes in both limbs and antennae, allow termites to be highly sensitive to the directional cue provide by the pull of gravity. Some termites sense the influence of gravity by feeling which way the distal portions of their antennae tend to droop (Howse 1970). As a result they can exhibit either positive or negative geotropism.
2. Heterogeneities resulting from the colony's activities, such as fluxes of individuals between the various sites of the colony, or trails, or structures already built (pillars, walls, and so on; a similar logic has been used by Camazine and co-workers (1990; Camazine 1991) to explain the organization of concentric patterns on the combs of honeybee colonies)), or simply a naturally inhomogeneous spatial distribution of individuals (corresponding to the functional organization of the colony or because the nest is more densely populated at some locations, possibly because of environmental heterogeneities).
3. Heterogeneity resulting from the presence of the queen. This heterogeneity is complemented by others that appear in the course of the construction of the royal chamber, because, for example, clusters of soil pellets form chemical and physical heterogeneities.

These different types of heterogeneities can be mutually dependent and lead to complex architectures (Deneubourg & Theraulaz 1997). We have shown that walls easily emerge along trails or along asymmetric fluxes of individuals. Furthermore, the intersection of trails leads to the formation of a chamber. This observation is extremely interesting because it shows that a relatively sophisticated structure, namely a chamber with two access trails, can result from the combination of simple effects: this indicates that more complex architectural patterns may be explained by the combination of a small number of simple mechanisms and the interplay of simple individual behaviours with varying external as well as internal conditions. For example, the formation of new galleries and chambers can create new air streams that transport pheromone particles and may modify individual behaviours: there is a feedback effect of structures on fluxes.

Colony growth can induce a flux of individuals from the centre of the colony to outside; this flux can lead to the formation of (possibly intersecting) structures which will in turn affect the environmental conditions influencing building behaviour (Deneubourg & Theraulaz 1997). In that respect, the dynamics of colony growth triggers the unfolding in space of an architecture (either continuously or by bursts (Deneubourg & Franks 1995; Franks & Deneubourg 1998)), the characteristic patterns of which may evolve because they are influenced by the structures already built: a large architecture may not necessarily be a juxtaposition of identical modules even though individual behaviours remain unchanged. As the nest gets bigger, the greater the heterogeneity in signals and cues it is likely to encompass. This may explain why the most populous termite societies have the most complex nests (Grassé 1984).

In a nutshell, a few simple behaviours repeated over and over again can generate a highly complex and diverse sequence of modules, because, in a sense, modules influence one another: different structures can arise because previous building actions have modified the building conditions. It is not unreasonable to speak of nest morphogenesis. The nest is the result of a supertemplate that emerges from the interplay between environmental and colony-generated (through behaviour or simply demography) heterogeneities, the stimuli (tactile, chemical, vibratory, and so on) produced by these heterogeneities and the responses of individuals to these stimuli (Deneubourg & Theraulaz 1997).

(c) *Conclusion*

The main goal of this paper was not simply to add new features to a simple model of the emergence of pillars in termites (Deneubourg 1977). This model was indeed used as a starting point to study the effects of various perturbations but a common property of all these perturbations was to break the homogeneity (or the symmetry) of the original model and to introduce new heterogeneities (or asymmetries). Furthermore, these various heterogeneities induced individual responses which, although qualitatively similar to the responses of the original model, produced very different patterns. Because heterogeneities can result from past construction, new patterns emerge in time, following, for example, colony growth, that are produced by the same qualitative behaviour applied to different conditions. Therefore, highly complex architectures can be produced by the unfolding in space and time of an emerging supertemplate which does not require individuals to be complex: we have emphasized the complexity and diversity of the signals and cues that the individual termite may encounter and not the complexity of its response. This is the main message of the present paper.

E.B. is supported by the Interval Research Postdoctoral Fellowship in Adaptive Computation at the Santa Fe Institute. N.R.F. wishes to thank the Leverhulme Trust for support. This work was supported in part by a grant from the GIS (Groupe d'Intért Scientifique) Sciences de la Cognition to E.B. and G.T.

APPENDIX A. LINEAR STABILITY ANALYSIS IN ONE-DIMENSION

Equations (1, 2 and 3) have a homogeneous stationary state (C_0, H_0, P_0) defined by equation (4*a*, 4*b*, 4*c*). Let us study how a small perturbation of the form $e^{\omega t}e^{ikx}$ on top of the homogeneous stationary state evolves. C_0, H_0, P_0 are transformed into $C_0 + \delta C$, $H_0, + \delta H$, $P_0 + \delta P$, respectively, with δC, δH, $\delta P^{\omega t}e^{ikx}$. The system of equations for (δC, δH, δP) is given by

$$\omega\delta C = (-k_1 C - D_C k^2)\delta C + \gamma k^2 C_0 \delta H, \tag{A1}$$

$$\omega\delta H = k_2\delta P - (k_4 C + D_H k^2)\delta H, \tag{A2}$$

$$\delta P = k_1\delta C - k_2\delta P. \tag{A3}$$

For a non-zero solution to exist, the following determinant must be equal to 0:

$$\begin{vmatrix} \omega + k_1 C - D_C k^2 & -\gamma k^2 C_0 & 0 \\ 0 & \omega + k_4 C + D_H k^2 & -k_2 \\ -k_1 & 0 & \omega + k_2 \end{vmatrix} = 0 \tag{A4}$$

that is:

$$\begin{aligned} &\omega^3 + \omega^2[k_1 + k_2 + k_4 + (D_C + D_H)k^2] \\ &+ \omega\ [(k_1 + k_4 + (D_C + D_H)k^2)k_2 + k_1k_4 + k_1 D_H k^2 \\ &+ k_4 D_C k^2 + D_C D_H k^4] + [k_1k_2k_4 + k_1k_2D_Hk^2 + k_2k_4D_Ck^2 \\ &+ k_2 D_C D_H k^4 - k_1k_2\gamma C_0 k^2] = 0, \end{aligned} \tag{A5}$$

which defines the dispersion relation $\omega(k)$. The condition for the growth of perturbations is $Re(\omega) \geqslant 0$. If one looks for marginal solutions characterized by $\omega(k) = 0$, equation (A5) becomes

$$D_C D_H k^4 + (k_1 D_H + k_4 D_C - \Phi\gamma)k^2 + k_1 k_4 = 0, \tag{A6}$$

since $\Phi = k_1 C_0$. This equation can also read

$$\gamma = \frac{D_C D_H k^4 + (k_1 D_H + k_4 D_C)k^2 + k_1 k_4}{\Phi k^2}. \tag{A7}$$

The minimal value γ_c of γ above which there exist marginal solutions is given by

$$\gamma_c = ((k_4 D_C)^{1/2} + (k_1 D_H)^{1/2})^2/\Phi. \tag{A8}$$

The associated wavelength is

$$k_c = \left(\frac{k_1 k_4}{D_C D_H}\right)^{1/4}, \tag{A9}$$

which gives the period of the characteristic pattern. When $\gamma > \gamma_c$, the characteristic wavenumber of the pattern is given by k such that $Re(\omega(k))$ is maximal.

The addition of an air stream transforms equation (1) into equation (6), so that equation (A5) becomes

$$\begin{vmatrix} \omega + k_1 C - D_c k^2 & -\gamma k^2 C_0 & 0 \\ 0 & \omega + k_4 C + D_H k^2 - iuk & -k_2 \\ -k_1 & 0 & \omega + k_2 \end{vmatrix} = 0, \tag{A10}$$

or

$$\begin{aligned} &\omega^3 + \omega^2[k_1 + k_2 + k_4 + (D_C + D_H)k^2] + \omega[k_1 + k_4 \\ &+ (D_C D_H)k^2)k_2 + k_1 k_4 + k_1 D_H k^2 + k_4 D_C k^2 + D_C D_H k^4] \\ &+ [k_1k_2k_4 + k_1k_2D_Hk^2 + k_2k_4D_Ck^2 + k_2D_CD_Hk^4 \\ &- k_1k_2\gamma C_0k^2] - iu[\omega^2 k + (D_C k^3 + (k_1 + k_2))\omega \\ &+ k_2 D_C k^3 + k_1 k_2 k] = 0. \end{aligned} \tag{A11}$$

The convection term therefore introduces an imaginary term in equation (A11), and no purely real solution exists for ω: all solutions will be transported in space along the direction of the air flow. The same type of calculation in the case where there is a flux of individuals in a given direction leads to the same conclusion: ω is never purely real so that structures are always displaced along the flux.

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