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Thermoregulation and ventilation of termite mounds

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Abstract Some of the most sophisticated of all animal-built structures are the mounds of African termites of the subfamily Macrotermitinae, the fungus-growing termites. They have long been studied as fascinating textbook examples of thermoregulation or ventilation of animal buildings. However, little research has been designed to provide critical tests of these paradigms, derived from a very small number of original papers. Here I review results from recent studies on *Macrotermes bellicosus* that considered the interdependence of ambient temperature, thermoregulation, ventilation and mound architecture, and that question some of the fundamental paradigms of termite mounds. *M. bellicosus* achieves thermal homeostasis within the mound, but ambient temperature has an influence too. In colonies in comparably cool habitats, mound architecture is adapted to reduce the loss of metabolically produced heat to the environment. While this has no negative consequences in small colonies, it produces a trade-off with gas exchange in large colonies, resulting in suboptimally low nest temperatures and increased CO₂ concentrations. Along with the alteration in mound architecture, the gas exchange/ventilation mechanism also changes. While mounds in the thermally appropriate savannah have a very efficient circular ventilation during the day, the ventilation in the cooler forest is a less efficient upward movement of air, with gas exchange restricted by reduced surface exchange area. These results, together with other recent findings, question entrenched ideas such as the thermosiphon-ventilation mechanism or the assumption that mounds function to dissipate internally produced heat. Models trying to explain the proximate mechanisms of mound building, or building elements, are discussed.

Introduction

Termite mounds have fascinated humans since the earliest journeys to tropical regions (e.g. Smeathman 1781). They are conspicuous features in the tropical savannahs of South America, Africa and Australasia, where they can reach very high densities (more than 100 mounds/ha; Korb and Linsenmair 2001) and mound heights of up to 8 m. Thus, millions of insects, each less than 1 cm in length, build complex structures up to 1,000 times their own size; approximately equivalent to humans constructing structures the size of mountains (Bölsche 1931). In Africa and Asia the most prominent mound builders are the fungus-cultivating termites, Macrotermitinae (Termitidae). Termites in this subfamily have evolved an ectosymbiotic relationship with basidiomycete fungi of the genus *Termitomyces*, which are cultivated within the nest in convoluted, greyish-brown combs that consist of plant material provided by the termites (for details see Badertscher et al. 1983; Gerber et al. 1988; Traniello and Leuthold 2000). The association between termites and fungus is an obligate symbiosis that offers many advantages (Wood and Thomas 1989), but also has the potential for conflict (Korb and Aanen 2003). Optimal conditions for the growth of these fungi are relative humidity near saturation, constant temperatures of about 30°C (Thomas 1987; Wood and Thomas 1989) and low concentrations of CO₂ (Sands 1969; McComie and Dharajan 1990), which the termites are known to regulate inside their mounds to achieve thermal homeostasis near optimal conditions (Lüscher 1961; Ruelle 1964). In addition, colonies need to exchange respiratory gases because the fungi and termites together have a high metabolism (e.g. Collins 1981; Darlington et al. 1992). Although thermoregulation and gas exchange have each received some consideration, resulting in classical textbook examples of ventilation and thermoregulation in animal housings (e.g. Hansell 1984; Heinrich 1993), they have rarely been considered concurrently. How they interact with each other and the environment and how the termites deal with them will be reviewed for one species, *Macrotermes bellicosus*

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Fig. 1 *Macrotermes bellicosus* mounds in the Comoé National Park (Côte d'Ivoire): **a** large savannah mound, **b** large gallery forest mound, and **c** small mound



(Smeathman). Causes and effects between environment, thermoregulation and gas exchange will be shown and feedback mechanisms discussed. These results question entrenched ideas of thermoregulation and ventilation. Therefore, other recent studies will be addressed to reveal interspecific differences as well as common principles on the architecture and function of termite mounds. Finally, proximate modelling approaches will be discussed; how termites might build mound structures by rules of self-organisation.

Interaction between environment, thermoregulation and gas exchange in *Macrotermes bellicosus*

Influence of ambient temperature on nest temperature and mound structure

Savannah mounds

In the savannah of the Comoé National Park (Côte d'Ivoire, West Africa; CNP), *M. bellicosus* reaches very high densities and builds impressive cathedral-shaped mounds with many ridges ('nids en cathédrale', see Fig. 1a; Grassé and Noirot 1961, Lepage 1984; Korb and Linsenmair 1998a, 2001). In accordance with other studies (Lüscher 1955, 1956, 1961; Ruelle 1964; Noirot 1970; for *M. carbonarius*: McComie and Dhanarajan 1990), the nest temperature of large mounds is relatively constant, near 30°C all year round, with a fluctuation of

less than 2°C, despite ambient temperature fluctuations of about 35°C (Korb 1997; Korb and Linsenmair 1998a). However, the nest temperature is also influenced by ambient temperature. In small mounds that harbour small colonies (Collins 1981), nest temperature positively correlates with ambient temperature (Korb and Linsenmair 1998a). Nest temperatures of small mounds reach 30°C only if ambient temperatures are high. Manipulation of ambient temperature confirmed the causal relationship between ambient temperature and nest temperature; shading mounds with grass roofs results in a drop of the ambient temperature followed by a decline in nest temperatures (Korb and Linsenmair 1998a). Multiple regression models of temperatures in inhabited and intact, uninhabited mounds showed that (1) mound structure alone results in the constancy of the nest temperature, (2) ambient temperature (abiotic heat production) provides a basal minimum nest temperature, but (3) that the heat produced by the metabolism of the fungi and termites (biotic heat production) is necessary to reach optimal nest temperatures of 30°C (Korb and Linsenmair 2000a).

Gallery forest mounds

The influence of ambient temperatures on nest temperatures can also be seen in mounds in the gallery forest in the CNP. Nest temperatures there are on average 2°C lower (i.e. 28°C) than those in the savannah. As the activity of the fungi decreases significantly below 30°C (Thomas 1987), nest temperatures in the gallery forest seem to be suboptimal and selection for insulation would be expected. In fact, mound architecture seems to be adapted to counteract the loss of heat. Mounds in the gallery are dome-shaped, earthen structures with thick walls ('*nids en dôme*', see Fig. 1b, c; Grassé and Noirot 1961) which have a lower surface complexity (i.e. ratio of the real surface area to the minimal possible surface) than mounds in the savannah (Korb and Linsenmair 1998a). This was also confirmed by experiments: when ambient temperatures were increased in the gallery forest by cutting shading trees, mound surface complexities increased and the resulting architecture resembled that of the savannah mounds (Korb and Linsenmair 1998a).

Influence of gas exchange on mound structure and thermoregulation

Despite the adaptation seen in mound structure, nest temperatures in the forest cannot be maintained optimally, suggesting the possible constraint of a constant necessity for gas exchange, especially for fungus cultivation. Lüscher (1955) calculated that a large colony needs at least about 240 l of O₂ per day, corresponding to 1,200 l of air (measurements for *M. jeanneli*: 100,000–400,000 l air per day or 800–1,500 l CO₂ per day; estimations for *M. subhyalinus*: 560 l CO₂ per day; *M. michaelseni*: 400–500 l CO₂ per day; Darlington et al. 1997). As *M.*

bellicosus has enclosed mounds without holes, the mounds' surface area corresponds to the gas exchange area. Thus, a reduction in surface area and increase in wall thickness to insulate the nest, bears the costs of decreased gas exchange and increased CO₂ concentrations. Although termites can tolerate high CO₂ concentrations (Lüscher 1955, 1961; Ruelle 1964; Matsumoto 1978), the metabolic activity of the fungi decreases with increasing CO₂ concentrations (Sands 1969; McComie and Dhanarajan 1990). This results in a reduced food supply for the termites and, more importantly, in a reduced production of metabolic heat that further reduces nest temperature. Thus, in a comparatively cool habitat, termites have to trade off nest insulation against effective gas exchange and increased heat production. The observed dome-shaped mounds with thick walls in the gallery forest seem to be the outcome of this trade-off with suboptimally low nest temperatures and elevated CO₂ concentrations (Korb and Linsenmair 1999a). Correspondingly, the experimental increase in ambient temperatures in the forest resulted in increased mound surface complexity and decreased CO₂ concentrations (Korb and Linsenmair 1999a). Ultimately, the suboptimal conditions in the forest lead to lower lifetime reproductive success of colonies in the forest compared with the savannah (Korb and Linsenmair 1999b) and seems to limit the distribution of *M. bellicosus* to open forest stands (Korb and Linsenmair 1998a). In areas with a dense canopy, ambient temperatures are probably too low to insulate mounds sufficiently and at the same time provide sufficient gas exchange.

Interaction between colony size, mound structure and ventilation

Savannah mounds

The differences in the mound structure and ambient temperatures between the gallery forest and the savannah nests have quantitative (a reduced surface area) and qualitative (an altered gas exchange mechanism) consequences for gas exchange that furthermore depend on mound size. Small colonies (Collins 1981) have a reduced capacity to generate heat and to maintain constant nest temperatures. Even in the savannah, the nest temperatures of small mounds are below the optimum of 30°C and vary with ambient temperatures (see above). In line with this, in both habitats small colonies build dome-shaped mounds with reduced surface complexity and thick walls (Fig. 1a). However, as gas exchange requirements in small colonies are low, this insulation does not compromise with gas exchange. This changes with increasing colony size. In the savannah, the then increasing demand for gas exchange is reflected by a reduction in wall thickness and an increase in surface complexity (Korb and Linsenmair 1998a), leading to cathedral-shaped mounds with ridges and an altered internal structure (Lüscher 1961; Figs. 1a and 2): The central, spherical nest is

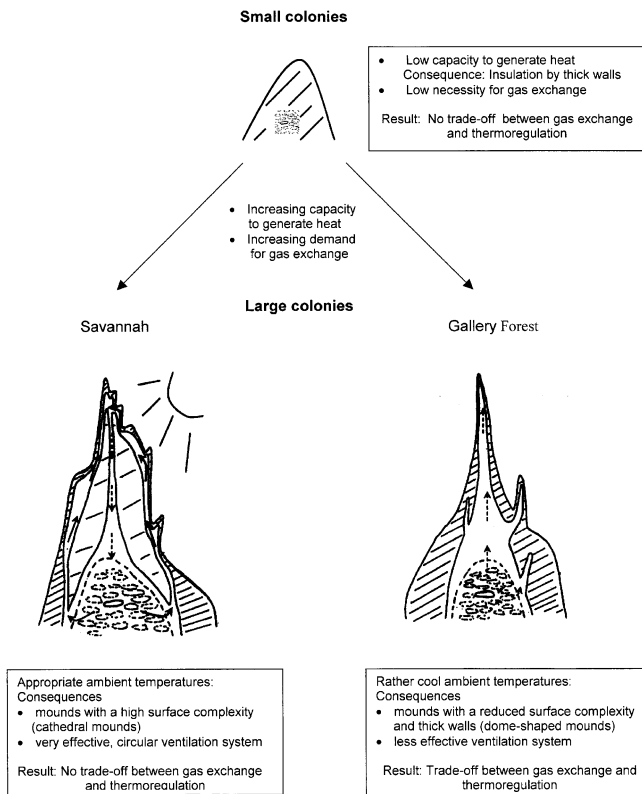


Fig. 2 Interaction between colony size, mound structure and ventilation. Small colonies have low metabolic rates. Therefore, they build dome-shaped mounds with thick walls which is not in conflict with the need for gas exchange. With increasing colony size the metabolic rates and the necessity for gas exchange increases. In the savannah, an externally driven circular ventilation system (see text) develops in cathedral-shaped mounds that provides efficient ventilation. In the rather cool gallery forest, well-insulated, dome-shaped mounds need to be built that bear the costs of a less efficient gas exchange

surrounded by a cavity, which at the apex of the nest opens into a central shaft that extends to the top of the mound. Peripheral air channels start closer to the bottom of the nest and run directly below the mound surface inside the ridges. This air channel system allows an efficient ventilation via circulation of air (Korb and Linsenmair 2000b). Warm ambient temperatures during the day cause temperature gradients between the cooler nest and the ambient air that lead to convection currents. Air rises inside the peripheral air channels of the ridges toward the top of the mound and ‘pulls’ CO₂-rich air from the nest into the ridges. As the air rises, respiratory gases are exchanged (‘externally driven ventilation’; Korb and Linsenmair 2000b).

At night, this gas exchange mechanism changes as temperature gradients invert when ambient temperatures fall below those in the nest (Korb and Linsenmair 2000b). Warm, CO₂-rich air flows upward inside the central shaft from the nest to the top of the mound (similar to a thermosiphon mechanism; Lüscher 1955), but without a prominent decline in the ridges. Gas exchange, therefore, seems to be restricted to the top of the mounds. This

change in the size of the gas exchange area between day and night is reflected in low CO₂ concentrations during the day and an increase of CO₂ during the night (Korb and Linsenmair 2000b).

Gallery forest mounds

As outlined above, in the cooler gallery forest, the increasing demand for gas exchange with increasing colony size is in conflict with an appropriate insulation of the nest. The resulting dome-shaped mounds also alter the mechanism of gas exchange (Korb and Linsenmair 2000b): Circulating air channels are lacking; only single, separated air channels of small diameters ascend from the nest to the mound wall, where they sometimes end in small turrets (Figs. 1 and 2). The largest of these channels is the central shaft that, similar to the cathedral-shaped mounds, rises from above the nest to the top of the mound, where it can extend into a turret of up to 2 m. Such turrets have comparatively thin walls, especially in the upper parts. Gas exchange seems to occur mainly through these central and the peripheral turrets; driven by convection currents, air rises from the nest upward to the turrets. This thermosiphon-like mechanism is indicated by temperature gradients, with ambient temperatures rarely exceeding nest temperatures. As the exchange area is limited, CO₂ concentrations are higher in the forest mounds than in the savannah.

Regulation of mound architecture

The interaction between ambient temperature, thermoregulation, gas exchange and mound architecture can be summarised as in Fig. 3a. Ambient temperature influences mound architecture. In relatively cool habitats, mounds are less complex to reduce the loss of metabolic heat. This reduction in mound complexity seems to be limited by the necessity for gas exchange. A negative feedback from gas exchange to thermoregulation occurs because increased gas exchange favours metabolic heat production. The result is a trade-off between thermoregulation and gas exchange.

It could be argued that the difference in mound architecture between the habitats is not caused by the necessity to insulate the nest, but by the mechanism for gas exchange (Fig. 3b). The circulatory ventilation mechanism of the savannah would rarely work in the gallery forest as it depends on temperature gradients caused by high ambient temperatures. Therefore, mounds with ridges would not be advantageous and mound structures would be selected that favour gas exchange via a thermosiphon mechanism, such as turrets do. As the gas exchange area of the turrets is smaller than those of ridges, CO₂ concentration in the nest might increase and result in diminished heat production. Thus, the lower nest temperatures as well as the increased CO₂ concentrations in the forest could be explained by the influence of

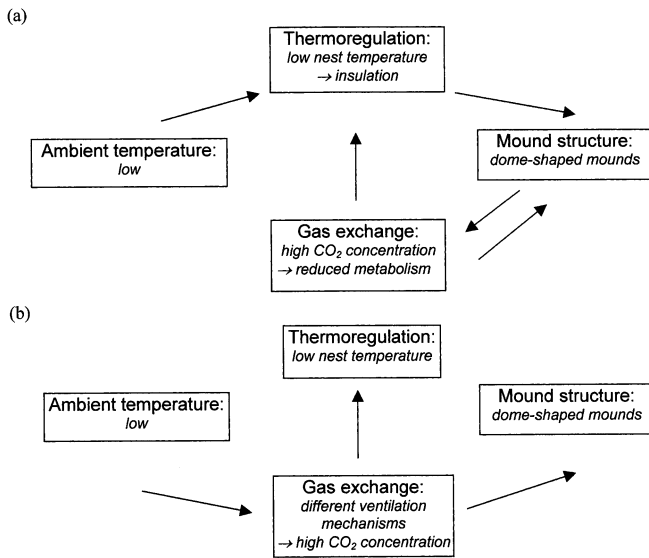


Fig. 3a–b Interaction between ambient temperature, thermoregulation, gas exchange and mound structure. **a** Likely interaction for *M. bellicosus* in the CNP: low ambient temperatures make it necessary to insulate the nest. This is achieved by building dome-shaped mounds with thick walls and reduced surface complexity. The change in the mound architecture results in elevated CO₂ concentrations in the nests which have a negative feedback on thermoregulation and constrain further insulation of the nest. The change of the internal mound structure is in accordance with the changed gas exchange mechanism, as a circular ventilation is not possible under low ambient temperatures. **b** Unlikely alternative scenario: low ambient temperatures change the ventilation mechanism for gas exchange. Firstly, this leads to increased CO₂ concentrations and a reduced metabolic heat production that results in low nest temperatures. Secondly, the change in the ventilation mechanism favours a change in mound structure. *Italic text* indicates consequences. For further information see text

ambient temperature on the physical mechanism for gas exchange, without invoking thermoregulatory causes.

However, several considerations suggest that the second scenario is not sufficient to explain mound architecture in the forest. First, why do the termites not build several large turrets to increase gas exchange area and reduce CO₂ concentrations, as the latter are critical for the maintenance of an optimal nest temperature? In other regions of the Côte d'Ivoire, *M. bellicosus* builds mounds with several large turrets (personal observation), indicating that the species has the behavioural repertoire to do so. Second, why do mounds of all sizes have reduced surface complexities? That is, why are mounds cone-shaped? This cannot be explained by the fact that ridges have no function. Even mounds without ridges can have a high surface complexity. Third, why do the thin turrets of large colonies not begin closer to the nest, but are separated from it by thick earth layers? In contrast, the ridges of cathedral mounds originate next to the fungus gardens. Forest nests are surrounded by thicker layers of compact mound material than savannah nests, independent of mound architecture (Figs. 1 and 2). These considerations strongly suggest that mound architecture in the gallery forest is a not just a consequence of the

ventilation mechanism, but a consequence of thermoregulatory constraints.

Implications from comparison with other studies

Comparing these results with those from earlier studies challenges the general validity of two entrenched ideas concerning mound-building, fungus-cultivating termites.

Keeping cool: do mounds dissipate heat?

Despite a lack of data, it is generally assumed that macrotermitid termites need to deal with overheating problems due to the high metabolism of the fungi and the termites (Darlington 1987, 1989; Weir 1973). In this context, ventilation of mounds was considered as a mechanism to dissipate excess metabolic heat (Collins 1979; Darlington 1987, 1989; Weir 1973; Schuurman and Dangerfield 1996; Noirot and Darlington 2000; Camazine et al. 2001).

The data for *M. bellicosus* in the CNP show that macrotermitine species can have problems in keeping warm which, due to physiological constraints, has consequences for the fitness of the colonies and the distribution of the species. The high demand for heat, despite the extensive metabolic heat production, could be explained by the high heat capacities of the mounds (Korb and Linsenmair 1998b).

This should not rule out cooling problems under some circumstances, but a careful analysis is necessary to address this topic. For example, in more arid regions, I would expect enhanced ventilation to occur through the ridges due to more pronounced temperature gradients. Optimal gas exchange and an extensive loss of heat would be the consequences. However, water loss would also be high and this might be difficult to replace. Therefore, at the upper temperature range of mound-building Macrotermitinae a similar trade-off as for the lower limit might be expected, except that gas exchange is traded against a reduction in water loss. This hypothesis could be tested.

The thermosiphon mechanism: a general mechanism for ventilation of enclosed mounds?

For the ventilation of enclosed mounds, Lüscher (1955, 1961) postulated a thermosiphon mechanism with air rising inside the central shaft and falling in the ridges, driven by convection currents. This mechanism became a classical textbook example of elaborate ventilation of animal structures (e.g. Heinrich 1993), although critical studies were lacking. The results for *M. bellicosus* in the CNP indicate that this mechanism only plays a minor role in enclosed cathedral-shaped mounds in the savannah, i.e. under the conditions that Lüscher proposed (Lüscher 1955, 1961). Moreover, preliminary results collected by

Loos (1964) are in line with the externally driven ventilation found for *M. bellicosus*.

A recent study on *M. michaelseni*, which also builds enclosed mounds, also lacks support for Lüscher's thermosiphon ventilation mechanism (Turner 2001). In contrast with *M. bellicosus*, however, *M. michaelseni* mounds seem to be mainly ventilated by a tidal movement of air driven by temporal variation in wind speed and wind direction, while thermosiphon-like metabolism-induced buoyant forces may promote social homeostasis.

Although the influence of wind was not quantitatively investigated in *M. bellicosus*, it is unlikely for several reasons that the ventilation mechanism working in *M. michaelseni* mounds is a major driving force in *M. bellicosus* in the CNP. First, *M. michaelseni* does not build cathedral-shaped mounds with ridges, but cone-shaped mounds with a tall, thin turret (i.e. spire) and a broad outwash pediment (Turner 2000). Thus, a circulatory ventilation system is missing in *M. michaelseni*, while it is present in *M. bellicosus* mounds of the savannah. Second, in *M. bellicosus* mounds air rises in the peripheral air channels (equivalent to Turner's surface conduits) during the day (Korb and Linsenmair 2000b); this is difficult to explain by Turner's tidal flow ventilation mechanism. And third, there was a daily cycle in the ventilation pattern of different ridges of the mounds. Those ridges having the most intense rise of air and ventilation were more exposed to the sun's radiation and therefore had the highest surface temperature (Korb and Linsenmair 2000b). Such a pattern can hardly be accounted for by tidal movement of air driven by wind conditions. Together, this indicates that in cathedral-shaped *M. bellicosus* mounds thermal radiation is the major driving force for ventilation during the day. However, it needs to be investigated whether the warming of the mound surface leads to an intensified movement of air that can cause air flow inside the mounds' peripheral air channels. Then wind-induced flow would play a role, but it would still gain its force mainly by solar radiation. So, in general, wind and solar power seem to be the driving forces for the ventilation of enclosed mounds, with convection currents – as proposed in the thermosiphon mechanism – probably playing a minor role. Which driving force is more important depends on the species and the environmental conditions.

Proximate mechanisms for the construction of mounds

The construction of mounds that seem to be adapted to local temperatures should not imply a purposeful design of the mounds with all termites having a blueprint of the nest 'hardwired' into the nervous system. There is no need to invoke individual complexity. Theories of self-organisation (i.e. the emergence of macroscopic patterns out of collective actions of relatively simple individuals) can explain how complex patterns may emerge from interactions among social individuals that exhibit simple

behaviours (for reviews see Bonabeau et al. 1997; Theraulaz et al. 1999; Camazine et al. 2001). Although self-organisation is not yet in a position to explain macroscopic features of termite mounds, several models have been developed to account for the construction of pillars and walls, the building elements of mounds (Grassé 1959; Deneubourg 1977; Bonabeau et al. 1998; O'Toole et al. 1999; Camazine et al. 2001). The most complex approach was probably to explain the construction of the royal cell by a combination of self-organisation and the use of a template (Bonabeau et al. 1998; Camazine et al. 2001), which was based on experimental data (Grassé 1959, 1984; Bruinsma 1979). The question how more complex structures, such as adaptive mound architecture, arise has not been addressed, probably also due to a lack of quantitative empirical data and cooperation between modellers and empiricists. How necessary such cooperation would be, might be illustrated by the following example. A recent simulation on the development of pillar-wall constructions pointed out that, in addition to stimulating factors, an inhibition mechanism is necessary to get 'a smooth surface of joining tips of growing pillars and a lateral extension of the pillars into walls' (O'Toole et al. 1999). This gave rise to a controversy, as former models did not need to include such an inhibition effect (Grassé 1959; Deneubourg 1977; Bonabeau et al. 1998). However, the differences in the simulation results are likely to be explained by biological differences between the species that served as model systems. O'Toole et al.'s (1999) model is based on *Nasutitermes costalis* (Jones 1979, 1980), while those of the former studies were based on Macrotermitinae; however, the former uses faecal pellets to build carton nests (Traniello 1981), while the latter use soil particles to build earthen nests (Grassé 1984). Furthermore, a smooth building surface is no general criterion for building processes in termites; the latter species not necessarily produce smooth surfaces during the building process (i.e. pillars do not grow evenly and may differ in height) (personal observation). Also a halting behaviour, claimed to be responsible for the inhibition effect in O'Toole et al.'s (1999) model, is not a general behaviour found in termites (see e.g. Grassé 1959, 1984). However, another general mechanism is quite likely to induce a similar inhibition effect during building: the crowding of termites when more termites enter a building site where other termites are working at existing pillars. Then, the newly arriving termites deposit their pellets just next to them. This mechanism probably prevents a disorganised growth of just a few pillars and leads to the lateral extension of pillars into walls which, however, are not completely smooth at the tip due to the attractive component of the building pheromone. A new, more realistic model which addresses different building materials and incorporates empirical data on crowding effects would be desirable. Furthermore, this example illustrates that models which predict an observed pattern do not necessarily reflect the processes working in the real system. To reveal relevant processes, each model needs to be tested by manipulating

one of the key parameters and comparing the results from the model with those in the field. Again, this demands a closer cooperation between modellers and empiricists.

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