

Do small cells help bees cope with Varroa? – A review

David Heaf

Published in *The Beekeepers Quarterly* (June 2011) No. 104, pp. 39-45
Addendum added in March 2019 to include two additional papers

Introduction

Ever since it was suggested by Erickson et al. (1990) that the foundation in common use might be unnaturally oversizing bees to the detriment of their health, a minority of beekeepers, especially in the USA, has applied various methods to reduce comb cell size.

The reasons originally given that small cells might be advantageous were:¹

- more brood per unit area of comb;
- shorter development times to hatching;
- faster build up in spring;
- reduced susceptibility of colonies to disease;
- reduced susceptibility to parasites – for example smaller tracheal openings in smaller bees might confer resistance to tracheal mites;
- reduced susceptibility to pesticides;
- winter mortality and other stress related losses;
- earlier drone production and thus mating.

The last point would conceivably allow longer for colonies to consolidate for winter.

Among the above points, it is the reduced susceptibility to parasites that concerns us here, in particular Varroa. Erickson et al. (1990) wrote:

Realization of the importance of cell size might also provide a management tool against the Varroa mite. Recently, Message and Goncalves [1985] reported that, in Brazil, cell sizes for Africanized and domestic (European) honey bees averaged 4.5 to 4.8 and 5.0 to 5.1 mm per cell, respectively. They further reported that Varroa infestation rates were 4.8 and 11.5 percent, respectively. Camazine [1988] calculated female Varroa replacement rates for Africanized and domestic honey bees at 1.2 and 1.8 with drones present and 0.8 and 1.5 without drones, respectively. (A female Varroa replacement rate of less than 1.0 indicates that the mite population is declining while a 1.0 rate is indicative of zero population growth). Thus, we think that it may be possible to suppress Varroa populations in domestic colonies by using small strains of bees with shorter development times reared in smaller cells.

Further support for the hypothesis that small cells help with Varroa suppression came with later work by Message and Goncalves (1995) who showed that 17-18 days after egg-laying in mosaic (composite) frames of large worker cell comb (4.9-5.1 mm) drawn by *Apis mellifera ligustica*, and small worker cell comb (4.5-4.6 mm) drawn by wild-type Africanised bees, the infestation rate of large cells by female mites was double that of small cells. To explain the difference, they suggested that the larger cells might receive more visits from nurse bees and therefore have a higher probability of infestation by mother mites.

An alternative or additional reason proposed for the difference is that Varroa reproduction is reduced the tighter the fit of developing workers in the capped cells. For a given colony, the smaller the cell, and assuming the size of the developing bee is not reduced in proportion to the cell size reduction, then the less successful would be Varroa reproduction. This is because the male mite egg is laid near the cell cap but to feed at the feeding area created by the mother mite on the bee's abdomen it must be able to pass between the bee and the cell wall.

Martin and Kryger (2002) had the opportunity to test this, not by reducing cell size, but by using workers of two different sizes in the same colony. It is worth examining this study in some depth because it is frequently cited by other investigators who have reported small cell experiments. Colonies of *Apis mellifera*

scutellata in a region of South Africa are often invaded by a pseudo-clone of *Apis mellifera capensis* workers which are 8% larger than workers of the host colony. In 2000, the authors established and selected six colonies of *A. m. scutellata*, three of which had already been invaded by the pseudo-clones. Colonies with very few pseudo-clones were used in order to avoid compromising colony dynamics. Frames of sealed brood were removed for a detailed characterisation of mite infestation in cells of host workers and of pseudo-clone and host drones. Reproductive success was higher in host drone cells than host worker cells, as would be expected, but lowest in the pseudo-clone worker cells. The authors accounted for this by the increased mite mortality due to the restricted space in the cells occupied by pseudo-clone workers.

Using a graph showing the high correlation between cell size and *Apis mellifera* race worker size, Martin and Kryger (2002) illustrated that their study involved one of the largest workers, i.e. the *A. m. capensis* pseudo-clone, in one of the smallest worker cells, namely those of *A. m. scutellata*. Referring to their graph the authors advised:

Although reproduction of *Varroa* sp. is affected by the space between the developing bee and cell wall, reducing cell sizes as a mite control method will probably fail to be effective since the bees are likely to respond by rearing correspondingly smaller bees which explains the close correlation between cell and bee size.

At the time when the article by Erickson et al. (1990) was published experiments were in progress to shrink ('downsize', 'retrogress', 'regress') bees by using foundation embossed with cell sizes smaller than in conventional foundation. Forty bee packages from conventional sources apparently had no problem drawing 5.12 mm foundation:

We assumed that, during the period when the packaged bees were disassociated from comb, the workers would lose their memory of previous cell size and thus ensure that the bees would quickly adapt to the new size.

Since then, not only has 4.9 mm foundation, wax or plastic, been successfully drawn, albeit sometimes passing through an intermediate stage of 5.1 mm foundation, but also bees have been raised on polypropylene artificial comb with 4.9 mm cells.² The proponents of 'small cell beekeeping', a following that could have increased to several thousand since 1990,³ appear convinced that this is part of the solution to keeping vigorous bees that can resist *Varroa* without the addition of acaricides or without using other anti-*Varroa* methods.

This idea has naturally attracted the attention of apiological scientists round the world and a number of studies have been carried out to investigate the role, if any, of small cell comb in the ability of *Apis mellifera* to cope with *Varroa*. The experimental designs have differed greatly, including having both large and small cell comb in the same test hives. The durations ranged from a few weeks to four years. A few studies showed a beneficial effect of small cells, and all but one of those lasted only a few weeks. In the following I examine the various studies in more detail.

Summaries of individual studies, with comments

Davidsson (1992) did a small study using 5.1, 5.5 and 6.0 mm (calculated by this reviewer from their data for cells per dm²) foundation and examined capped cells for mite families. Mite numbers were slightly, though not significantly higher in the small cell group.

In investigating why Africanised honey bees in South America cope better with *Varroa* than European races, Piccirillo and De Jong (2003) provided six test Africanised bee colonies with comb of three sizes: 1) natural Africanised bee comb (4.84 mm inner width); 2) comb from Italian bee 5.4 mm foundation (5.16 mm inner width); 3) natural Carniolan bee comb (5.27 mm inner width). Combs of emerging brood were taken for laboratory examination. The percentages of emerging bee cells infested were 10.3, 13.9 and 19.3 respectively and this series was reflected in the number of mites per 100 cells. In four of the colonies there was a highly significant positive correlation between cell size and infestation rate. The authors concluded: 'The small width comb cells produced by Africanized honey bees may have a role in the ability of these bees to tolerate infestations by *Varroa destructor*, furthermore it appears that natural-sized comb cells are

superior to over-sized comb cells for disease resistance.' Despite the short duration of this study – only one brood cycle – it is regarded by some as supportive of the small cell hypothesis.

Fries (2004), in a study not often cited by other investigators, possibly because it was reported in a Swedish beekeeping journal, prepared large cell (5.45 mm) and small cell (5.05 mm) bees in 2001 and infested them with *Varroa* in 2002. In 2002 and 2003 he recorded mite drop, mites per 100 bees, and bee weight. Mite drop rose during 2002 and stayed at high levels in 2003. It was higher in the large cell bees in 2003 but by the July, August, and September sample times this difference had disappeared. Mites per 100 bees rose from about eight in October 2002 to 70-80 in October 2003, with no significant differences between large and small cell bees. Some frames in small cell colonies had an uneven cell pattern. Fries acknowledged that this could have resulted in more drone cells. However, that was not observed. Neither was there a measurement of the amount of drone brood in the experimental groups.

Liebig & Aumeier (2007) reported in a short article to a German beekeeping journal an experiment at Munich with 4.9, 5.1 and 5.5 mm foundation during a single season. The size of the cells had no effect on the pre-treatment natural mite drop and the degree of infestation of cells. They confirmed this with their own work at Bochum and concluded that small cells are inappropriate as a weapon against *Varroa* mites.

Dahle (2008) reported on a 4-year study with 90 colonies which finished in 2007 and was conducted by the Norwegian Beekeepers Association involving the apiaries of several participating beekeepers. Colonies had 4.9, 5.1 or 5.4 mm foundation in the brood nest, and precautions were taken to remove influences of drifting, climate, and bee genetics. Colonies were given occasional oxalic acid treatment as a moderate control of *Varroa* infestation. This means that the bees were not exposed to the full selective pressure of *Varroa* and its associated pathogens. Multifactorial statistical analysis was applied to the results. Mites per 100 bees were significantly lower in colonies with 5.1 mm cells. A similar tendency was observed with 4.9 cells but the difference was not statistically significant. The author concluded that, on the basis of an experiment of limited scope, reducing the cell size is no alternative to oxalic acid treatment, but may be a possible supplement.

A preliminary report on the Norwegian study by Johnsen (2005), a commercial beekeeper participating in the study, who was also cited by Seeley and Griffin (2010), recounted more favourable results for the small cell group. In a subsequent press release, the Norwegian Beekeeping Association distanced itself from Johnsen's article, saying that the results were taken without approval out of the context of a wider and longer experiment.

Taylor et al. (2008) gave ten nuclei colonies mosaic frames each containing comb from five foundation cell sizes from 4.7 mm upwards. Between eighteen and twenty days later they took the frames for counting *Varroa* in capped cells. More cells from 4.8 mm foundation were infested compared with the larger sizes. Brood cell size, measured internally, had no significant effect on mite reproduction or infestation. The authors acknowledged two problems in the design and execution of the experiment: 1) the Italian bees used did not draw the smaller cell sizes evenly, and 2) the waxes used in the different foundations were from very different sources.

Oliver (2008) compared plastic comb of 4.9 mm cell size (Honey Super Cell) with plastic foundation with 5.35 mm cell bases (Plasticell), ten colonies in each case. The hives were populated in May with about 2.7 kg bees pretreated with an effective acaricide but thereafter no treatments were used. The hives were arranged to minimise drifting and were opened as little as possible. The colonies were generously fed to stimulate build up and mite reproduction. From July to October, hive weights, visual grading of frame strength and natural mite drops were recorded. There were no measurements of brood cell infestation or mites per 100 bees. However, Seeley and Griffin (2010), who also used Honey Super Cell for their small cell colonies, did measure mites per 100 bees and found no difference between small and large cell colonies. Their paper is discussed in more detail below. Oliver (2008) found that small cell colonies gained only 65% in weight compared with large cell colonies. By October there was no difference in frame strength between large and small cell colonies. Despite checking mite drop in the 20 colonies at several points in time, a statistical analysis of the results was not performed. However, it is clear from the graph of the results that the

small cell colonies had mite drops grouped at or well below the bottom end of the range for the large cell colonies. The apparently increased mite drop in controls was not attributable to drone comb.

Ellis et al. (2009) claim to have made the first refereed quantitative investigation in the USA into the efficacy of small cells as a *Varroa* control method. In a 13-month study they established 15 hives with small cell bees on fresh 4.9 mm foundation and 15 with standard cell bees on fresh 5.4 mm foundation as a control. Test and control apiaries were 680 m apart. Bees were of mixed European race dusted with icing sugar to lower initial mite counts. Small cell foundation did not significantly affect the total area of brood, the total number of mites per colony, mites per brood cell, or mites per adult bee. There were more bees in the small cell colonies at some time points in the study, but not at others. The authors concluded that they 'cannot recommend use of small cell comb as a tool in an integrated pest management program aimed at controlling *Varroa*'.

The study of Wilson et al. (2009), so far published only as a short communication, failed to test whether small cells affect *Varroa* populations, although this appears to have been one of the intentions behind it. In two successive experiments spread over two years using bees reared on natural cells drawn under waxed wooden starter strips in frames, the authors compared colonies on natural cells with those on foundation. However, the worker cells in the natural comb averaged 5.4 mm and cells did not decrease in size despite the bees having had a total of three seasons freedom to build the cell size of their choice and being given fresh starter strips in the third season. In contrast, the two experiments' control groups which were on foundation-based comb had an average cell size of 5.3 mm. *Varroa* populations from the two types of comb, assessed by 72-hour mite falls, did not differ in the first year but were significantly lower from natural comb colonies that had been started the previous year. Most of the parameters of colony productivity studied did not differ between the two types of comb with the exception that the control colonies produced almost five times the amount of surplus honey compared with controls. The main contribution of this study seems to lie in the fact that the foundationless system used did not achieve a reduced cell size.

Next we consider two papers by McMullan and Brown (2006a & b) who are co-authors in the Coffey et al. (2010) paper. Before conducting mite studies, McMullan and Brown (2006a) first carried out morphometric analysis of *Apis mellifera mellifera* reared on small cell foundation (4.9/5.0 mm nominal) compared with standard foundation (5.5 mm nominal). The bees, previously in nuclei on standard foundation, satisfactorily drew small cell foundation in three test hives each of which also contained frames of large cell foundation. Adjacent large and small cell frames with emerging brood from the centre of the brood nest were taken for measurement of the callow bees. Although there were significant differences in many of the parameters measured, the 7-8% reduction in brood cell size gave only about 1% reduction in bee linear dimensions. The authors noted that their results were consistent in two separate seasons (2003 & 2005) and that the change was a step change rather than a gradual one. However, their results differed markedly from those of other researchers who, using other strains or races of *Apis mellifera*, obtained bee size reductions of up to 13.5%.

It is worth briefly mentioning here the findings of McMullan and Brown (2006b), even though they apply not to *Varroa* but to the tracheal mite *Acarapis woodi*. In their morphometry paper, discussed above, the authors concluded that the small reduction in tracheal diameter they obtained from 191 to 189 microns is unlikely in itself to affect access or reproduction in the trachea of female tracheal mites as these mites are only 70 microns wide. Indeed, in their tracheal mite paper the authors concluded that there was 'no evidence of any difference in the overall susceptibility between the bees raised in the standard-sized cells versus small-sized brood cells'.

Coffey et al. (2010), citing three peer reviewed papers which reported no beneficial effect of small cells vis-à-vis *Varroa*, focused in their introduction on the possibility that, with *A. m. mellifera*, a tighter fit for the young bee developing in a smaller cell would reduce the reproduction success of *Varroa*. In their earlier paper, co-authors McMullan and Brown (2006b) had found that the 'fill factor' for *A. m. mellifera* rose from 73% to 79% with the use of small cell comb, whereas in studies in the USA the fill factor⁴ was in the 50-60% range. In April 2007, frames of pre-drawn small cell (4.91 mm) and large cell (5.38 mm) combs were alternated in each of the test brood boxes which were placed on the test colonies on sheets of newspaper, and 500 bees with more than 20% infestation were added. *A. m. mellifera* had no problem with drawing out

small cell foundation. Four test colonies were included in the analysis. Three days later the queens were moved into the respective top boxes, and by four weeks later the lower boxes were removed, the brood having hatched. From July to September, they sampled comb in such a way as to be able to calculate: (a) prevalence – the number of infested cells per number of cells x 100; (b) abundance – the number of varroa mites (mother or offspring) per number of cells and (c) the intensity – the number of varroa mites (mother or offspring) per infested cell. Mite prevalence was slightly higher in small cells but overall mite abundance and intensity were not significantly affected by cell size. Abundance was higher in three of the four colonies but this was not reflected in the abundance of female offspring. The authors concluded that reduced worker brood-cell size is unlikely to have any value as a control strategy in *A. m. mellifera* under European conditions.

In 2006-2008, Berry et al. (2010) conducted three experiments with bees pooled from colonies with various rearing histories transferred either to small or large cell comb drawn by bees accustomed to the respective size, or, in one experiment, to large or small cell foundation. Colony and Varroa data were collected after 12, 16 or 40 weeks depending on the experiment. Cell density data were reported from which the mean cell sizes of 5.4 mm and 5.0 mm, for large and small cells respectively, can be calculated. Small cell bees were 9% lighter than large cell bees. At the end of each experiment the number of mites in brood, the percentage of the mite population in brood, and the number of mites per 100 adult bees were significantly higher in small-cell colonies. There were more bees in the small cell colonies in two of the three experiments. As this study comprised three experiments with different start dates, one experiment running for as long as 40 weeks and all involved a relatively holistic examination of colony development and Varroa reproduction, the authors seem very justified in their conclusion that 'small cell comb technology does not impede Varroa population growth'.

The study by Maggi et al. (2010) was conducted entirely on comb drawn the previous year on 4.5 mm (cell base) foundation,⁵ by an unspecified race of *Apis mellifera*. The authors investigated six colonies by sampling frames of capped brood from each, and opening all cells to take a census of the mite families therein. They found a range of worker cell sizes, measured internally, from 4.17 mm to 6.86 mm.⁶ There was a positive linear correlation between brood cell width and intensity of infestation by mother mites. For example, from their plot of those variables they found that an increase in cell size from 4.17 mm to 5.03 mm approximately doubles the probability of finding mites in a capped cell. Infertile mother mites were more common in the smaller cells, but there was no correlation between mite progeny and cell size. The rate of increase for viable mother mites was 0.96 viable female descendants, i.e. just below the replacement rate. This paper could be taken to indicate that it would be advantageous to have a significant proportion of smaller worker cells in the brood nest.

As already mentioned, Seeley and Griffin (2010) used Honey Super Cell plastic comb to obtain their small cell colonies. This is because preliminary experiments failed to get the bees to draw out small cell foundation satisfactorily. In June, they populated seven hives on small cell comb (4.82 mm average cell size) paired with seven hives with standard cell comb (5.32 mm average cell size), taking care to standardise the initial mite loads. From mid-June to mid-October they monitored colony strength, mite drop, mites per 100 bees (powdered sugar method) and worker sizes. Thorax widths were measured the following year in the standard cell colonies and in two new small cell colonies, as all seven of the original ones had died out over winter. The colonies were managed for honey production and drone comb was removed when it formed. Although the number of mites per 100 bees fell in both groups over the summer only to rise again, there were no significant differences between large and small cell colonies. Mite drops increased steadily but were never significantly different between the two groups. When the mite drops were adjusted for colony strength, there was an indication that, towards autumn, the small cell colonies had a higher mite drop than standard cell colonies, mainly on account of the reduced strength of the small cell colonies.

As a possible mechanism for any effect of small cells on Varroa reproduction, Seeley & Griffin (2010) focused on the fill factor. They found that although their small cells were 10.4% smaller than their standard cells, their small cell bees were only 2.1% (head width) or 3.5% (thorax width) smaller than their standard cell bees. They found that the fill factors of standard cells and small cells were 73% and 79% respectively, identical to the figures of McMullan and Brown (2006a). They concluded that as cell filling was rather low

and not greatly different between the two cell sizes, it was not surprising that they failed to show an effect of small cells on Varroa reproduction.

Overview

The following table is an attempt to make the somewhat conflicting findings of the various studies described above more surveyable.

Studies that can be regarded as supporting or not supporting the hypothesis that small cells help bees cope with Varroa

Supporting

Message & Goncalves (1995)*
Martin & Kryger (2002) – African bees
Piccirillo & De Jong (2003)* – Africanised bees
Oliver (2008)
Maggi et al. (2010)*

Not supporting

Davidsson (1992)
Fries (2004)
Liebig & Aumeier (2007)
Dahle (2008)
Taylor et al. (2008)
Ellis et al. (2009)
Wilson et al. (2009)
Coffey et al. (2010)
Berry et al. (2010)
Seeley & Griffin (2010)

Clearly the studies that do not support the small cell hypothesis are in the majority. However, the South American studies, shown with an asterisk in the above table, and the African bee study convincingly show that Varroa infestation and/or reproduction is less effective in small cells. The study by Oliver (2008) lacks completeness because the results were not analysed statistically. Furthermore, he used the same plastic comb for its small cells as that used by Seeley and Griffin (2010) who showed no advantage for small cells.

We are confronted with several short-term studies that suggest that small cells should 'work', but which are countered by many other studies, some running for several years, that show the opposite. Add to that the anecdotes of hundreds of beekeepers, especially in the USA, who use small cells as part of acaricide-free management, and there seems some justification for regarding the small cell hypothesis as still standing. However, the viability of the management system used by proponents of small cells may be nothing to do with the small cells per se. There could be other reasons for it. One possibility raised is that their bees are Africanised, therefore are already inherently able to cope with Varroa. This is easily refuted by the fact that success is claimed for small cell beekeeping in regions not yet reached by Africanised bees. Another possible reason is that the bees concerned have long been exposed to the full force of Varroa, without the shield of acaricides, and therefore have been naturally selected for resistance over a period of several years. Indeed, there are anecdotes of initial massive colony losses after switching to small-cell acaricide-free management (Flottum 1998), indicative of a powerful selective pressure at work, partly due to Varroa and partly to the viruses the mite carries.

A possible reason for most of the experiments by apiological scientists failing to support the small cell hypothesis is that they have not been conducted for long enough. If the bees used have not had a long period in advance of the experiment to adjust to comb with small cells, then they are already at a disadvantage compared with controls reared on the same kind of comb that they have been used to for many decades. How long any period of adaptation to small cells should be is a matter of debate, but it could take several years. In the experiments where a season of adaptation was given before commencing studies, for example those of Fries (2004) and Dahle (2008), the period may have been too short. It is noteworthy that the study of Piccirillo and De Jong (2003), supportive of the small cell hypothesis, employed bees that were already long adapted to small cells.

Conclusion and suggestion for further work

In view of the fact that 20 years of apiological research appears not to have finally settled the debate as to whether small cells help European bees cope with Varroa, yet another experiment seems warranted. In order to accommodate the aforementioned objection regarding adaptation to small cells, the experiment would need to last several years, preferably considerably longer than the 4-year experiment reported by Dahle (2008). Factors such as bee genetics, initial mite loads, apiary location, drifting, foundation wax source, hive format, drone comb, management and feeding would need to be standardised. As regards apiary location, several apiaries with local bees in different climatic regions would be needed. Deadouts would have to be replaced, ideally from bees of either group already within the experiment. If the bees used are not capable of drawing small cell foundation at first go, then an adaptation period, already with control colonies under observation, should include a stepwise reduction to small cell foundation. The data collected should at least include measurement of phoretic mites and brood infestation and any other parameters of interest that do not make data collection overly intrusive into colony life. Above all, the interest would be the survivor rate in the two groups in the absence of acaricides. This would be the primary holistic parameter to measure. Secondly, and because it is of particular interest to commercial beekeepers, honey yields would provide a second holistic parameter.

It would of course be of interest to apiology to know how any possible advantage conferred by small cells actually works. Influences such as pre- and post-capping times, cell fill factors, bee sizes (visits by nurse bees) etc. could be studied, although ideally not at the expense of colony health. Furthermore, it would be of value to assess whether any of the reasons put forward by Erickson (1990), cited at the beginning of this review, apply.

Such a study would of course make heavy demands on funding resources, and might even be impracticable for any groups within the apiological science community because of the often short-term nature of research grants and, with that, the very limited tenure of the people who would do the field work.

It may be argued that such a worldwide experiment by commercial and hobby beekeepers is already in progress and has been for over two decades, especially in the USA. However, such an experiment lacks controls and thus cannot convincingly show that small cells 'work'.

Nevertheless, the goal is surely a form of beekeeping with European bees that does not rely on acaricides. I quote Alsopp (2006):

In both Cape [*A. m. capensis*] and Savanna [*A. m. scutellata*] bees,⁷ the absence of varroacide applications and a live-and-let-die approach to the wild and commercial honeybee populations was crucial to the development of population-wide varroa tolerance, in contrast to the selective breeding and pesticide treadmill practised in most parts of the world in an effort to get rid of the varroa mite. Varroa destructor is concluded not to be a serious threat to honeybees and beekeeping in Africa, and efforts should be made to prevent the use of pesticides and techniques that could hinder the development of natural mite tolerance in Africa.

The small-cell 'school', however uncertain the basis of its success, has already made an effort in this direction. For its practices to become more widespread, the kind of controlled study described above would no doubt help.

References

Allsopp, M (2006) Analysis of Varroa destructor infestation of Southern African honeybee populations. Dissertation, University of Pretoria

Berry, J. A., Owens, W. B., and Delaplane, K. S. (2010). Small-cell comb foundation does not impede Varroa mite population growth in honey bee colonies. *Apidologie* 41: 40-44.

Camazine, S. (1988) Factors affecting the severity of *Varroa jacobsonii* infestations in European and Africanized honey bees. In *Africanized honey bees and bee mites*, Ch. 59, 444-451.

- Coffey, M. F., Breen, J., Brown, M. J. F. & McMullan, J. B. (2010). Brood-cell size has no influence on the population dynamics of Varroa destructor mites in the native western honey bee, *Apis mellifera mellifera* *Apidologie* 04 February 2010; DOI: 10.1051/apido/2010003.
- Dahle, B. (2008) Er det noe å hente på å redusere cellestørrelsen? *Birøkteren* **124**, 216-218.
- Davidsson M (1992). Betydelsen av vaxcellornas storlek hos bina, *Apis mellifera*, för varroakvalsterets, *Varroa jacobsoni*, reproduktion. Examensarbete 49. Husdjurens utfodring och vård. Sveriges Lantbruksuniversitet, Uppsala.
- Ellis, A. M., Hayes, G. W., and Ellis, J. D. (2009). The efficacy of small cell foundation as a varroa mite (*Varroa destructor*) control. *Experimental and Applied Acarology* 47(4): 311-316.
- Erickson E.H., Lusby D.A., Hoffman G.D. & Lusby E.W. (1990) On the size of cells: speculations on foundation as a colony management tool, *Glean. Bee Culture* **118**, 98-101, 173-174. This two part article can be accessed at <http://www.beesource.com/point-of-view/ed-dee-lusby/historical-data-on-the-influence-of-cell-size/on-the-size-of-cells-part-1/>. Scroll down to link for part 2.
- Flottum, K. (1998) Beekeeping on the Fringe, with Ed & Dee Lusby. *Bee Culture*, January, 34-35.
- Fries, I. (2004) Cellstorlek och varroakvalster. *Bitidningen* **103**, March, 18-20.
- Johnsen, H.-O. (2005) Commercial Beekeeping in Norway. *Bee Culture*, September, **133:37-40**. See Beesource version: <http://www.beesource.com/point-of-view/hans-otto-johnsen/survival-of-a-commercial-beekeeper-in-norway/>.
- Liebig, G., Aumeier, P., 2007. Helfen kleine Zellen gegen Varroa? [Do small cells help against Varroa?] maandblad voor bijenhouders [magazine for beekeepers] July/August 2007. From: Liebig, G., Aumeier, P., 2007. Helfen kleine Zellen gegen Varroa? Dtsch. Bienenjour. 04, 32–33.
- Maggi, M., Damiani, N., Ruffinengo, S., De Jong, D., Principal, J. & Eguaras, M. (2010) Brood cell size of *Apis mellifera* modifies the reproductive behavior of *Varroa destructor*. *Experimental and Applied Acarology* Volume 50, Number 3, 269-279.
- Martin S.J. & Kryger P. (2002) Reproduction of *Varroa destructor* in South African honeybees: does cell space influence *Varroa* male survivorship? *Apidologie* 33, 51–61.
- McMullan, J. B., Brown, M. J. F. (2006a). The influence of small-cell brood combs on the morphometry of honeybees (*Apis mellifera*). *Apidologie* 37: 665-672.
- McMullan, J. B., Brown, M. J. F. (2006b). Brood-cell size does not influence the susceptibility of honey bees (*Apis mellifera*) to infestation by tracheal mites (*Acarapis woodi*). *Experimental and Applied Acarology* 39: 273-280.
- Message, D. & Goncalves, L. S. (1985) The effect of the size of the honey bee cells on the rate of infestation by *Varroa jacobsonii*. *XXXth International Apicultural Congress of Apimondia*, Nagoya, Japan. 250.
- Message, D. & Goncalves LS (1995) Effect of the size of worker brood cells of Africanized honey bees on infestation and reproduction of the ectoparasitic mite *Varroa jacobsoni* Oud. *Apidologie (Celle)* 26:381–386. doi:[10.1051/apido:19950503](https://doi.org/10.1051/apido:19950503)
- Oliver R (2008) A trial of HoneySuperCell small cell combs. *Am Bee J* 148:455 458.
- Piccirillo G.A., de Jong D. (2003) The influence of brood comb cell size on the reproductive behaviour of the ectoparasite mite *Varroa destructor* in Africanized honeybee, *Genet. Mol. Res.* 2, 36–42.

Seeley, T. D. & Griffin, S. R. (2010) Small-cell comb does not control Varroa mites in colonies of honey bees of European origin. *Apidologie* (in press)

Taylor, M. A., Goodwin, R. M., McBrydie, H. M., and Cox, H. M. (2008). The effect of honey bee worker brood cell size on Varroa destructor infestation and reproduction. *Journal of Apicultural Research* 47(4): 239-242.

Wilson, M. W., Skinner, J., Chadwell, L. Measuring The Effects Of Foundation On Honey Bee Colonies: *American Bee Journal*, June 2009.

Acknowledgement

I thank the following for their help in various ways during the writing of this document: Bjørn Dahle, Ingemar Fries, Matias Maggi, Randy Oliver, Tom Seeley and Michael Wilson.

Contact

David Heaf is a hobby beekeeper in North Wales, UK. He can be contacted via his web site <http://www.bee-friendly.co.uk>.

ADDENDUM

Since this review was written two further papers have appeared on this theme, firstly Olszewski et al. (2014)⁸ who showed an increase in hygienic behaviour in bees transferred to small-cell comb and secondly Oddie et al. (2019)⁹ published a paper showing some reduction in mite reproduction indices caused by giving small cell comb to mite-susceptible colonies of bees.

In the Olszewski et al. (2014) study, bees from colonies treated for Varroa, or from colonies naturally selected over several years following withdrawal of Varroa treatment, were transferred to comb built on 4.93 mm foundation. Controls comprised both colony types but kept on standard 5.56 mm foundation. The bees on small-cell foundation derived comb showed significantly increased hygienic behaviour in the pin kill test, but this could not be linked to Varroa sensitive hygiene. This paper is therefore taken as not supporting the hypothesis that small cells help bees cope with Varroa.

In the Oddie et al. (2019) study, mite-surviving colonies, i.e. stocks from 17 years of treatment-free natural selection, did not show this effect. The essential design was to prepare 10 pairs of capped brood combs derived from foundation of either 4.93 mm or 5.3 mm, by caging queens on them in heavily mite infested colonies, and, on the 9th day from laying, put 5 of the pairs in 5 mite-surviving colonies on 4.93 mm foundation comb and 5 of the pairs in mite-susceptible colonies on 5.3 mm foundation comb. After 10 days in the two colony types the 20 combs were frozen pending determination of the actual drawn cell sizes, the developmental stage of the young bee and the status of mite reproduction. During those 10 days the bees were of course free to interfere with the mite reproduction, e.g. by uncapping/recapping etc. In the susceptible colonies, mite fecundity was positively correlated with actual cell size, but not with the foundation size given. This and the meticulousness of the study, covering several parameters of mite reproductive success, justifies it being included amongst the papers supporting the hypothesis discussed herein.

With these two papers we have six supporting and 11 not supporting the hypothesis.

¹ Erickson et al. (1990)

² Honey Super Cell – <http://www.honeysupercell.com>

³ At the time of writing this review, Dee Lusby's e-group at <http://groups.yahoo.com/group/Organicbeekeepers/> had a membership of 3,965 and was still growing.

⁴ Fill factor is thorax width/cell width expressed as a percentage.

⁵ Maggi, Matías. Personal communication (2011).

⁶ Maggi, Matías. Personal communication (2011). "At the time of the study, the sampled combs ranged in age between 6 month and 2 years. It is very probable that smaller cells correspond to old combs or zones of the combs where numerous bee larvae were raised."

⁷ Alsopp (2006) estimates that the development of resistance to Varroa took 3-5 years in *A. m. capensis* and 6-7 years in *A. m. scutellata*. We can expect it to take at least 6-7 years for European *A. mellifera* to co-adapt with Varroa and there is already some evidence that the damage done by the mite is less than when it first arrived.

⁸ Olszewski K., Borsuk G., Paleolog J., Strachecka A., Bajda M. (2014) Hygienic behaviour of colonies kept on small-cell combs. *Med. Weter.* **70** (12), 774-776.

⁹ Oddie, M. A. Y., Neumann, P. & Dahle, B. (2019) Cell size and *Varroa destructor* mite infestations in susceptible and naturally-surviving honeybee (*Apis mellifera*) colonies. *Apidologie* doi: 10.1007/s13592-018-0610-2.