Chapter 3
Self-Organization of Nest Contents

Abstract The arrangements of the contents of both single, vertical and horizontally arranged parallel combs are very similar among all species of honeybees, and different areas of the combs are repetitively used for the same functions. They principally differ in the formation of their patterns, which have been tacitly assumed for centuries, to derive in some mysterious way as "in the nature of bees". Camazine (1991) conducted a series of experiments to validate one of two mutually exclusive hypotheses for the comb patterns of *A. mellifera*; (1) a blueprint hypothesis in which patterns develop in some pre-ordained and specified way intrinsic to bees; or, (2) a self-organization hypothesis (a reaction–diffusion system), by which patterns emerge spontaneously from the dynamic interactions among the processes of placing, and then displacing, the different elements of the nests. Camazine's original self-organization hypothesis has been challenged, modified, and ultimately, supported by rigorous mathematical analyses of this problem. The model and the self-organization hypothesis appear extremely robust and parsimonious and remains the prevailing paradigm (Montovan et al. 2013). Explanations for pattern formation in the single-comb dwarf and giant honeybee species are perhaps less difficult. Development of an *A. florea* vertical, single comb nest is accomplished in 4 months after a swarm settles. In only a few days the nest has already been partitioned into areas for honey (top of comb), an underlying pollen layer below, and a central area which both capped and uncapped larval cells occur. This basic pattern remains until the mature colony swarms some 4 months later. The major challenge is the construction of the crown comb.

3.1 Introduction

Honeybees are a group of largely wild insects of which only the two medium-sized, cavity-nesting species, *A. cerana* and *A. mellifera,* have successfully been semi-domesticated to the extent that they can be maintained in artificial cavities such as woven skeps, clay or log hives or man-made boxes, such as the ubiquitous

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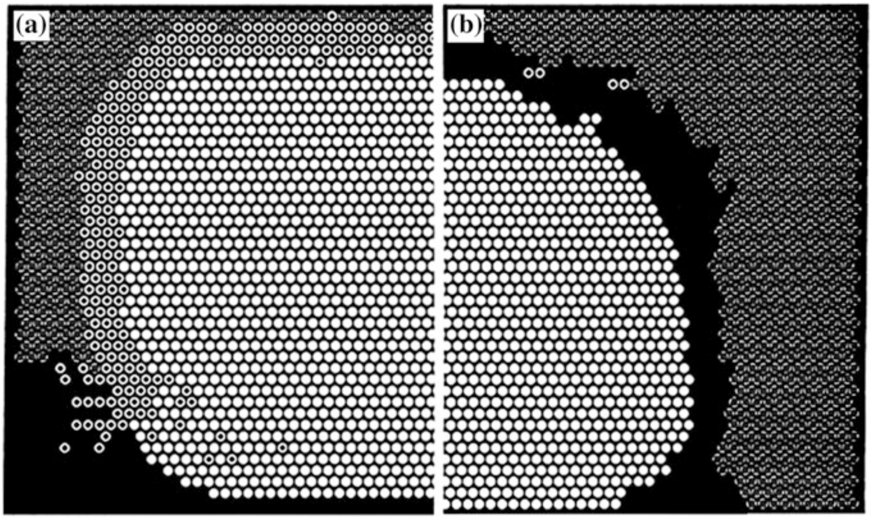


Fig. 3.1 **a** Characteristic nest pattern of *A. mellifera*: centrally located brood, a band of pollen above and to the side of the brood area and a honey storage region at the periphery (*left*). **b** Comb pattern when little pollen was available with an empty area where pollen was previously stored (*right*). *White circles*—brood; *white circles with black dot*—pollen; *grey areas*—honey; and *black*—empty cells (Camazine 1991)

Langstroth hive (Free 1982; Crane 1999), while the other species are entirely wild. Nonetheless, the arrangement of comb contents are very similar among all species of honeybees, whether the nest be a single vertical comb (*A. andreniformis, A. dorsata, A. florea* and *A. laboriosa*), or collections of horizontally arranged parallel combs (*A. cerana, A. koschevnikovi, A. nigrocincta* and *A. mellifera*). For the latter, brood, honey and pollen are stored in a series of parallel wax combs so that a characteristic, well-organized pattern develops on the combs, consisting of three distinct concentric regions: a central brood area, a surrounding rim of pollen, and an outer large, peripheral region of honey (Fig. 3.1a and b). For the cavity-nesting species this pattern is most pronounced on the central combs, which intersect a large portion of the roughly spherical volume of brood (Camazine 1991).

The arrangement and distribution of the contents of European bees' nests, *A. mellifera*, seems to have been basically understood by the middle of the eighteenth century (Dublin Society 1733; Thorley 1744). Indeed, there was a proliferation of texts on honeybees in the early nineteenth century and some of the more important, subsequently influential, and still pertinent ones are those of Huber (1814), Dzierzon (1852) and Langstroth (1857). Among the more recent works describing the natural nests of honeybees and the distribution of their contents are: for *A. andreniformis* (Wongsiri et al. 1997); *A. cerana* (Tokuda 1924, 1935; Sakagami 1959); *A. dorsata* (Koeniger et al. 2010); *A. florea* (Sakagami and Yoshikawa 1973; Rinderer et al. 1996; Duangphakdee et al. 2013); *A. laboriosa* (Underwood 1986) and *A. mellifera* (Seeley and Morse 1976). Oddly enough, natural (non-beehive) nests of *A. mellifera* have seldom been investigated, but Seeley and Morse (1976) did so and also provided a summary of the characteristics of the nests of *A. florea* based on data from Benton (1896), Rahman and Singh (1946), Lindauer (1956), Ruttner (1968), Sakagami and Yoshikawa (1973); as well as *A. dorsata* based on data from Benton (1896), Grassé (1942), Rahman and Singh (1946), Kallapur (1950), Lindauer (1956), Singh (1962), Ruttner (1968), Morse and Laigo (1969) and *A. mellifera* (Seeley and Morse 1976).

3.2 Pattern Formation in Combs

3.2.1 Reaction–Diffusion Systems Pattern Formation

It is evident that different areas of the comb are used repeatedly for the same functions in all honeybee species. It has been tacitly assumed for centuries that the patterns observable in the arrangement of nest contents in *A. mellifera* are in some mysterious way “in the nature of bees”; or as Pappus suggested, “bees have a certain geometrical forethought by which the most economical container to be made of wax was, in fact, the hexagonal configuration”. However, the observations that pollen and honey are regularly deposited in empty cells within the brood area during the day, only to be removed to their ‘proper’ places during the night, led to an especially seminal paper on pattern formation of comb use in honeybees by Camazine (1991). While Camazine’s ideas are certainly original, they stem from two sources; his childhood wonderment as to why sand dune ripples looked so much like patterns of clouds in the sky (so-called cloud streets—Camazine, pers comm.), and the application of reaction–diffusion equations formulated by Turing (1952) to explore pattern formation. Turing’s model demonstrates self-organization, and remains a classical paradigm in studies of morphogenesis.

Camazine (1991) conducted a series of experiments to validate one of two mutually exclusive hypotheses: (1) a blueprint or template hypothesis, in which patterns develop in some pre-ordained and specified way intrinsic to bees; or (2) a self-organization hypothesis in which patterns emerge spontaneously from the dynamic interactions among the processes of placing and then displacing the relevant nest elements. In a series of classically simple and illuminating observations and experiments, Camazine (1991) noted that the brood pattern is initiated by the laying habits of the queen, who must take into account the presence of nearby brood and, perhaps, the comb boundaries. This given, the queen lays eggs and the bees deposit both nectar and pollen haphazardly among the combs in the first instance. Possibly informed by the presence of young nurse bees, the queen does not lay eggs outside the nascent brood area, but continually searches for empty cells near other eggs or brood.

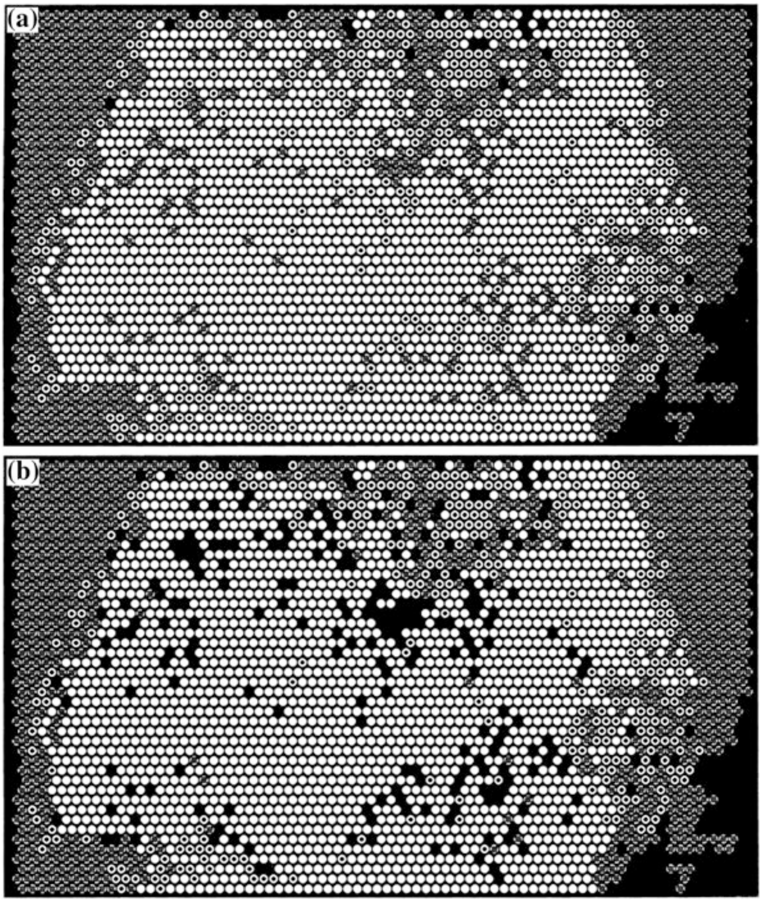


Fig. 3.2 Comb of an *A. mellifera* nest showing preferential removal of honey and pollen away from brood: **a** *upper trace* made at 19:00 at the end of foraging; **b** *lower trace* of the same comb the following morning at 08:00. Cell symbols as in Fig. 3.1 (Camazine 1991)

Cells in the brood area filled with honey or pollen are preferentially emptied of their contents. This was experimentally shown by the distribution of cell emptying from the brood area, which is a function of distance from the nearest brood cell (Fig. 3.2a and b).

Brood cells emptied of nectar and pollen, are then found by the queen who lays in them, and so the pattern develops. Camazine and colleagues (Jenkins et al. 1992) then proceeded to develop a computer simulation model to establish pattern-forming rules, as estimated from the actual experiments. Using the empirical events from observation hives as the parameter values, they were able to reveal interacting processes that contribute to pattern formation. The simulation also produced the final pattern observed in observation hives and confirmed the interpretation of pattern formation (Fig. 3.3a–c). The model and the self-organization

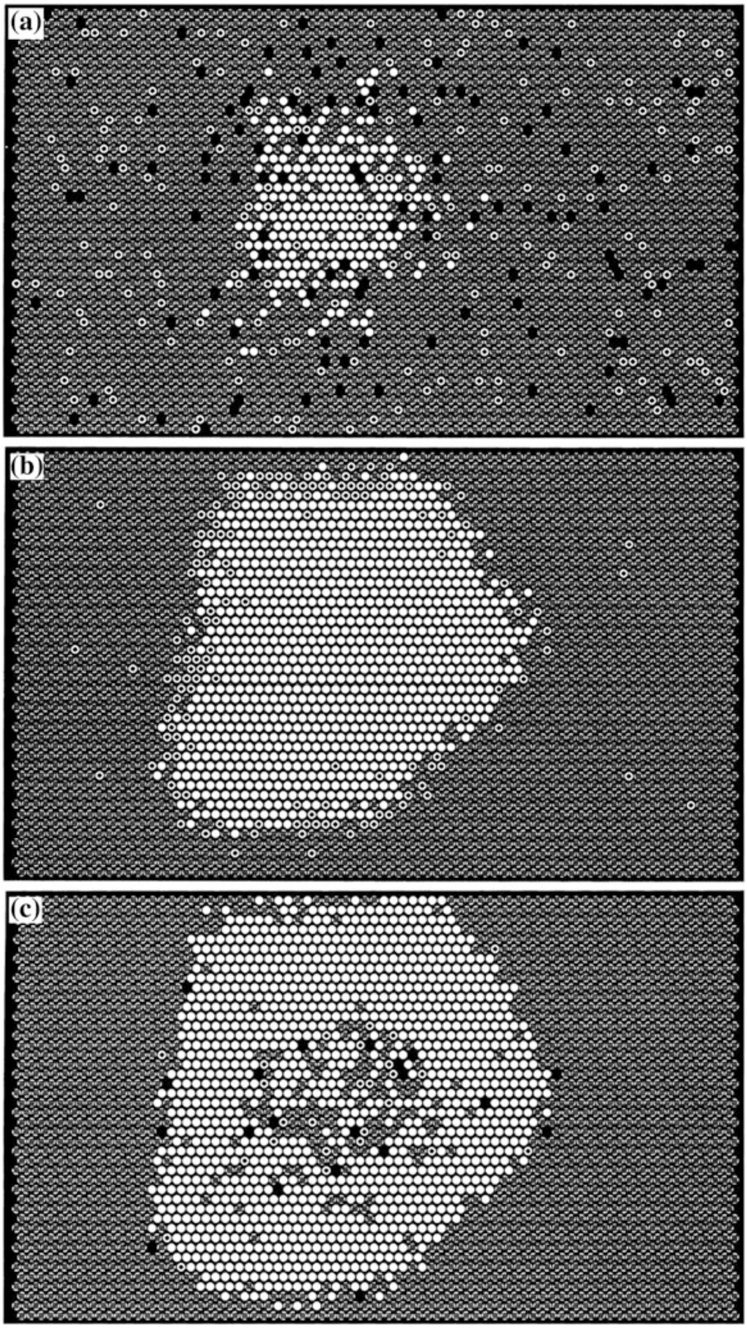


Fig. 3.3 Computer simulation of pattern formation of *A. mellifera* comb: **a** day 1; **b** day 7; **c** day 22. Cell symbols as in Fig. 3.1 (Camazine 1991)

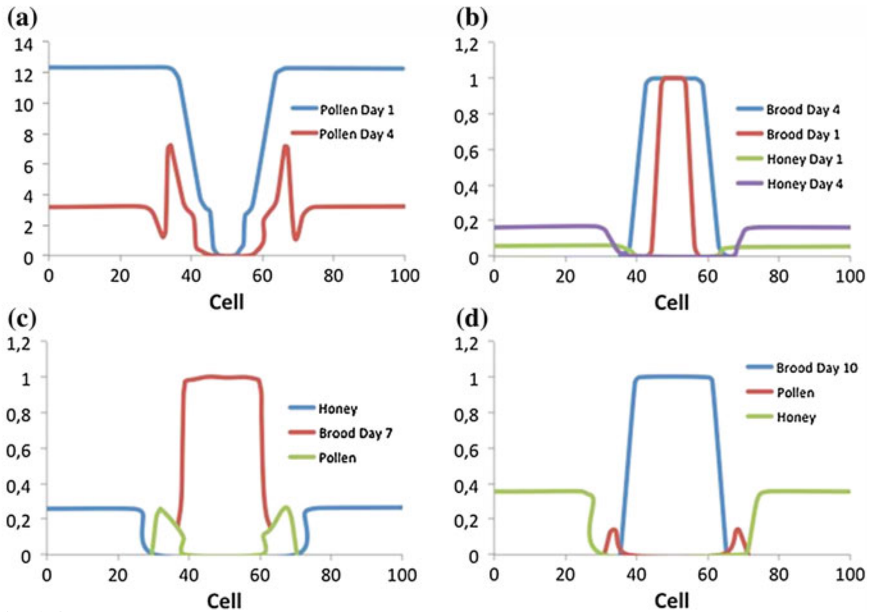


Fig. 3.4 Sequence of events in Camazine's (1991) self-organization model showing the formation patterns of brood, pollen, and honey, observed in a drawn frame in an observation hive of *A. mellifera*. **a** Pollen distribution when input is low; the concentration of pollen initially increases at the periphery, but then decreases and is low everywhere; **b** the brood area has expanded over the first few days with an increase in honey at the periphery of the comb. (In this particular model there was a 3-day pollen burst over days 5–7). The interface between honey and pollen consists of a zone of empty cells due to a low level of pollen; **c** by day 7, the pollen band has developed rapidly and a typical pattern of brood, pollen and honey has formed. Honey concentration is increasing at the periphery of the comb, and the brood area is expanding; **d** by the end of day 10, the pattern is intact, but the pollen band is slowly decreasing. Equilibrium is reached when the brood is surrounded by honey and pollen and the queen can find no empty cells in which to lay eggs (after Camazine 1991; Jenkins et al. 1992)

hypothesis appear extremely robust and parsimonious. This idea has been further analyzed mathematically by Jenkins et al. (1992), who derived rate constants for the removal and re-deposition of honey and pollen in order to achieve their characteristic bands and positions above the brood area (Fig. 3.4). Camazine's approach and interpretations have subsequently been endorsed by Bonabeau et al. (1997) and Theraulz et al. (2003).

3.2.2 Template Effects?

In the intervening years since the works of Camazine (1991), Bonabeau et al. (1997) and Theraulz et al. (2003) were published more detailed knowledge of worker behaviour has been reported. For example, Johnson and Baker (2007) observed that nectar-receiving bees tend to deposit their nectar loads near the top

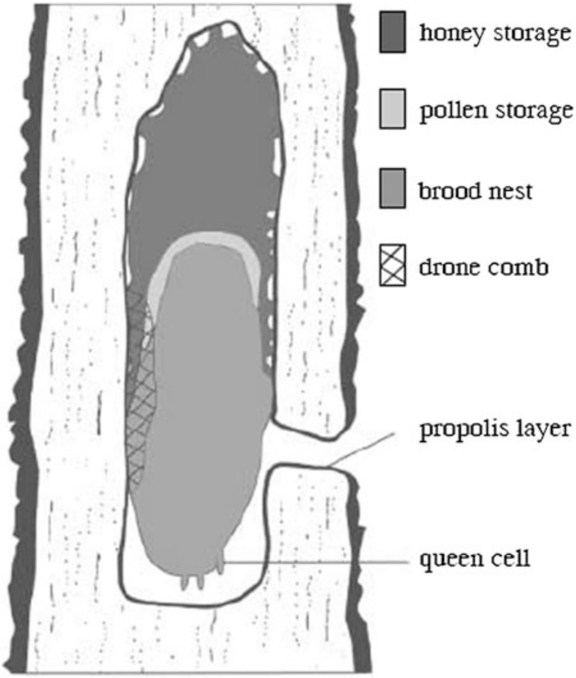


Fig. 3.5 Characteristic pattern of comb organization in a tree cavity occupied by an *A. mellifera* nest (Johnson 2009, after Seeley and Morse 1976)

of the comb where the nectar band occurs. Likewise, Dreller and Tarpy (2000) showed that foragers must have direct contact with the brood and pollen areas to regulate their foraging for pollen and preferentially deposit pollen in cells near the brood area. Inevitably, these observations and subsequent analyses required some refinements. Johnson (2009) re-examined pattern formation on combs in relation to four groups of bees: the queen, nectar-receiving bees, pollen foragers and nurse bees. He concluded that the vertical pattern of honey at the top of the comb and brood at the bottom is owing to a gravity-based template effect, while the band of pollen depends on both a self-organization effect as well as a queen-based template. Johnson's model is based on the distribution of comb contents in a tree-dwelling colony, described by Seeley and Morse (1976) and illustrated in Fig. 3.5.

In models, colonies using the more complex scheme (proposed by Johnson 2009), during a period of high nectar inflow is shown in Fig. 3.6. It is followed by pattern formation obtained by a self-organization model and two template effects during a period of high nectar inflow shown in Fig. 3.7.

3.2.3 Recent Models

The modifications that Johnson's (2009) scheme suggests remain open to argument and debate. In a rigorous mathematical analysis of this problem by Montovan et al. (2013), these authors support Camazine's original proposition, that the combined

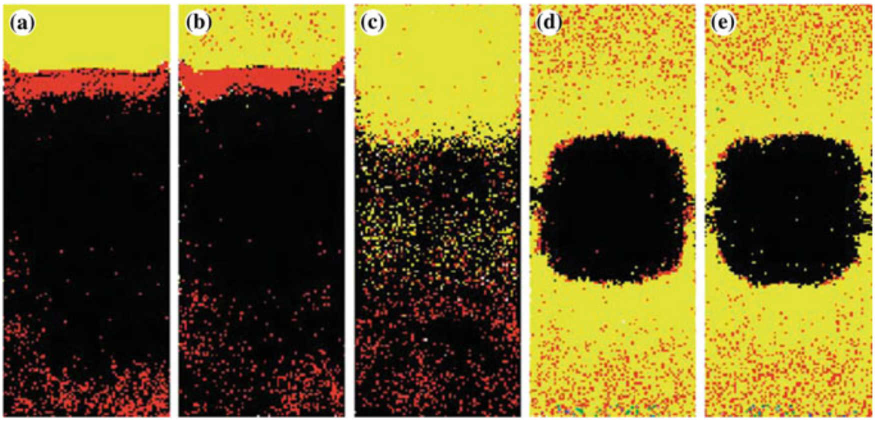


Fig. 3.6 Mechanisms underlying comb pattern formation in an *A. mellifera* nest: SO—self-organization, T1—gravity-based template, T2 queen-based template. Each of the frames (**a**–**e**) shows the pattern at 14 days. The full model (with rain) is shown in (**a**) so (SO + T1 + T2); **b** without the queen-based template, pollen is scattered throughout the honey zone (SO + T1); **c** without the self-organizing mechanism, a pollen band does not form, and the brood and honey areas are indistinct (T1 + T2); **d** without the gravity-based template, the pattern remains concentric as opposed to vertical so that (SO + T2); **e** original self-organization model of Camazine does not lead to pattern formation under realistic parameter settings (SO) (Johnson 2009)

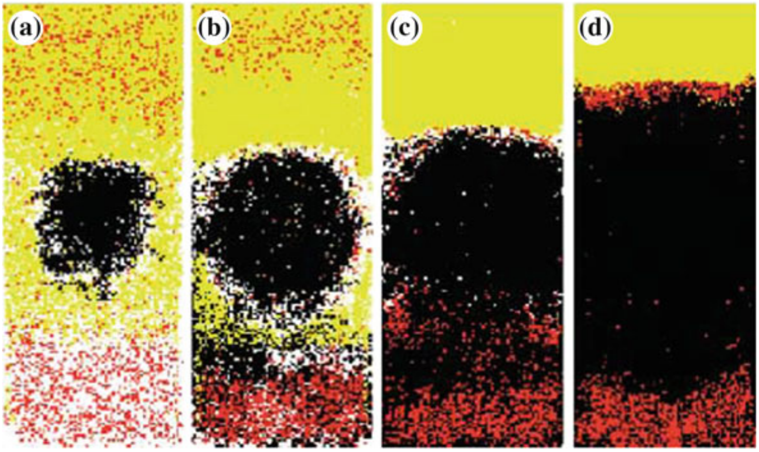


Fig. 3.7 Johnson's (2009) pattern formation in an *A. mellifera* nest obtained by self-organization and two template effects during a period of high nectar inflow: **a** day 1, **b** day 4, **c** day 7, and **d** day 14. Cells of honey are *yellow*, those of pollen *red* and brood cells *black*. On day 1, pollen was scattered about the comb but once brood was present, pollen was shifted to the bottom of the comb. Nectar was preferentially unloaded near the top of the comb by the nectar-receiving bees. By day 7 the comb pattern was almost formed except for the band of pollen cells, which had formed by day 14 (Johnson 2009)

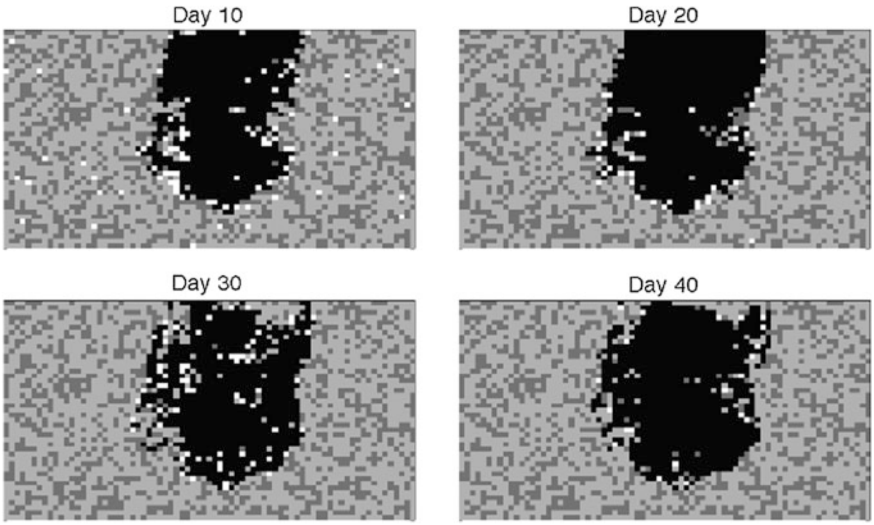


Fig. 3.8 Simulation of Model 4 beginning with an empty comb but after 20 days the pattern is maintained when the emerging adults leave their cells (Montovan et al. 2013)

actions of many individual bees could produce the comb pattern with which we are familiar, using rather simple but biologically meaningful rules. However, as they pointed out, the Camazine model does not explain how the comb pattern is maintained with subsequent generations of brood. In their analyses, their Model 1 is the original Camazine model; in Model 2, an alternate queen movement method is employed while leaving the remaining rules identical to those of Model 1. Model 3 uses alternate honey/pollen consumption rules while all other rules are identical to those of Model 1. Model 4 employs the alternate methods of both queen movement and honey/pollen consumption (Fig. 3.8). Model parameter values were varied over a wider range than were used, so that the sensitivity of the model to choices of parameter values could be assessed. For queen movements, Montovan et al. (2013) used a Gaussian distribution of directions with a mean toward the centre of the comb. For honey and pollen they defined the probability of selecting a particular cell that is linearly proportional to the number of brood cells within a chosen distance, which includes the idea that nurse bees take more honey/pollen from cells nearer to brood, without assuming that nurse bees make multiple trips from the same cell.

The model of Montovan et al. (2013) contains the basic processes that Camazine described, but to check that their models would in fact create the initial pattern of a compact brood region surrounded by a ring of pollen, they simulated the first 20 days for all four models. For the Camazine model, their simulations reproduced Camazine's results in Model 1, but the desired pattern formed in the first 20 days gradually dissolved as brood cells are vacated. They found that all the models were able to form the initial pattern. In a simulation of Model 4, the initial

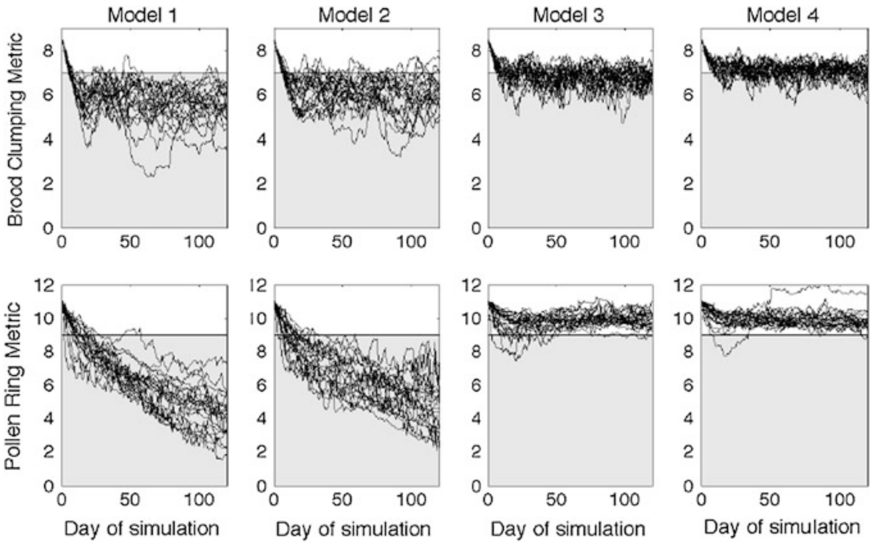


Fig. 3.9 Trajectories for all four models which illustrates that the combined modifications for queen movement and honey/pollen removal used in Model 4 provides the best result for *A. mellifera* nests (Montovan et al. 2013)

pattern is not perfect, but a compact brood region forms, as does a ring of pollen. Models 1 and 4 form similar patterns initially, but Model 1 cannot maintain the pattern, while Model 4 is able to both create and maintain the pattern. The overall differences between the four models lie in the ability to maintain a compact brood region and a pollen ring over time and are apparent in the trajectories of the brood and pollen metrics through 120 days of simulation for each model (Fig. 3.9). To conclude this section, Camazine's work showed a highly developed prescience when he was able to demonstrate that the centuries-old belief "in the nature of bees" (which equates to "a certain geometrical forethought" as postulated by Pappus) as an explanation for patterns in combs, could be bettered.

3.3 Developmental Cycles of *Apis florea* Nests

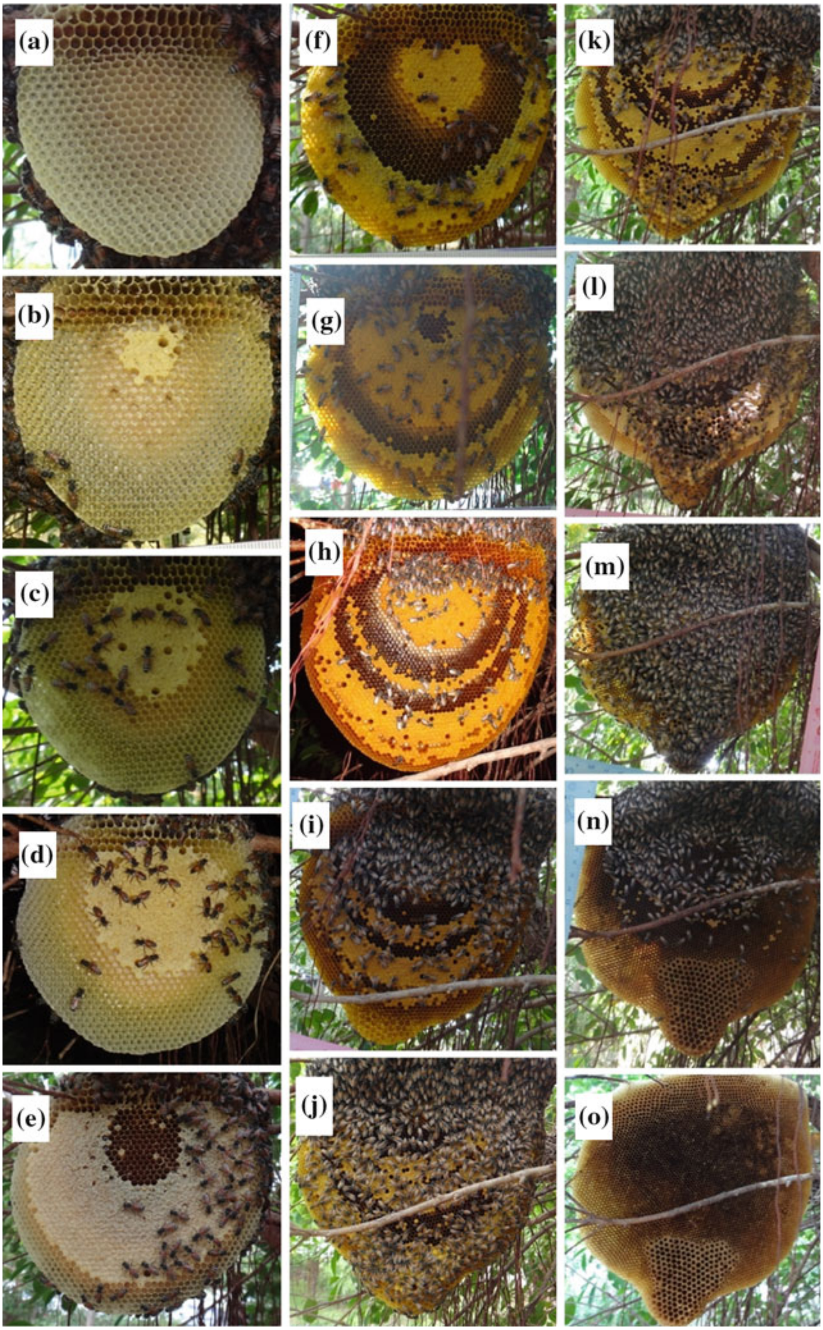
When we consider that Camazine's observations were made on *A. mellifera* combs in observation hives, there is a more natural comparison which can be made to the nests of the dwarf honeybees, *A. florea*, and we present this material for its heuristic value. *A. florea* nests are single, exposed combs, vertically attached to one or two thin branches in trees or bushes throughout Southeast Asia, and have been described quite thoroughly many times (cf. Hepburn and Hepburn 2011). Analyses of the structure of these nests have been comprehensively reported in an especially relevant publication by Sakagami and Yoshikawa (1973), who described and illustrated the arrangement of honey, pollen, worker and drone brood cells as well as reproductive queen cells. Further details on the nests of *A. florea*, the arrangement and dimensions of cells and their physical relationships to one another were tabulated by Rinderer et al. (1996).

Although we now have accurate descriptions of the nest structure of *A. florea* as reported by Sakagami and Yoshikawa (1973) and Rinderer (1996), virtually all the nest specimens of *A. florea* that they and others examined were purchased at Chatuchak Market in Bangkok. Because of the presence of drone cells at the bottom of the combs purchased, they were rightly adjudged to be mature nest specimens. So, these works provide what are literally ‘snapshots’ in time of mature nests on their day of harvest for market. More recently, Duangphakdee et al. (2013) photographically documented the chronological growth and development of *A. florea* nests at Chom Bueng, Thailand, by newly settled swarms, from their inception until their final days before reproductive swarming or absconding.

The areas of brood comb in examples of the dwarf, medium-sized and giant honeybees, all consist of concentric regions in the plane of the comb. However, in the medium-sized, cavity-nesting honeybees, the use of multiple parallel combs means that, in a three-dimensional perspective, the concentric rings of sequential brood combs approximate a sphere, while those of honey and pollen are ovals or inverted saucers. Because the dwarf honeybees usually construct a single comb, we use this species to illustrate the chronological changes that occur from the onset of building to maturity of the comb and its final abandonment as documented by Duangphakdee et al. (2013). However, the vertical arrangement of specialized areas is the same as in *A. mellifera,* as described by Seeley and Morse (1976).

A. florea nests were collected and moved at dusk. They were hung on small trees, maintaining the vertical position of the combs. Colonies were allowed to adapt to their new environment and resumed normal activities and foraging. After few days the brood comb, extending below the crown, was cut away at dusk, and removed to induce absconding (Woyke 1976; Duangphakdee et al. 2012). The following day, a new nest site selection process was conducted when the whole colony took off to a new nesting site. The authors then followed each swarm until the colony settled in a new nesting tree. Their results are shown in a chronological series of photographs (Fig. 3.10).

The dimensional growth curves of the nests of two colonies of *A. florea* show daily changes in comb length, width and area from inception of the nest to its maturity and completion (Figs. 3.11, 3.12 and 3.13). Initially, both the lengths and widths of the nests double in parallel, following a logarithmic form over the first 10 days (Figs. 3.11 and 3.12). Then the rates of change gradually begin to decrease in subsequent weeks, but nonetheless do so in tandem. In consequence, the rate of change in the area of the comb yields a linear constant (Fig. 3.13).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◀ **Fig. 3.10** Development of an *A. florea* vertical, single comb nest of over 16 weeks once a swarm settled. By day 4 (**b**) the nest has already been partitioned into an area for honey (top of comb), an underlying pollen layer, below which both capped and uncapped brood cells occur. This basic pattern remains until the mature colony swarms some 4 months later. In the sequence of photographs shown: **a** on day 2, the darker wax honey crown is being developed above the brood area which contains eggs and larvae in a concentric pattern; **b** by day 4, some of the brood cells have been capped and more eggs and larvae are in the cells below, maintaining the concentric pattern; **c** on day 6 the progression of cell cappings continues as does the expansion of the uncapped brood area; **d** by day 8 the concentric rings of capped and uncapped brood increased and workers began storing nectar in the crown; **e** on day 16 the oldest patch of brood emerged as adults, and extensive capping of brood cells continued (note that the brood area does not extend to the periphery of the comb); **f** on day 23, the previously empty cells of (**e**) now contained capped brood of what will be the second generation of adults, the cells in the area surrounding this contains newly laid eggs, while the outer band contains capped brood; **g**–**k** sequential occurrences between days 30 and 93, showing the staggered distribution of concentric brood of various ages and generations with drone cells finally constructed by day 93; **l** by day 100 drones emerged from their cells at the bottom of the comb; **m** on day 107 the drones have left the nest; **n** by day 114 there are no new eggs, no uncapped brood and only very few capped cells; **o** on day 121 the colony absconded (Duangphakdee et al. 2013)

Fig. 3.11 Change in length of *A. florea* comb

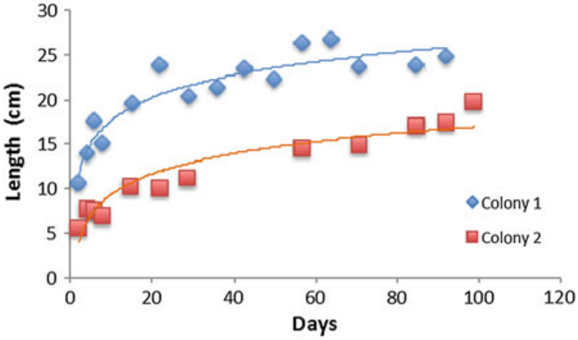


Fig. 3.12 Change in width of *A. florea* comb

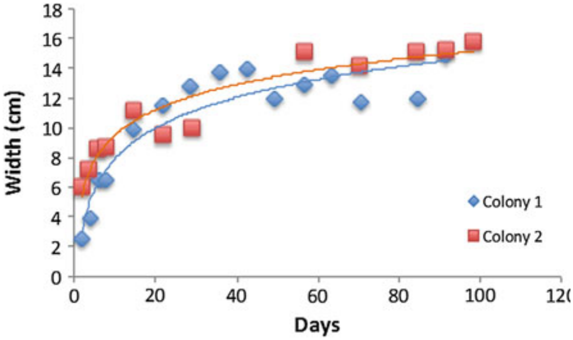
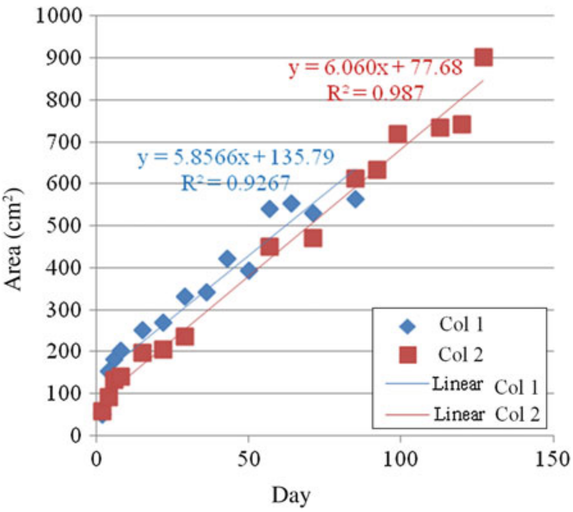


Fig. 3.13 Change in area of *A. florea* comb



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