

## Chapter 2

# Nesting: Sites, Space and Density in Comb-Building

**Abstract** The nesting sites of open- and cavity-nesting honeybees are reviewed in terms of nest sites, space and honeybee density. Space comprises building space for new combs and living space for clustering bees. In a container of a fixed volume, a strong colony constructs more than a colony with a smaller population; but, the amount of comb constructed per bee decreases with increased density and increases in colony size. The quality aspects of space as a stimulus for comb-building include illumination and air movement. Volume, space and density will only operate on wax production when the colony has reached some critical, if yet indefinable, threshold. Wax bees move throughout the nest so there is a close synchrony between the ‘needs’ of specific comb-building areas and the presence of bees producing wax scales. During comb-building there are concomitant changes in population size, population density, nectar and pollen influx, all of which affect honeybee/comb interactions.

### 2.1 Introduction

Nesting is critical for the homeostasis, stability and ultimately the survival of honeybee colonies, and provides an arena in which colony growth unfolds in the usual annual colony cycle of swarming, reproduction and migration (Hepburn 2011). Once a swarm of bees has left its maternal nest it must find a new home, and descriptions of the process for *A. mellifera* abound as early as the early 18th century (Thorley 1744). The first studies of the ways in which colonies of the Asian *A. cerana*, *A. dorsata* and *A. florea* find new nest sites, have been described in a charming monograph by Lindauer (1961). Basically, the scout bees of a colony scour the countryside for potential nest sites and convey the information that they have reconnoitred to their nestmates. In the mother colony, this information is shared and “debated” until a consensus is reached as to the ‘best’ of the sites offered. Major studies on the nature of these debates, their duration and intensity, began with early studies on *A. mellifera* some 30 years ago, by Seeley and Morse (1978; Seeley et seq.), and have been recently summarised (Seeley 2010). These matters are discussed in detail below. ‘Best’ is the gist of the problem in a nutshell, and we suggest that ‘best’ can largely,

but not entirely, be gleaned from a survey of natural honeybee nest sites (specifically excluding beekeeping hives) among the species of honeybees.

This is a review of the nesting sites of honeybees and the peculiarities and constraints of open-nesting and cavity-nesting. The honeybees comprise three groups with respect to nesting: the dwarf honeybees, *A. andreniformis* and *A. florea*, are single comb, open-nesting species; the medium-sized species, *A. cerana*, *A. koschevnikovi*, *A. mellifera*, *A. nigrocincta* and *A. nuluensis*, are multiple comb cavity-nesting bees; and the giant honeybees, *A. dorsata* and *A. laboriosa*, are also single comb open-nesting species (Phiancharoen et al. 2011). The ways in which the nests of these species are attached to a substrate further differentiate them: (1) there are no horizontal surfaces in the nests of the medium-sized and the giant honeybees, so communication using the dance language occurs in the vertical mode for both groups; whereas (2) in the dwarf species, dance language communication occurs in the horizontal mode. These factors clearly determine the suitability of potential nesting sites in the first instance for these species. Both open-air nesting and cavity-dwelling nesting sites further constrain the honeybees in terms of colony defense and micro-environmental homeostasis (Fuchs and Tautz 2011; Kastberger et al. 2011). Of equal importance is the nature of the nesting sites, mode of comb construction (Hepburn 1986) and the physico-chemical properties of the actual construction materials (Hepburn 1986; Phiancharoen et al. 2011).

## 2.2 Nesting Sites

### 2.2.1 *The Dwarf Honeybees*

Nests of *A. florea* occur in wooded areas, urban settings, areas with intensive agricultural activity as well as in the savanna (Franssen 1932; Free 1981; Matsuura 1983; Booncham et al. 1995; Nagaraja and Rajagopal 1999). *A. florea* nests are attached to a wide variety of plants (Basavarajappa 1998), and partially exposed to sunlight, wind and rain, and often have one surface of the comb exposed to direct sunlight for several hours a day (Fig. 2.1). *A. florea* are more likely to nest in diverse places, such as high up in tall trees in Southeast Asia, while in arid Western Asia they commonly nest in caves and buildings as well (Whitcombe 1984; Mossadegh 1990). *A. andreniformis* nests throughout Southeast Asia are most commonly observed in and near undisturbed, mixed deciduous and evergreen forests. Their nesting habitats are usually dark and shady places (20–35 % sun), well hidden and widely spaced. *A. florea* and *A. andreniformis* usually build single-comb nests in shrubs, bushes, and small trees, but double-comb nests have occasionally been reported for *A. florea* (Douglas 1886; Akratanakul 1977; Free 1981; Whitcombe 1984). *A. florea* nests are typically about 0.5–10 m above ground, but in towns and cities they are commonly found up to 15 m (Wongsiri et al. 1996; Wongsiri et al. 1997). *A. florea* are very adaptable and seem to find suitable nesting sites under extremely varied conditions (Mogga et al. 1989; Moritz et al. 2010).



**Fig. 2.1** *Apis florea* nests with (left) and without (right) workers. On the right, one can see the differentially utilised parts of the comb. The crown with sealed honey above the twig, open brood or empty cells in the centre surrounded by sealed brood and newly constructed cells that are empty

Neither *A. florea* nor *A. andreniformis* form nest aggregations in the same tree or shrub (Wongsiri et al. 1996). However, they can achieve a relatively high concentration ranging between 7.1 and 14.3 colonies/km<sup>2</sup> (Duangphakdee et al. 2013a). Nesting density of *A. andreniformis* remains unreported; however, casual observations in Sabah State, Borneo (Duangphakdee, pers. obs.) and Sumatera, Indonesia (Hepburn, pers. obs.) indicate that they are diffusely distributed. Studies in north-western Thailand, have shown that *A. florea* have a wide range of nesting habitats and food sources, estimated from the number of tree species used for nesting (Akratanakul 1977; Oldroyd et al. 2008; Basavarajappa 1998). However, Rinderer et al. (2002) reported that *A. andreniformis* and *A. florea* colonies have a tendency to locate their nests near nests of their own species in south-eastern Thailand. *A. andreniformis* and *A. florea* colonies select similar nest sites, but the spatial correlations of these sites were significantly negative, indicating that colonies may avoid areas containing nests of the other species. It is rare to find nests of *A. florea* in the same tree as another honeybee species; but, curiously, an *A. florea* nest was once seen in the same tree as an *A. dorsata* nest, the former was about 6 m from the ground, the latter 13 m (Duangphakdee and Hepburn, unpubl. obs.). However, it has been stated that *A. florea* colonies build nests aggregated near one another forming spatial clumps (Rinderer et al. 2002; Wattanachaiyingcharoen et al. 2008).

### 2.2.2 The Cavity-Nesting Honeybees

The cavity-nesting bees show preferences for nesting sites which vary within races and among *Apis* species. Among the sympatric cavity-nesting species of Indonesia, different species nest in distinctly different habitats. *A. cerana* mainly nest in

agricultural or disturbed areas, while *A. nigrocincta* nest more deeply in the forests (Matsuura 1983; Kuntadi 1989; Hadisoesilo 1997). Similarly, *A. koschevnikovi* occur in primeval forests while *A. cerana* occur mostly in secondary forests, agricultural and urban areas in Peninsular Malaysia (Otis 1996). It is not evident whether these species specifically avoid aggregated nest sites, but some reports are suggestive to the contrary (Hadisoesilo 1997; Bakker 1999). There is no published information on nesting of *A. nigrocincta*, *A. koschevnikovi* and *A. nuluensis* as of yet.

Nest density is probably related to topographical variations and the availability of profitable forage. Nest density for *A. mellifera* ranges from 0.5 to 7.8 nests per km<sup>2</sup> whereas nest density in tropical bees is greater. For example, Inoue and Adri Salmah (1990) measured nest density of *A. cerana* in Padang, Sumatra and found 22 nests/km<sup>2</sup> with a mean distance of about 100 m between nests. Aggregations of nests are not well known in cavity-nesting bees; nevertheless, Rinderer et al. (2002) suggested that there is a tendency in *A. cerana* to form aggregated nests. The nest cavity volume of *A. cerana* is usually about 10–15 l, but ranges from 4.5 to 97 l (Inoue and Adri Salmah 1990; Oldroyd and Wongsiri 2006). Nest entrances may be about 1–2 m above ground, but they seem to have no real preference for height, because nests can also be many meters above ground or in cavities within the ground. Entrance sizes range between 2 and 100 cm<sup>2</sup> (Seeley et al. 1982; Inoue and Adri Salmah 1990; Oldroyd and Wongsiri 2006). Such studies are extremely few, but Bakker (1999) reported that *A. nigrocincta* may be less specific in its choice of nest sites. The first study of feral nests of European-derived *A. mellifera*, of which we are aware, is that of Seeley and Morse (1976), who analysed the structures of 21 such nests and found that nest cavities are vertically elongate, more or less cylindrical and 30–60 l in volume.

### 2.2.3 *The Giant Honeybees*

Unlike other *Apis* species, the giant bees, *A. dorsata* and *A. laboriosa*, build very exposed and easily visible nests (Starr et al. 1987; Reddy and Reddy 1989; Sattigi 2001; Woyke et al. 2001; Neupane et al. 2004; Reddy 1983). *A. dorsata* builds nests in inaccessible places, like vertical rock faces (hence the name ‘rock bee’ in India), in gorges along hill profiles, tall man-made structures such as water towers and buildings, and in the higher branches of remarkably, emergent tall trees which are highly visible in their surroundings (Fig. 2.2—Deodikar et al. 1977). Unusual nests, only 1 m above ground, have also been observed (Duangphakdee and Hepburn, unpubl. obs.). *A. dorsata* tend to build their combs in a north–south direction, minimising the exposure to strong wind and sunlight (Deodikar et al. 1977; Woyke et al. 2004). *A. laboriosa* apparently always build their nests beneath unweathered, light-coloured clear cliffs or rock overhangs, which have recently been analysed and described in great detail (Woyke et al. 2012). They have never been reported to nest on the branches of trees (Roubik et al. 1985;



**Fig. 2.2** A tree with several *A. dorsata* nests and one unoccupied comb in the foreground

Underwood 1986); but, there is simply no information as to whether they are able to do so. Colonies of *A. dorsata* re-use preferred trees after an absence of several months (Neumann et al. 2000; Paar et al. 2000). Previous work has suggested that visual information is used by migratory colonies to relocate places where nesting has proven successful, although odour and tactile or chemical cues associated with the material of old combs seem more likely in determining the final choice (Neumann et al. 2000; Paar et al. 2000).

Giant honeybees vary quite considerably in their nesting habits and relative nest densities. *A. dorsata* and *A. laboriosa* are extremely gregarious species and 20–30 nests in a single tree are fairly common for the former, as are cliff overhangs for the latter (Roubik et al. 1985; Joshi et al. 2004; Woyke et al. 2004, 2012). Reports include a range of 67–256 colonies per tree for *A. dorsata* (Butani 1950; Lindauer 1956; Singh 1962; Deodikar et al. 1977). Oddly, Morse and Laigo (1969) found almost no aggregations in the Philippines. It could well be that the Philippine population is a distinct species (Lo et al. 2010), which would explain the difference in behaviour. In an extensive survey of *A. laboriosa* at 54 cliff sites in western Nepal, Joshi et al. (2004) reported an average aggregation of 6 nests per cliff, with a range of 1–37. Woyke et al. (2012) analysed some 23 nesting sites in Nepal, India and Bhutan, on which 587 colonies were established, with an average of about 25 colonies per site.

*A. dorsata* colonies nest gregariously; however, placing empty combs in previously occupied trees, or on nearby trees of the same species, did not attract more swarms; the same number of colonies that left trees returned to previously

occupied trees (Liu et al. 2007). Although it is believed that few individuals probably live long enough to make a return journey to their original nest site, some colonies nonetheless return to their exact former trees (Neumann et al. 2000; Paar et al. 2000; Liu et al. 2007). Because the longevity of workers has not been determined under field conditions, it may prove that there is nothing really ‘magical’ about a migrating swarm of *A. dorsata* returning to their original nests.

*A. laboriosa* is the largest species of *Apis* and is distributed along the Himalayas from Nepal to Vietnam (Hepburn and Radloff 2011). It builds exposed nests under rock ledges in deep, vertical river valleys, most commonly at 1,200–3,500 m (Roubik et al. 1985; Underwood 1986) and seems confined to areas higher than 2,500 m in the central and western areas of the Himalayas. The nests at 1,200–2,000 m could possibly be occupied throughout the year, but nest sites above 2,800 m are only occupied for a few months in summer (Underwood 1990). By late November, dropping temperatures make even the lower altitude cliff sites unsuitable for colony survival, and the colonies migrate to the forests and settle near the ground where they remain as combless winter clusters until late January (Underwood 1990). Those that nest below 1,200 m are reported not to migrate (Woyke et al. 2001).

### 2.3 Nest Cavities

The documentation for virtually every subspecies of African *A. mellifera* shows that the bees simply occupy cavities, natural or otherwise, including the hollows of trees and among their roots, in rock crevices, ridges of limestone, stony ground and even termite heaps (termitaria) excavated by aardvarks. The principal conclusion about nest site selection for this group of bees is that they will use any appropriate shelter that the natural terrain has to offer (Hepburn and Radloff 1998). Nest site preference is another matter, and is illuminated by interesting results from simple experiments using trap boxes to collect wild swarms of *A. m. scutellata* in Zambia, Kenya, Malawi (Nightingale 1983; Clauss 1992; Berg 1996) and *A. m. capensis* in South Africa (Hepburn and Radloff 1998), in which there was about a 10:1 greater catch in boxes 3–4 m above ground on building roofs, than at ground level. This fact is routinely exploited in traditional African beekeeping, the rule of thumb being “the higher the hive, the higher the occupation rate” (Mwangi 1985; Zulu 1970). Wherever tall trees occur in sub-Saharan Africa is where traditional beekeepers site their hives. Pressures for high sites include frequent fires, periodic flooding and predators.

When *A. mellifera* scout bees of European set out to find a new nest site, one of the criteria they use in selection is a measure of nest cavity volume (Seeley 1985; Seeley 1995). Here, the differences between European races and African races of *A. mellifera* are in stark contrast. Seeley and Morse (1976) found that natural cavity size preference for the former averaged about 45 l. The nest volumes of African *A. mellifera* ranged from about 5–150 l for *A. m. scutellata* in southern

Africa, but over 90 % of dozens of such measurements show that the average cavity volume hovers around 20 l, or only half that of European subspecies (Johannsmeier 1979; Berg 1996; McNally and Schneider 1996). As an aside, it is worth noting that various European experts, assessing the hives of traditional beekeeping in Africa, from Morocco and Ethiopia to Zimbabwe, state that they are too small. However, traditional man-made cylinders of straw, clay or log have a cavity size of about 25 l on average and are excellent facsimiles of nature.

Qualities, such as the compass direction of cavity opening with respect to the sun and possible distinctness of the apertures, have also been noted. Tests of trap boxes with distinct markings attracted no more colonies than unmarked boxes, nor did degree of a roof-overhang matter (Berg 1996). An analysis of compass orientation for the opening direction of about 140 wild nests in the Botswana swamps showed that they were randomly distributed (McNally and Schneider 1996). The actual nest size in nature is more problematical and it is doubtful as to whether many colonies stay at a fixed site for more than a season or two. In measurements of actual comb areas, based on about 80 established wild nests of *A. m. scutellata* in Botswana, McNally and Schneider (1996) found that the average comb area was about 6,000 cm<sup>2</sup>, while Hassan and Bradbear (1994) recorded an average of about 5,000 cm<sup>2</sup> in Tanzania. Working with wax recovery figures from various parts of the continent, comprising decades of wax export trade, average recovery ranged between about 300 and 900 g of wax per colony (Estève 1932; Irvine 1957; Sheriff 1963; Silberrad 1976). These figures were calculated to be about 519 g/wax/colony/harvest/year (totally destructive harvest). Using a wax yield figure of 100 mg wax/cm<sup>2</sup> of comb (for *A. m. capensis*, *A. m. scutellata* and *A. m. adansonii*), Hepburn and Radloff (1998) estimated that nest comb area ranged from about 2,600–8,000 cm<sup>2</sup> for hundreds of thousands of colonies in Africa, and averaged about 4,500 cm<sup>2</sup>, based on tonnage of beeswax exported (Hepburn and Radloff 1996).

Because there is a reasonable relationship between cavity volume and nest size, it appears that traditional beekeepers in Africa emulated nature well. But, there is also a southern hemisphere perspective, which is often lost on temperate zone biologists. Hepburn and Radloff (1996) performed time series and regression analyses of rainfall and beeswax exports from the woodland savanna of east central Africa, and determined that these two variables are most significantly and highly correlated when phase-lagged by one ‘bee year’ (running from July of year 1 to June of year 2). Rainfall and honey production are highly significantly correlated when lagged by one ‘bee year’. Honey and wax production are also highly correlated on a same ‘bee year’ basis. Thus, the beeswax harvest of any 1 year depends on the rainfall of the previous ‘bee year’. This is consistent with general effects of climate on vegetation, specifically to the fact that the bee trees of the African miombo flower in the dry season (Hepburn and Radloff 1996), as do the dipterocarp forests of Southeast Asia (Ridley 1901; Ashton et al. 1988; Sakai et al. 2002; Corlett 2011; Rattanawane et al. 2012).

## 2.4 Colony Space and Density

### 2.4.1 Arrangement of Space

The importance of space for building combs in *A. mellifera* was observed by Huber (1814), who noted that when the nest cavity is packed with combs, building is curtailed; and, conversely, an absence of combs is an inducement to build. Gundelach (1842) asserted that when there is nectar afield, the bees are driven to build. Thus, nectar both arouses the drive to build and provides the fuel to do so. It was noted that bees only built when they hung under the combs (in a skep), and this only happened when there was not enough space to accommodate them among the combs. The drive to build is most notable in newly settled swarms on the branches of trees, rock overhangs or in empty skeps or hive boxes, where a whole nest of combs can be constructed within a week. Here, space can be considered in two ways: building space available for new comb construction and living space for clustering amongst the combs.

During summer, in the Caucasus, Muzalewskij (1933) experimentally extended the observations of Gundelach (1842). Using twenty 'average' *A. mellifera* colonies, he gave half of them a single building frame each, placed adjacent to the last frame of brood comb; each of the other ten colonies was given three such frames. Muzalewskij's basic thinking was that, if space is only a passive aspect of colony life, then one ought to obtain roughly the same amount of wax in the two experimental groups; however, if space acts in some way as an active stimulus for comb production, then clearly the hives with three empty frames should differ in the total amount of wax produced (Muzalewskij 1933). The results showed that those colonies given three empty frames produced around  $808 \text{ g} \pm 24$ , which is some 32 % more than those given only one frame ( $550 \text{ g} \pm 77$ ; Muzalewskij 1933). To eliminate any source of error that might have arisen from inequalities among the colonies, Muzalewskij simply performed the reciprocal experiment, and again, the colonies with three frames produced more wax (Muzalewskij 1933). One can also distinguish between the effects of space on comb-building and on the actual synthesis and secretion of wax scales (Hoffmann and Werner-Meyer 1960).

Given the perhaps unusual circumstances, in which there was simply no available space in which to construct new combs at a time when there was an autumn nectar flow, Dönhoff (1854) reported an extraordinary secretion of wax scales in *A. mellifera*. These scales were said to form large blocks of wax (possibly 2–3 mm in thickness) which greatly distended the abdomen. Similar examples, with the same interpretation as to cause were also noted in *A. mellifera* by von Buttell-Reepen (1900, 1915); Gwin (1931) and Minderhoud (1933), but this phenomenon has not been studied experimentally. These very large scales are probably genuinely distinct from other examples which appear to be either teratological or pathological in nature (Sendler 1938). Similarly, thick scales have also been observed on *A. cerana* workers in Zhejiang Province, China (cf. Fig. 2.3) and



**Fig. 2.3** **a** A swarm of *A. cerana* settle in a stave barrel hive; **b** and **c** workers with wax pieces attached to them can be seen among other members of the swarm; **d–h** dead workers found at the entrance of the hive with wax pieces attached to their abdomens; **g** and **h** view of the same worker from opposite sides; **i** the swarm was able to construct comb with regular geometry (Zheng et al. 2011)

which could be a reason why some workers are sometimes trapped in wax during comb construction (Zheng et al. 2011).

The matter of spacing in the dwarf and giant honeybee species is peculiarly different from that of the cavity-nesting bees, because the former are not constrained by the sides of a cavity as are the latter. Nonetheless, ‘space’ as a ‘nearest neighbour’ problem still holds for cavity-nesting colonies, which translates to carrying capacity/km<sup>2</sup>; but, there are no demographic studies of this kind for wild colonies of cavity-nesting bees. In the red dwarf honeybees, *A. florea*, it would appear that ‘space’ may well be a ‘nearest neighbour’ distance rule (Duangphakdee et al. 2013b). In a year long study of emigration and immigration of *A. florea* colonies in secondary, dry dipterocarp forests at Chombueng, Ratchaburi, Thailand, the standing population of *A. florea* colonies ranged from 20 to 41, with a mean of 34.25 colonies occupying a nesting area of 2.8 km<sup>2</sup>. In terms of movement, this equates to a range of 7.1–14.3 colonies month/km<sup>2</sup> and an average carrying capacity of 12.2 colonies month/km<sup>2</sup> (Duangphakdee et al. 2013a).

Given significant immigration and emigration data, it is also of interest to consider the spacing of the colonies over the year. No two colonies occupied the same tree and a frequency calculation of the distances between ‘nearest neighbouring’ nests for 202 colonies over each month showed that over 90 % of the colonies were no more than 100 m apart, with an average distance between neighbouring colonies of  $53.9 \pm 114.74$ ; the magnitude of the standard deviation being the result of the greater distance from ‘nearest neighbours’ by only 10 % of the colonies.

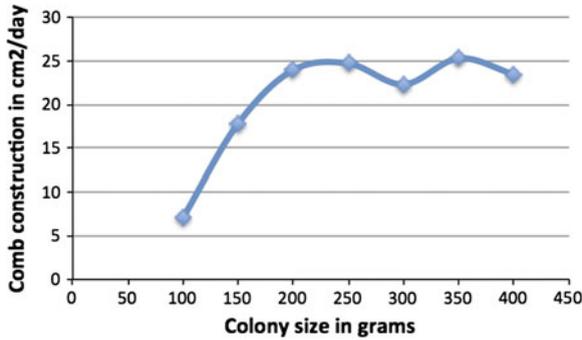
Unlike the dwarf bees, *A. dorsata* nest in aggregations and as many as 256 colonies have been observed in a single tree (Deodikar et al. 1977). Space in this context could include an average ‘nearest neighbour’ distance, so that nests do not overlap but enhance the defensiveness of densely packed clusters. A recent study by Kastberger et al. (2011) used stereoscopic motion analysis to obtain a three-dimensional analysis of the shimmering behaviour of clumped colonies of giant honey bees, which is an extremely accurate, non-invasive approach that holds much promise for spatial distribution studies.

### 2.4.2 Density Versus Space

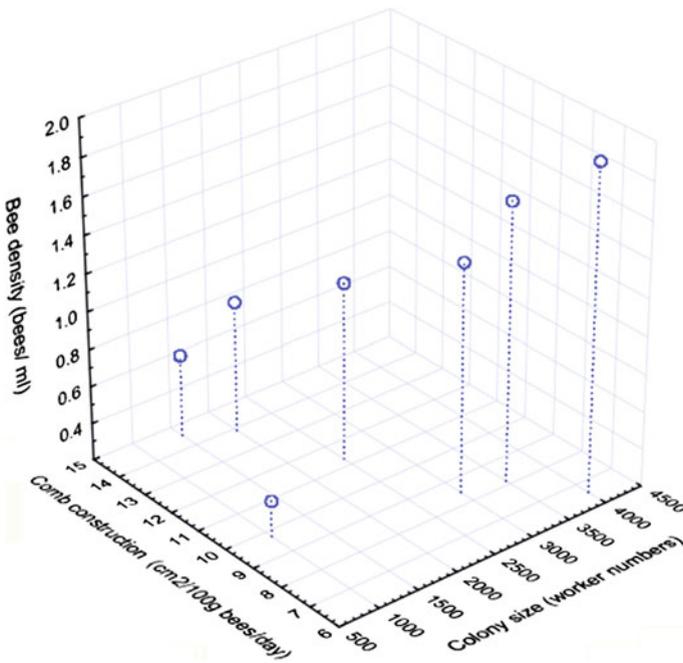
In the experiments discussed above, the relative density (unmeasured) of bees would have changed with the construction of new combs, but without information on natural attrition or increase in the work force through brood production, the importance of density per se cannot yet be evaluated. The only study thus far that has attempted to assess the significance of the density of bees in a nest container is that of Freudenstein (1961). Using young bees of about the same age, he hived queenright colonies of *A. mellifera* in one-frame hives. These hives were either 0.5 l or 2 l in volume. Freudenstein first calculated how the amount of comb constructed per day varied with the size of the colony (Fig. 2.4).

Although the original data were presented in such a way as to preclude any rigorous statistical analysis, it is apparent that the small colonies of 500–1000 bees constructed about 7 cm of comb/day, while the larger colonies of 1000–4000 bees built three times that amount. Given a nest container of a fixed volume, the larger number of bees constructed relatively more comb; however, the density of bees per unit volume was increasing as was the population. If the data is viewed slightly differently (Fig. 2.5), one observes that the amount of comb constructed per bee decreased with increasing colony size and density in colonies exceeding 1000 bees. In either comparison, both density and the number of bees varied simultaneously. This of course is a conflation of variables thus precluding more precise interpretations.

To overcome these difficulties, Freudenstein (1961) then established colonies of *A. mellifera* of varying sizes, in either large (2 l) or small (0.5 l) nest boxes, to compare the performance of paired colonies of the same strength under a fourfold difference in density. In these experiments he measured only the mean height of



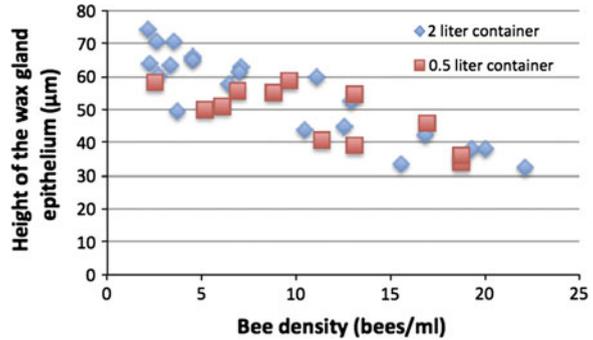
**Fig. 2.4** Comb construction by *A. mellifera* colonies as a function of colony size (Freudenstein 1961)



**Fig. 2.5** Average comb construction by *A. mellifera* per 100 g/bees/day in relation to colony size and population density (Freudenstein 1961)

the wax gland epithelium as a function of bee density. He did not, unfortunately, provide any experimental data on the area or mass of wax comb—information rather crucial to the assessment of volume in relation to population density. Nonetheless, Fig. 2.6 shows that the height of the wax gland epithelium was

**Fig. 2.6** Height of the wax gland epithelium of *A. mellifera* in relation to the bee density (Freudenstein 1961)



greater the lower the density of bees; the height of the epithelium decreased by half with an order of magnitude increase in bee density.

Szabo (1977) tried to establish the relationship between colony size and wax production. After the autumn flow had finished in Canada, he established 24 *A. mellifera* colonies ranging in size from 2 to 8 kg; to each of which he gave a single frame of brood and 19 frames of beeswax foundation. Each of the colonies was fed 14.5 kg of a 60 % sugar solution, and after 8 days the area of comb constructed was measured. Szabo (1977) found that wax construction was linearly related to the size of the colony and that there was an additional 50 g of wax produced with each kilogram increase in colony size. Unfortunately, the experiment was dominated by colonies of about 4.5 and 6.5 kg so that it was not possible to extrapolate the data any further, nor were possible individual contributions taken into account.

### 2.4.3 Reduction of Nest Size

Dealing with space in a slightly different way, Taranov (1959) suggested that the production of wax occurs only as a reaction of the colony to the absence of a nest (e.g. swarms newly arrived in an empty skep, reminiscent of Gundelach 1842), the unsuitability of an existing one, or serious disruption of the nest (e.g. colonies deprived of their combs as in Gontarski 1930). To test the effects of available space (perhaps better seen as nest shortage) Taranov (1959) established eight *A. mellifera* colonies, each of about 10,000 young bees of the same age. Four of these colonies contained a single frame full of honey (Group A), while in the other four, intact combs alternated with frames from which a portion of the comb had been cut away (Group B). Thus, all eight nests had been disrupted in some way. In Group A there was virtually no place for brood-rearing, while in B there was adequate space for food storage and brood-rearing. At the end of the experiment, duration unstated, the Group A colonies had produced an average of 728 g of wax, slightly more than double that of the Group B colonies which averaged 318 g of wax per colony (a highly significant difference). Interestingly enough, the two groups

differed by only 5 % or so in the average amount of brood reared: Group A produced an average of 23,546 young and group B some 22,197. The density of bees in a given space can obviously vary throughout the day and across the seasons.

An interesting observation from practical beekeeping with *A. m. scutellata* suggests, at first sight, that high density through heavy bee traffic may affect comb-building. Many producers of honeycomb know that bees tend to cap honeycombs in the back of a super in a Langstroth hive in preference to those closest to and just above the entrance. In consequence, beekeepers simply rotate the supers back to front once the back portion is almost complete, so giving the bees a new unworked back section. A natural experiment bearing on this problem came to light concerning a hive that was securely locked in a heavy-gauge steel cage but had been overlooked for 2 years. On its rediscovery, it was found to have three supers of completely capped honeycomb; however, the front quarters of those frames in the bottom super, nearest the entrance, were unworked and contained no honey (Hepburn 1986).

These observations recalled Dadant's (1926) hypothesis, that returning nectar-laden foragers probably go up into the super just above the entrance, resulting in sufficiently dense traffic to prevent work in that area. This was tested on 12 hives as follows. A third of the hives were maintained as controls; in another third, a piece of fibre-board was placed so that incoming bees had to go one-third the length of the hive before reaching the super; in the remaining four hives, the bees were forced to go two-thirds the length of the hive to reach the super. The point of this little experiment was simply to shift the bees further into the hives during a spring flow, the anticipated effect of which would have been unworked comb at the experimentally induced new traffic jam sites. After several months the surprising result was that the front parts of the frames remained unworked, regardless of the point at which the bees could attain access the super (Hepburn 1986).

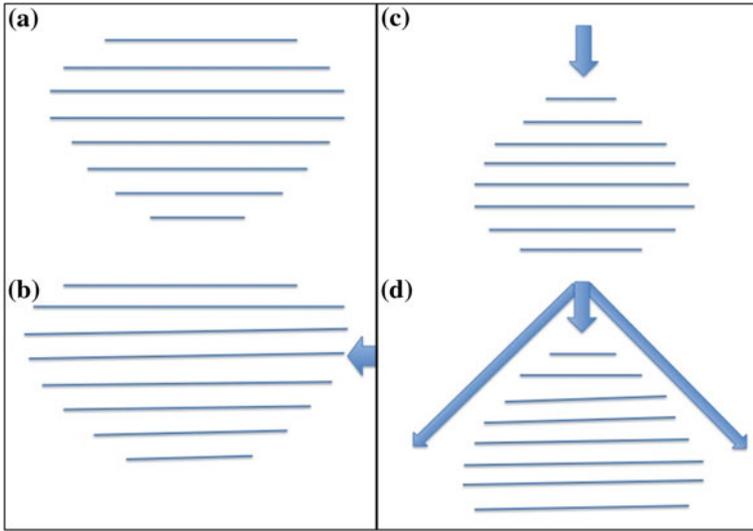
The quality aspects of space as a stimulus for comb-building can be partially derived from a related but slightly different experiment by Taranov (1959). Again using 10,000 queenright *A. mellifera* bees as a colony unit, he divided them into three groups of three colonies each: Group A had the bottom halves of their alternate combs cut away; Group B the top halves of alternate combs removed; and Group C was given a single comb filled with honey. At the end of the summer experiment, during which the bees were fed a 60 % sugar syrup, Taranov found that wax production varied enormously: Group A, which started without the bottom halves, averaged 155 g of wax; Group B, the one without the top halves 234 g, and Group C, with one full frame 385 g—all comparisons between groups being highly significantly different. The absence of a nest in Group C was a strong stimulus to construct comb. Finally it is probably fair to say that volume, space and density will only operate on wax production provided that the colony of bees has reached some critical threshold, even if we cannot yet specify such a limit.

#### 2.4.4 Other Qualities of “Space”

It has been determined that a group of 50 bees and a queen are just sufficient for the production of comb by *A. mellifera* (Darchen 1957; Darchen 1957; Goetze and Bessling 1959). The factors that might affect this population level in the induction of wax working are open to discussion. The word ‘space’ has been used in several different ways in the preceding pages. Moreover, the qualities of space are extremely difficult to specify. Two additional aspects of this quality are wind or air currents and light, as well as the relative density of bees in different parts of the nest. These aspects are of obvious importance to *A. andreniformis* and *A. florea*, but have not as yet been investigated. However, open-air nesting by cavity-dwelling *A. cerana* is sufficiently infrequent that periodic notes on its occurrence have been reported (Sasaki and Okada 1988; Lazar 1995; Sugahara 1998; Akimoto 2000; Soman and Sawant 2001). The same applies to a description by Bouvier (1906) of *A. mellifera* colonies nesting in the open air in Paris, following which Darchen (1959a) investigated similar nests experimentally. His ‘open air’ nests were actually situated in very large clear boxes with open bottoms. He blew in a continuous current of air at a rate of 2–3 ms<sup>-1</sup> in a direction parallel to existing combs (Fig. 2.7), and observed that the bees shifted away from the direct air current and confined their constructions downwind (Fig. 2.7b). Similar downwind building resulted when the direction of air was normal to the combs, as shown in Fig. 2.7.

The importance of illumination to comb construction is roughly indicated by the fact that we virtually never find nests of cavity-nesting bees like *A. mellifera* or *A. cerana* built in full sunlight, nor even the open-nesting species like *A. florea* or *A. andreniformis*. Colonies of *A. mellifera* found out-of-doors are invariably lodged below the limbs of trees or in bushes, where they receive dappled shade (Rau 1931; Avitabile 1975). In a brief note on swarms, Morse (1963) found that only one of 50 colonies kept in full sunlight built comb, even during a heavy nectar flow. Similarly, two colonies housed in transparent polyethylene cages did not build comb for an 8 week period, but they had synthesized wax, as evidenced by the many dropped wax scales that accumulated beneath their clusters. In another series of experiments on *A. mellifera*, Morse (1965) continued his studies on the effects of light and comb construction. Using about 10,000 bees per colony, he simulated the early April of New York in his flight room, with a daytime temperature of 22 °C. The bees were exposed to light and could forage for sugar syrup in the room. The bees constructed no combs but secreted wax. When the colony was covered with a wooden box lacking one side, it constructed about 50 cm of comb in the ensuing week. Morse then raised the temperature to 29 °C and in the following week the colony constructed 80 g of comb. He then exposed the bees to light (2250 lx) and they continued building combs.

Shifting to the field, Morse (1965) established six swarms, each with a caged queen, as follows: (1) each of two colonies was confined in its own box, from which one side had been removed, the consequent opening facing north; (2) two



**Fig. 2.7** The effect of a continuous current of wind on comb-building: **a** The existing comb structure at the onset of the experiment; **b** comb constructed after application of the air current. The effect of a continuous current of wind on comb-building by *Apis mellifera* where the direction of the air was normal to the combs; **c** combs before application of wind; and **d** combs constructed after the colony was subjected to wind (Darchen 1959a, b)

others were kept in gauze cages with one side open; and (3) two others were kept in wooden boxes. At the end of 3 weeks during a heavy nectar flow, the bees in Group (1): one colony had constructed only little comb, and the other none; for Group (2): there was no construction; finally, for Group (3): extensive combs were built with the exclusion of light. Thus Morse (1965) found that comb construction decreased with increasing (if unmeasured) light intensity. But in all three situations, wax scales had been produced, as evidenced by the scales beneath the colonies that had not built and the combs of those that had. Unlike wind, it appears that the direction of a light source has no effect on the pattern and arrangement of combs (Ifantidis 1978). Given the intensity of full sun, swarms of bees may well secrete wax but will not build combs. If, however, they have begun construction in darkness and are then exposed to light, construction continues; whether this will be at the same pace as that in darkness is unknown.

The fact that bees should first be kept in darkness, to stimulate comb construction, and then exposed to light for viewing has been known since Gundelach (1842), and is today a basic form of management for the use of observation hives (Showler 1978). It would appear that varying light intensity does not prevent the development of and secretion by the wax gland complex, but it certainly modifies building behaviour. The question of light naturally leads to a consideration of whether bees secrete wax and build combs during the daytime or during the night. To assess this, Darchen (1959a) set two colonies in huge glass boxes out of doors

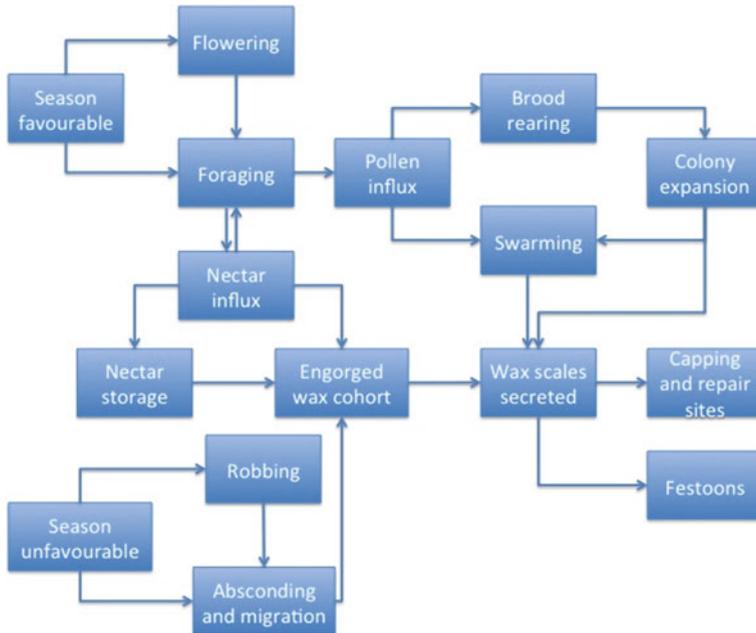
and collected the debris that fell from the nests, assuming that the quantity of fallen wax scales was proportional to building activity. Dividing 4 days into nearly equal halves, he found that one colony dropped about twice as much wax during the day as at night, while the performance of a second colony was exactly the opposite. While light intensity exerts effects on comb construction, the day-night comparison also raises the question of circadian rhythms. How these factors operate together is simply unknown.

## 2.5 Seasonality, Space and Density

It has been well established experimentally that newly settled swarms of *A. mellifera*, *A. cerana* (Okada and Sakai 1960; Hadisoesoilo 1990), *A. florea* (Duangphakdee et al. 2013b) and *A. mellifera* (Lee and Winston 1985; Hepburn 1986) are prodigious comb builders, but in a framework of space and time, comb-building only reaches parity with other wax working (capping and repairing) at the height of the colony growth cycle (Muller and Hepburn 1992). Comb-building is conducted in different areas of the nest by many individuals, some clustered in festoons, others not, while other wax works are often the efforts of individual bees (Lindauer 1952; Yang et al. 2010). Changing ratios of what work there is to be done and where it is carried out can be assessed by following the raw wax in a colony with the changing seasons.

Muller and Hepburn (1992) found that in the course of a year just as much wax is found on *A. mellifera* bees elsewhere among the combs as on festoon bees, but seasonal pictures are quite different (Fig. 2.8). It is our impression that the same, or a very similar scheme, would apply to *A. cerana* as well. It appears that wax-bearing bees can be found in the right places at the appropriate times (Pratt 2004). The wax bees shift from one area of the nest to another, for example, with heavy nectar flow for capping honey cells or to areas requiring brood capping. This ensures a close synchrony between comb area ‘needs’ and the presence of bees with wax scales. Although not all would agree (Fergusson and Winston 1988), the distribution of these wax bees is largely predicated on an underlying age-based cycle of glandular secretion (Hepburn et al. 1991).

The effects of storage space are elegantly illustrated in the statement “that strong nectar flows fuel comb-building”, an explanation proposed for this relationship was formulated by Butler (1954), and, indeed is an old axiom of practical beekeeping (Langstroth 1853). Butler argued that the greater the influx of nectar into the colony, the longer the house bees must retain nectar in their honey stomachs. This, of course, requires the right combination of available storage space and ratio of foragers to house bees. Serving as distended reservoirs over time, these bees assimilate some of the nectar sugar and become stimulated to secrete wax. Enquiries were made at Rothamsted to find out whether these ideas had ever been tested, but had remained unpublished. In reply, we were informed in the negative. This sensible idea has proven far easier to appreciate than to test.



**Fig. 2.8** Flow diagram for the stimulation of wax secretion in *A. mellifera*. The favourable season sequence should apply to all *A. mellifera*; but the unfavourable one only to the tropical races in Africa (Hepburn 1998)

Using queenright colonies in which comb available for nectar storage was experimentally reduced or entirely eliminated, a correlation between engorgement of the honey stomach and wax secretion was obtained (Hepburn and Magnuson 1988). This experiment did not distinguish between physical distension of the honey stomach and the time such a bee might spend in trying to disgorge and store the nectar. Nonetheless, the observation is indirectly supported by experiments in which either the deprivation of combs (Fergusson and Winston 1988), or lack of sufficient storage space (Seeley 1995), both led to increased foraging, accelerated wax secretion and, ultimately, comb-building. Collectively, the experimental data lead to a simple feedback system: forager dancing effectively recruits more nectar-foragers; when the incoming nectar is difficult to off-load, a special tremble or stop dance is performed, which inhibits further recruitment (Seeley 1992; Nieh 1993).

During comb-building there are concomitant changes in population size, population density, nectar and pollen influx, all of which affect honeybee-comb interactions. Of these, Harbo (1988) examined the relationship between colony size, brood production and combs for colonies that were equalized. He found that those *A. mellifera* colonies which had produced the largest amount of comb, also produced the largest number of brood and adult workers. To separate queens from comb effects, he performed a second experiment using large and small combs as the variables of interest. Comb effects were significant (queens not) and small

combs resulted in reduced brood production. But there is more to a colony in a cavity, and the variables richer than has thus far been assessed.

Harbo (1993) extended his findings to examine the effects of nest cavity (hive) volume on growth and productivity by adjusting the population density against volume. In winter, crowded bees consumed less honey per bee and reared less brood than less crowded colonies. During the flows of spring through autumn, the crowded colonies produced more honey but less brood than the less crowded ones. In another experiment, comb effects were tested against space effects. Both affected brood rearing and honey production. Colonies with combless, extra space produced less honey and more brood than those with the same amount of comb but less space (Harbo 1993). These results complement those of Taranov (1959) and Szabo (1977) who had shown that brood production and comb construction are not competitive activities: the exclusion of one activity does not accelerate the other.

If creativity in biology is partially the result of the discovery of variables, then we can take some solace from the status quo of our current knowledge on space and density. We know that space, volume, density and colony size all affect wax production. From first principles we also know that gas exchange and heat transfer weigh heavily in the equation. We also know that a scout can obtain information about an empty cavity that we translate into a measure of volume. Likewise, we have a few experimental observations to hand. It will be very rewarding indeed to see the development of experiments that might, 1 day, integrate them all.

## References

- Akimoto T (2000) Winter temperature in the exposed nest of the Japanese honeybee, *Apis cerana japonica*. Honeybee Sci 21:31–34 (in Japanese)
- Akratanakul P (1977) The natural history of the dwarf honey bee, *Apis florea* F. in Thailand. Thesis, Cornell University, Ithaca
- Ashton PS, Givnish TJ, Appanah S (1988) Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the seasonal tropics. Am Nat 132:44–46
- Avitabile A (1975) Exposed combs of honey bees. Am Bee J 115(436–437):456
- Bakker DW (1999) Foraging and habitat selection by two species of honey bee near Lore Lindu National Park in Sulawesi, Indonesia. Thesis, University of Guelph, Guelph
- Basavarajappa S (1998) Status of natural colonies of *Apis dorsata* in Maidan region of Karnataka, India. Indian Bee J 60:143–146
- Berg S (1996) Investigations to increase the attractiveness of the Malawi standard hive for natural colonisation through bee swarms. Department of National Parks and Wildlife, Rumphii
- Booncham U, Wongsiri S, Thirakupt K (1995) Niche differences between *A. florea* and *A. andreniformis* in dry-evergreen forest Thailand. In: Proceedings of international conference tropical bees environment, Pedu Lake, Kedah, p 33
- Bouvier EL (1906) Nouvelles observations sur la nidification des abeilles l'air libre. Ann Soc Entomol Fr 75:429–444
- Butani DK (1950) An *Apis dorsata* colony in New Delhi. Indian Bee J 12:115
- Butler CG (1954) The world of the honeybee. Collins, London

- Clauss B (1992) Bees and beekeeping in the north western Province of Zambia. Mission Press, Ndola
- Corlett RT (2011) Honeybees in natural ecosystems. In: Hepburn HR, Radloff SE (eds) Honeybees of Asia. Springer, Berlin, pp 215–225
- Dadant HC (1926) Behavior of bees in comb-building. No. 2. Am Bee J 26:278–280
- Darchen R (1957) La reine d'*Apis mellifica*, les ouvrières pondueuses et les constructions cirières. Insectes Soc 4:321–325
- Darchen R (1959a) Observation et experimentation sur un essaim nidifiant artificiellement à l'air libre. Ann Abeilles 1:5–11
- Darchen R (1959b) Un des rôles des chaînes d'abeilles: la torsion des rayons pour les rendre parallèles entre eux. Ann Abeilles 2:193–209
- Deodikar GB, Ghatge AL, Phadke RP, Mahindre DB, Kshirsagar KK, Muvel DS, Thakar SS (1977) Nesting behaviour of Indian honeybees. III Nesting behaviour of *Apis dorsata* Fab. Indian Bee J 39:1–12
- Dönhoff E (1854) Ueber den uebergang der wachslättchen in wachstlumpchen. Schweiz Bienen-Ztg 15:279
- Douglas JC (1886) The hive-bees indigenous to India and the introduction of the Italian bee. J Asia Soc Bengal Sci 55:83–96
- Duangphakdee O, Hepburn HR, Rod-im P (2013a) Seasonal movements of the red dwarf honeybee, *Apis florea* (in ms.)
- Duangphakdee O, Hepburn HR, Rod-im P (2013b) Development of the nest of *Apis florea*. (In ms.)
- Estève G (1932) L'apiculture au Tchad. Agron Colon 21:161–165
- Fergusson LA, Winston ML (1988) The influence of wax deprivation on temporal polyethism in honey bee (*Apis mellifera* L.) colonies. Can J Zool 66:1997–2001
- Franssen CJH (1932) Notes on *Micrapis florea* F. Natuurk Tijdschr Ned-Indie 92:55–63
- Free JB (1981) Biology and behaviour of the honeybee *Apis florea*, and possibilities for beekeeping. Bee Wld 62:46–59
- Fuchs S, Tautz J (2011) Colony defence and natural enemies. In: Hepburn HR, Radloff SE (eds) Honeybees of Asia. Springer, Berlin, pp 369–395
- Freudenstein H (1961) Entwicklung und leistung der wachsdriisen der honigbiene. Biol Zentralbl 80:479–492
- Goetze G, Bessling BK (1959) Die wirkung verschiedener fütterung der honigbiene auf wachserzeugung und bautätigkeit. Z Bienenforsch 4:202–209
- Gontarski H (1930) Über das baualter und die wachserzeugung der bienen. Leipz Bienen-Ztg 45:284–286
- Gundelach FW (1842) Die naturgeschichte der honigbiene. JJ Bohné, Cassel
- Gwin CM (1931) Wax production by the honey bee colony. Wisc Beekeep 7:109–110
- Hadisoesilo S (1990) A preliminary study on a swarm of *Apis cerana* at kuok, riau province, Indonesia. Bull Penelitian Kehutanan 5:357–363
- Hadisoesilo S (1997) A comparative study of two species of cavity-nesting honey bees of Sulawesi, Indonesia. Thesis, University of Guelph, Guelph
- Harbo JR (1988) Effect of comb size on population growth of honey bee (Hymenoptera: Apidae) colonies. J Econ Entomol 81:1606–1610
- Harbo JR (1993) Worker-bee crowding affects brood production, honey production, and longevity of honey bees (Hymenoptera: Apidae). J Econ Entomol 86:1677–1678
- Hassan LAM, Bradbear N (1994) Designs of low-cost and low-technology hives for beekeepers in the tropics. In: Proceedings of the 5th international conference Apic tropical climate, Trinidad and Tobago, pp 30–34
- Hepburn HR (1986) Honeybees and wax: an experimental natural history. Springer, Berlin
- Hepburn HR (1998) Reciprocal interactions between honeybees and combs in the integration of some colony functions in *Apis mellifera* L. Apidologie 29:47–66
- Hepburn HR (2011) Absconding, migration and swarming. In: Hepburn HR, Radloff SE (eds) Honeybees of Asia. Springer, Berlin, pp 133–158

- Hepburn HR, Magnuson P (1988) Nectar storage in relation to wax secretion by honeybees. *J Apic Res* 27:90–94
- Hepburn HR, Radloff SE (1996) Beeswax exports and rainfall in the savanna woodlands of east central Africa. *Apidologie* 27:473–478
- Hepburn HR, Radloff SE (1998) Honeybees of Africa. Springer, Berlin
- Hepburn HR, Radloff SE (2011) Biogeography. In: Hepburn HR, Radloff SE (eds) Honeybees of Asia. Springer, Berlin, pp 55–67
- Hepburn HR, Bernard RTF, Davidson BC, Muller WJ, Lloyd P, Kurstjens SP, Vincent SL (1991) Synthesis and secretion of beeswax in honeybees. *Apidologie* 22:21–36
- Hoffmann I, Werner-Meyer W (1960) Wachsdruisenentwicklung und Wachsbedarf bei der Honigbiene. *Zool Beitr* 5:337–343
- Huber F (1814) Nouvelles observations sur les abeilles. (English translation (1926)) Dadant, Hamilton
- Ifantidis MD (1978) Wabenorientierung im nest der honigbiene (*Apis mellifica* L.). *Apidologie* 9:57–73
- Inoue T, Adri Salmah S (1990) Nest site selection and reproductive ecology of the Asian honey bee, *Apis cerana indica*, in central sumatra. In: Sakagami SF, Ohgushi R, Roubik DW (eds) Natural history of social wasps and bees in equatorial Sumatra. Hokkaido University Press, Sapporo, pp 219–232
- Irvine FR (1957) Indigenous African methods of beekeeping. *Bee Wld* 38:113–128
- Johannsmeier MF (1979) Termite mounds as nesting sites for colonies of the African honeybee. *S Afr Bee J* 51:9
- Joshi SR, Ahmad F, Gurung MB (2004) Status of *Apis laboriosa* populations in kaski district, western Nepal. *J Apic Res* 43:176–180
- Kastberger G, Maurer M, Weihmann F, Ruether M, Hoetzl T, Kranmer I, Bischof H (2011) Stereoscopic motion analysis in densely packed clusters: 3D analysis of the shimmering behaviour in giant honey bees. *Front Zool* 8:833–856
- Kuntadi TH (1989) Nesting habit of *Apis cerana* F in nature. *Bull Penelitian Kehutanan* 5:21–26 (in Indonesian)
- Langstroth LL (1853) Langstroth and the hive and the honeybee. (Facsimile, 1977) Root, Medina
- Lazar M (1995) *Apis cerana* nesting in the open. *Indian Bee J* 57:146
- Lee PC, Winston ML (1985) The effect of swarm size and date of issue on comb construction in newly founded colonies of honeybees (*Apis mellifera* L.). *Can J Zool* 63:524–527
- Lindauer M (1952) Ein Beitrag zur Frage der Arbeitsteilung im Bienenstaat. *Z Vergl Physiol* 34:299–345
- Lindauer M (1956) Communication among the honeybees and stingless bees of India. *Z Vergl Physiol* 38:521–557
- Lindauer M (1961) Communication among social bees. Harvard University Press, Cambridge
- Liu F, Roubik DW, He D, Li J (2007) Old comb for nesting site recognition by *Apis dorsata*? Field experiments in China. *Insectes Soc* 54:424–426
- Lo NH, Gloag RS, Anderson DL, Oldroyd BP (2010) A molecular phylogeny of the genus *Apis* suggests that the giant honey bee of the Philippines, *A. breviligula* maa, and the plains honey bee of southern India, *A. indica* Fabricius, are valid species. *Syst Entomol* 35:226–233
- Matsuura M (1983) Notes on the nesting habits of the three honeybee species in Sumatra. *Honeybee Sci* 4:117–122 (in Japanese)
- McNally LC, Schneider SS (1996) Spatial distribution and nesting biology of colonies of the African honey bee *Apis mellifera scutellata* (Hymenoptera: Apidae) in Botswana, Africa. *Envir Ent* 25:643–652
- Minderhoud A (1933) Over de aanwezigheid van wasschubjes bij de bijen. *Maandschr Bijent* 36(3–7):29–30
- Mogga JB, Abdin AMZE, Nagi SKA, Ali AM (1989) *Apis florea* in Sudan: some biological observations. In: Proceedings of the 4th international conference Apic tropical climate, Cairo, pp 422–424

- Moritz RFA, Haddad N, Bataineh A, Shalmon B, Hefetz A (2010) Invasion of the dwarf honeybee *Apis florea* into the near East. *Biol Invasions* 12:1093–1099
- Morse RA (1963) Swarm orientation in honeybees. *Science* 141:357–358
- Morse RA (1965) The effect of light on comb construction by honeybees. *J Apic Res* 4:23–29
- Morse RA, Laigo FM (1969) *Apis dorsata* in the philippines. Philippine Association of Entomologists Inc, Laguna
- Mossadegh MS (1990) Nesting behaviour of *Apis florea* F (Hymenoptera: Apidae) in Khuzestan, Iran. In: Proceedings of the 11th international Conference IUSSI, New Delhi, pp 669–670
- Muller WJ, Hepburn HR (1992) Temporal and spatial patterns of wax secretion and related behaviour in the division of labour of the honeybee (*Apis mellifera capensis*). *J Comp Physiol* 171:111–115
- Muzalewskij BM (1933) Wie ein leerer raum im nest die wachsausscheidung der bienen beeinflusst. *Arch Bienenkd* 14:1–145
- Mwangi RW (1985) Reasons for the low occupancy of hives in Kenya. In: Proceedings 3rd International Conference Apic Tropical Climate, Nairobi, pp 61–63
- Nagaraja N, Rajagopal D (1999) Colony establishment, nesting and foraging activity of the little honey bee, *Apis florea* F (Hymenoptera: Apidae). *J Ent Res* 23:331–338
- Neumann P, Koeniger N, Koeniger G, Tingek S, Kryger P, Moritz RFA (2000) Home-site fidelity in migratory bees. *Nature* 406:474–475
- Neupane KR, Hartfelder KH, de Jong D, de Pereira RA, Santos Cristino A, dos Morais MM, Tanaka ED, Silva AP, da Almeida GF, do Nascimento AM (2004) Nesting behavior of giant honey bees (*Apis dorsata*). VI Encontro sobre abelhas, Ribeirão Preto 351–357
- Nieh JC (1993) The stop signal of honey bees: reconsidering its message. *Behav Ecol Sociobiol* 33:51–56
- Nightingale J (1983) A lifetime's recollection of kenya tribal beekeeping. IBRA, London
- Okada I, Sakai T (1960) A comparative study on natural comb of the Japanese and European honeybee, with special reference to cell number. *Bull Fac Agric Tamagawa Univ* 1:1–11 (in Japanese)
- Oldroyd BP, Wongsiri S (2006) Asian honey bees. Harvard University Press, Cambridge
- Oldroyd BP, Gloag RS, Even N, Wattanachaiyingcharoen W, Beekman M (2008) Nest-site selection in the open-nesting honey bee *Apis florea*. *Behav Ecol Sociobiol* 62:1643–1653
- Otis GW (1996) Distributions of recently recognized species of honey bees (Hymenoptera: Apidae; *Apis*) in Asia. *J Kans Ent Soc* 69:311–333
- Paar J, Oldroyd BP, Kastberger G (2000) Giant honeybees return to their nest sites. *Nature* 406:475
- Phiancharoen M, Duangphakdee O, Hepburn HR (2011) Biology of nesting. In: Hepburn HR, Radloff SE (eds) *Honeybees of Asia*. Springer, Berlin, pp 109–131
- Pratt SC (2004) Collective control of the timing and type of comb construction by honey bees (*Apis mellifera*). *Apidologie* 35:193–205
- Rattanawanee A, Chanchao C, Lim J, Wongsiri S, Oldroyd B (2012) Genetic structure of a giant honey bee (*Apis dorsata*) population in northern Thailand: implications for conservation. *Insect Conserv Diver* 6:38–44
- Rau P (1931) Exposed combs of the honeybee. *Ecology* 12:615–616
- Reddy CC (1983) Studies on the nesting behaviour of *Apis dorsata* F. In: Proceedings of the 2nd international conference apic tropical climate, New Delhi, pp 391–397
- Reddy MS, Reddy CC (1989) Height-dependent nest site selection in *Apis dorsata* Fabr. *Indian Bee J* 51:105–106
- Ridley HN (1901) The timber of the Malay Peninsula. Agric Bull Straits and Federated Malay States 1. Government Printing Office, Singapore
- Rinderer TE, Oldroyd BP, de Guzman LI, Wattanachaiyingcharon W, Wongsiri S (2002) Spatial distribution of the dwarf honey bees in an agroecosystem in southeastern Thailand. *Apidologie* 33:539–543
- Roubik DW, Sakagami SF, Kudo I (1985) A note on distribution and nesting of the Himalayan honeybee *Apis laboriosa* smith (Hymenoptera: Apidae). *J Kans Ent Soc* 58:746–749

- Sakai S (2002) General flowering in lowland mixed dipterocarp forests of South-east Asia. *Biol J Linn Soc* 75:233–247
- Sasaki M, Okada I (1988) Feral nest of *Apis cerana japonica* constructed in an open space. *Honeybee Sci* 9:77–78 (in Japanese)
- Sattigi HN (2001) Nesting behaviour of rock bee selection of nesting height. *Karnataka J Agric Sci* 14(3):664–667
- Seeley TD (1985) *Honeybee ecology*. Princeton University Press, Princeton
- Seeley TD (1992) The tremble dance of the honey bee: message and meaning. *Behav Ecol Sociobiol* 31:375–383
- Seeley TD (1995) *The wisdom of the hive*. Harvard University Press, Cambridge
- Seeley TD (2010) *Honeybee democracy*. Princeton University Press, Princeton
- Seeley TD, Morse RA (1976) The nest of the honey bee (*Apis mellifera* L.). *Insectes Soc* 23:495–512
- Seeley TD, Morse RA (1978) Nest site selection by the honey bee, *Apis mellifera*. *Insectes Soc* 25:323–337
- Seeley TD, Seeley RH, Akwatanakul P (1982) Colony defense strategies of the honeybees in Thailand. *Ecol Monogr* 52:43–63
- Sendler O (1938) Über ungewöhnliche wachs-ausscheidung der honigbiene. *Nat Volk Frankf* 68:87–92
- Sheriff JS (1963) Beeswax and honey production—the Nyasaland potential. Ministry of National Resources and Surveys, Zambia
- Showler K (1978) *The observation hive*. Bee Books New and Old, Steventon
- Silberrad REM (1976) *Bee-keeping in Zambia*. Apimondia, Bucharest
- Singh S (1962) *Beekeeping in India*. Indian Council of Agricultural Research, New Delhi
- Soman AG, Sawant SB (2001) Nesting of Indian hive bees in open. *Indian Bee J* 59:240
- Starr CK, Schmidt PJ, Schmidt JO (1987) Nest-site preferences of the giant honeybee, *Apis dorsata* (Hymenoptera: Apidae), in Borneo. *Pan-Pac Entomol* 63:37–42
- Sugahara M (1998) Feral colonies of Japanese honey bees in the northeastern part of Osaka Prefecture. *Honeybee Sci* 19:37–41 (in Japanese)
- Szabo TI (1977) Effect of colony size and ambient temperature on comb-building and sugar consumption. *J Apic Res* 16:174–183
- Taranov GF (1959) The production of wax in the honeybee colony. *Bee Wld* 40:113–121
- Thorley J (1744) *Melissologia or, the female monarchy: being an enquiry into the nature, order, and government of bees*. Thorley, London
- Underwood BA (1986) *The natural history of Apis laboriosa* Smith in Nepal. Thesis, Cornell University, Ithaca
- Underwood BA (1990) *The behaviour and energetics of high-altitude survival by the Himalayan honeybee, Apis laboriosa*. Thesis, Cornell University, Ithaca
- von Buttel-Reepen H (1900) Sind die bienen reflexmaschinen? *Biol Zentralbl* 20:1–82
- von Buttel-Reepen H (1915) *Leben und wesen der bienen*. Vieweg, Braunschweig
- Wattanachaiyingcharoen W, Wongsiri S, Oldroyd BP (2008) Aggregations of unrelated *Apis florea* colonies. *Apidologie* 39:531–536
- Whitcombe RP (1984) *The biology of Apis spp in Oman with special reference to Apis florea* Fab. Thesis, University of Durham, Durham
- Wongsiri S, Thapa R, Oldroyd BP, Burgett MD (1996) A magic bee tree: home of *Apis dorsata*. *Am Bee J* 136:196–199
- Wongsiri S, Lekprayoon C, Thapa R, Thirakupt K, Rinderer TE, Sylvester HA, Oldroyd BP, Booncham U (1997) Comparative biology of *Apis andreniformis* and *Apis florea* in Thailand. *Bee Wld* 78:23–35
- Woyke J, Wilde J, Wilde M (2001) Swarming, migration and absconding of *Apis dorsata* colonies. In: *Proceedings of the 7th international conference apic tropical climate*, Chiang Mai, pp 183–188

- Woyke J, Wilde J, Reddy CC (2004) Open-air-nesting honey bees *Apis dorsata* and *Apis laboriosa* differ from the cavity-nesting *Apis mellifera* and *Apis cerana* in brood hygiene behaviour. *J Invert Path* 86:1–6
- Woyke J, Wilde J, Wilde M (2012) Swarming and migration of *Apis dorsata* and *Apis laboriosa* honey bees in India, Nepal and Bhutan. *J Apic Res* 56:81–91
- Yang MX, Tan K, Radloff SE, Phiancharoen M, Hepburn HR (2010) Comb construction in mixed-species colonies of honeybees, *Apis cerana* and *Apis mellifera*. *J Exp Biol* 213:1659–1664
- Zheng HQ, Hu FL, Pirk CWW (2011) Errors in comb-building behaviour in *Apis cerana cerana* that result in entrapped workers. *Insectes Soc* 58:413–415. DOI: [10.1007/s00040-011-0158-x](https://doi.org/10.1007/s00040-011-0158-x)
- Zulu GM (1970) Bark-hive beekeeping in Zambia. Bull 2A. Forest Department, Lusaka