Brood-cell size has no influence on the population dynamics of Varroa destructor mites in the native western honey bee, Apis mellifera mellifera

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Apidologie 41 (2010) 522–530
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DOI: 10.1051/apido/2010003

Available online at:
www.apidologie.org

Original article

Brood-cell size has no influence on the population dynamics of *Varroa destructor* mites in the native western honey bee, *Apis mellifera mellifera**

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Received 10 July 2009 – Revised 22 October 2009 – Accepted 23 October 2009

Abstract – The varroa mite (*Varroa destructor*) is an ectoparasite of the western honeybee *Apis mellifera* that reproduces in the brood cells. The mite will generally kill colonies unless treatment is given, and this almost universally involves the use of chemicals. This study was undertaken to examine the effect of small cell size on the reproductive success of the mite, as a method of non-chemical control in the Northern European honeybee *Apis mellifera mellifera*. Test colonies with alternating small and standard cell size brood combs were sampled over a three-month period and the population biology of the mites evaluated. To ensure high varroa infestation levels, all colonies were infested with mites from a host colony prior to commencement. A total of 2229 sealed cells were opened and the varroa mite families recorded. While small-sized cells were more likely to be infested than the standard cells, mite intensity and abundance were similar in both cell sizes. Consequently, there is no evidence that small-cell foundation would help to contain the growth of the mite population in honeybee colonies and hence its use as a control method would not be proposed.

***Apis mellifera* / *Varroa destructor* / cell size / natural mite fall / prevalence**

1. INTRODUCTION

The varroa mite (*Varroa destructor*) and its associated viruses remains a primary factor in colony losses world wide. The problem has been compounded by the extensive use of chemical treatments such as acaracides which has led to the evolution of resistance (Thompson et al., 2002). Consequently, the development of an integrated pest management control incorporating non-chemical approaches is becoming increasingly important.

Non-chemical control relies upon an understanding of the biology of *V. destructor*, the key aspect of which is invasion of and reproduction in the worker and drone brood cells of the host. *V. destructor* has evolved specific time activity budgets and space structuring (Donzé and Guerin, 1997) which maximises the number of fertilised females produced per reproductive cycle. Martin (1994) reported that a female varroa mite can deposit five or six eggs in a worker cell, of which four (1 male and 3 female) may reach maturity before the bee emerges from the cell. However, due to offspring mortality, the estimated number of female offspring reaching maturity is only 1.45 per cell. Many claims have been made about the potential benefit of using small-cell comb (Message and Gonçalves, 1995; Martin and Kryger, 2002; Piccirillo and de Jong, 2003) to reduce the space inside the cell, thus impeding movement of the mites and causing an increase in

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mortality of mother mites and offspring, both male and female. However, the scientific evaluation of them has been limited. Three recent papers, Taylor et al. (2008) in New Zealand and Ellis et al. (2008) and Berry et al. (2010) in the US, have attempted to test potential benefits. While Taylor et al. (2008) found no effect of cell size, they acknowledged that their study was confounded both by an inability of the bees to draw out small cells, resulting in only a small difference in the actual cell sizes being tested, and by the use of different grades of wax for different cell sizes which may have influenced mite migration into the cells. Ellis et al. (2008) evaluated infestation in colonies in two different apiaries, one apiary having exclusively standard-cell sized combs and the other exclusively small-cell sized combs. Consequently, while no effect of cell size was found (apart from adult bee population doubling in the first year in the small cell-size apiary), they acknowledged that their results are somewhat confounded by the experimental design. Finally, Berry et al. (2010) conducted three experiments comparing colonies with small-cell or conventional-cell foundation. They found that colonies with small-cell foundation had higher numbers of mites in brood and on adults at the end of the season. While they did not report the strain of honeybee used, they also found that honeybee size reduced with small foundation and thus suggested that this was behind the lack of a controlling effect of small-cell brood on mite populations. However, McMullan and Brown (2006) showed that such reductions are not proportional, particularly in the native northwest European *Apis mellifera mellifera*. This leaves open the possibility that potential benefits of small-cell foundation may vary depending upon how a given honeybee sub-species responds to a reduction in brood cell size.

In this study, we examine the impact of small cell size on the reproductive success of *V. destructor* using a split-colony design and assess its possible use as a non-chemical treatment. Earlier work in Ireland showed that the indigenous honeybee, *Apis mellifera mellifera* had no difficulty in moving from the standard-cell size of 5.4 mm to the small-cell size of 4.9 mm (McMullan and Brown, 2006). Also, as *Apis mellifera mellifera* is a large bee and has a high ratio of thorax width to cell width ('fill factor'), the potential benefit of using small cell combs would be greatest in this subspecies.

2. MATERIALS AND METHODS

2.1. Preparation of test colonies

Six test colonies of bees of the subspecies *Apis mellifera mellifera* were established in April 2007 in an apiary in County Carlow, Ireland. The wax comb used in these colonies was prepared by placing new brood boxes with wax foundation over the brood boxes of 'wax-drawing' colonies which were located in an alternative apiary. This foundation was arranged in the new brood boxes alternately 4.9 mm nominal size, to be called 'small' cells, and 5.4 mm nominal size, to be called 'standard' cells (Dadant wired foundation F350503SC and F35050, respectively). The foundation in each mixed brood box was drawn out by the same colony to reduce the potential bias of different colony odours being present on combs in the same brood box. A period of 2–3 weeks was taken to draw out the 11 brood combs per colony. Combs were removed from the centre of the brood box when drawn and replaced with new foundation. Consequently, there was little or no honey present in the drawn combs prior to their placement into the test colonies. Frames were marked with the date the foundation was fitted, cell size and identification number of the wax-drawing colony.

A brood box of the drawn mixed-cell combs was placed on top of each test colony. Small and standard combs were inter-digitised within the brood box. Approximately 500 bees from an inoculation colony (with > 20% varroa mite prevalence) were introduced into the new brood boxes and a sheet of newspaper placed between the boxes to aid acceptance (Janmaat and Winston, 2000). Three days later the queens were moved into each of the top brood boxes. The lower boxes were removed within four weeks when all of the brood in these boxes had emerged. Test colonies were screened prior to the experiment for hygienic behaviour (for another experiment, which required hygienic colonies), and observations provided no evidence for the presence of such behaviour in our test colonies. Furthermore, during the experiment there were no signs of eaten or removed pupae, and brood clumps were compact, indicating a lack of hygienic behaviour.

2.2. Collecting test samples

Twice per month from July to September 2007, two 8 × 8 cm areas of worker brood containing eggs (or open brood of similar age if eggs were not available) were identified in facing small and standard combs in each colony. A template was used to record the coordinates of these areas for later removal. Selecting in this way ensures that both samples are exposed to the same temperature, humidity and bee movements with the only variable being the cell size. After a period of 16/17 days (adjusted if open brood were used instead of eggs), the two adjacent brood sample sections were identified using their coordinates and the comb sections cut out. The samples were put into cardboard boxes, sealed, marked and frozen at –18 °C. Prior to each sampling date, the natural mite fall was estimated by placing an insert underneath the brood box for three days. The total mite drop was counted and expressed as the number of mites per day. This was used as a proxy for the total mite population in each of the test colonies.

2.3. Laboratory analysis

Brood comb sizes were measured for both cell sizes. Measurements of ten cells across the flats were taken for the three axes displaced at 60°, and the cell sizes were expressed in mean linear distance per cell size. In each of the test brood samples, 50 to 100 cells (depending on availability) were uncapped. For each sealed-cell opened, the following data were recorded; (1) the number of live and dead mother mites, (2) the number of male and female mite offspring, (3) the developmental stage (egg/larva, protonymph, deutonymph and adult) of each offspring (Ifantidis, 1983) and (4) the bee brood development stage (Jay, 1962). Mother mites were classified as dead (prior to freezing) if the idosoma of the mites was shrivelled and/or partly decomposed. The bee brood's stage of development was used to provide a time reference from the time the cell was sealed. The duration for the full sealed brood stage was taken as 12.0 days, which was measured in the UK by Jay (1962) for *Apis mellifera*. This aligns closely with the corresponding measurements taken in Ireland of 12.4 days (McMullan, unpubl. data).

The terms used in the paper are defined here to make it clear that in some cases we are not dealing with parasite infestation per host (bee), but infestation per brood cell. Hence, (a) prevalence is defined as the number of infested cells per number of cells in a sample of test comb (and expressed as a percentage), (b) abundance is the number of varroa mites (mother or offspring) per number of cells in a sample of test comb and (c) the intensity is the number of varroa mites (mother or offspring) per infested cell.

2.4. Statistical analyses

Prevalence data were analysed using binary logistic regressions. The forward log-likelihood procedure was used, with cell size (indicator), colony (deviance), and time (continuous) and their interactions used as predictor variables. Generalized linear models were used to analyse abundance and intensity data. Abundance data were analysed using a log link function and a negative binomial error distribution. Intensity data were analysed using a log-linear link function and either a Poisson or a negative binomial error distribution. Cell size and colony were considered as fixed effect factors, while time was a covariate. In the models, we initially considered full factorial models before using a step-down simplification procedure. At each step, the term with the largest *P*-value was excluded from the model, starting with the higher order interactions. Simplification ended when all terms in the model were significant, or, for lower order terms, was involved in significant interaction terms.

3. RESULTS

A total of six colonies (designated 1 to 6) were used at the commencement of this experiment. However, poor weather prior and during the experimental period caused significant queen laying related problems in test colonies 2 and 3, resulting in a lack of data across multiple sampling points. Colonies 1, 4, 5 and 6 showed typical seasonal development and were sampled on each of the five sampling dates (Julian days 202, 220, 237, 258, 263). Thus, only data from these four colonies are reported and analysed in this study, but it represents approximately 80% of the total data set. While mother and offspring mite categories could generally be identified with ease, in a few cases (less than 1%) it was not

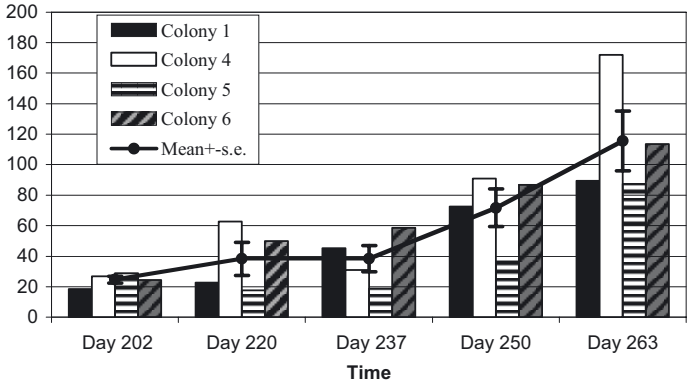

Figure 1. Natural mite fall (mites/day) in the four test colonies during July–September 2007 (the line shows mean ± SE across colonies). Mite fall increased significantly across the season (see results for statistics).

possible to allocate mites with 100% reliability to one of these categories. Consequently, we removed these cells from the dataset prior to analyses of intensity and abundance. For the prevalence analyses we reverted to the full four colony dataset, as in all cases, cells with unidentifiable mites also contained clear mother mites.

3.1. Cell size

Cell measurements indicate that test colonies successfully drew 4.9 mm foundation ($t_{[119]} = 0.831$, $P = 0.408$ and 5.4 mm foundation $t_{[119]} = 1.067$, $P = 0.288$). The mean ± s.e. for small and standard cells in the present experiment was 4.91 ± 0.02 and 5.38 ± 0.01, respectively.

3.2. Natural mite fall

The natural mite fall, a proxy for the total mite population in a colony increased in all colonies over the experimental period (Fig. 1; $F_{[4,19]} = 14.74$ $P < 0.05$). The mean (±SE) natural mite fall (mites/day) in the four test colonies at the beginning of the experimental period was 24.6 ± 2.29, increasing to 115.1 ± 19.2 by September. However the growth rate varied between colonies ($F_{[3,19]} = 4.02$ $P < 0.05$).

3.3. Prevalence

Contrary to our expectations, smaller cells were significantly more likely to be infested with mother mites of *Varroa destructor* (Tab. Ia). 47.1% of 4.9 mm cells were infested compared to 43.6% of 5.4 mm cells. There was a significant effect of time (i.e., the day on which a cell was capped), with the probability of being infested increasing throughout the season at a rate of 5% per day (Tab. Ia). There was also a significant effect of colony (Tab. Ia), with cell infestation varying from 33.8% in colony 1, through 39.8% in colony 5, to 50.2% in colony 6 and 56.7% in colony 4. Colony prevalence varied significantly with time (Tab. Ia).

3.4. Intensity

Colonies 1 and 5 only had one infested 5.4 mm cell on sampling date 202. Therefore, for this analysis the dataset was reduced to the last four sampling dates. There was a significant effect of time on intensity, with mite intensity increasing across the experiment (Tab. Ib), and colonies varied significantly in their intensity of infestation (Tab. Ib), but there was no effect of cell size (Tab. Ib). However, mite intensity varied depending upon a cell size by colony interaction (Tab. Ib) Results were qualitatively the same if live mother mites were used to calculate intensity.

Table I. The effect of cell size, colony, time and inter-group interactions on prevalence, intensity and abundance of mother mites in four test colonies during July–September 2007.

(a) Prevalence	B±SE	Wald	DF	*P*	Exp(B)
Cell size	0.216 ± 0.097	5.005	1	0.025	1.242
Colony		13.163	3	0.004	
Time	0.046 ± 0.002	360.9	1	< 0.001	1.047
Colony × Time		14.291	3	0.003	
(b) Intensity		Wald χ^2		*P*	
Cell		1.217		0.27	
Colony		35.456		< 0.001	
Time		21.443		< 0.001	
Cell × Colony		10.355		0.016	
(c) Abundance		Wald χ^2		*P*	
Cell		0.356		0.5	
Colony		13.041		0.005	
Time		315.545		< 0.001	
Cell × Colony		11.048		0.011	
Cell × Time		0.353		0.553	
Colony × Time		12.134		0.007	
Cell × Colony × Time		12.432		0.014	

3.5. Abundance

3.5.1. Female mother mite abundance

The number of mother varroa mites per number of cells was not affected by cell size (Tab. Ic), while over time the abundance increased significantly (Tab. Ic). Individual colonies showed significant differences in mite abundance (Tab. Ic). Interestingly, there was a significant interaction between cell size and mother mite abundance (Tab. Ic), with mother mites being more abundant in the larger cells in colonies 1, 4 and 5, and less abundant in the larger cells in colony 6.

3.5.2. Female offspring abundance – population level

The older offspring (⩾210 hrs post capping) were analysed as these reflect the growth in mite population. There were significant effects of time (Wald = 132.264, $P < 0.001$), colony number (Wald = 19.158, $P < 0.001$) and the number of mother mites (Wald = 351.246, $P < 0.001$) on the number of female offspring in a cell. Unsurprisingly, the number of female offspring increased across time (from 0.32 ± 0.057 to 2.26 ± 0.15) between the beginning and end of the experiment and exhibited an initial increase, followed by a decrease, with an increase in the number of mother mites (from 2.38 ± 0.083 with 1 mother, to 5.76 ± 0.452 with 5 mothers, and then down to 2.5 ± 0.5 with 7 mothers). There was no effect of cell size on the abundance of female offspring (Fig. 2; Wald = 1.045, $P = 0.307$). Similarly, the interaction between cell size and colony was non-significant and therefore removed from the model prior to the final model stage (see Methods). When the data were split into data sets with either one mother mite, or more than one mother mite/cell, there were no significant effects of any of the factors on female offspring abundance.

3.5.3. Male offspring presence-absence – population level

The final model contained 2 significant main effects, and 2 significant interactions, and predicted 86.2% of the cells correctly (that is, in 86.2% of cases it was able to predict whether male offspring were or were not present), in comparison to a null model prediction of 69.4%. However, the majority of

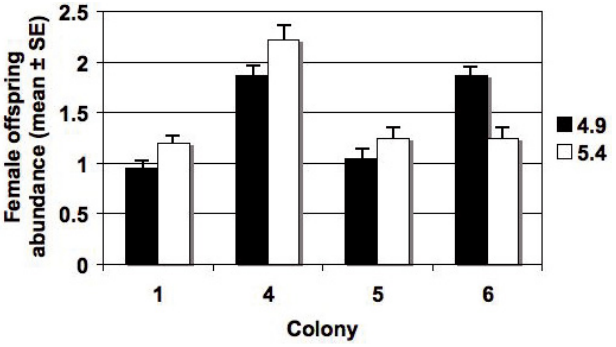

Figure 2. The abundance (mean ± SE) of *V. destructor* female offspring across colonies in the small and normal cell sizes. There was no significant effect of either cell size or the cell size by colony interaction (see results for statistics).

this increase was due to the number of mother mites present in a cell, which was the first factor to be incorporated into the model and, on its own, increased the probability of correction prediction to 83.9%. In the final model, number of mother mites (Wald = 47.452, $P < 0.001$), colony identity (Wald = 16.565, $P = 0.001$), the interaction between mother mites and time (Wald = 14.608, $P = 0.006$) and the interaction between mother mites, colony and time (Wald = 48.256, $P < 0.001$) were all significant. The probability of a male offspring being present in a cell increased over time (from 0.08 to 0.44 across the season) and with the number of mother mites per cell (from 0.57 to 1.00 at 5 mothers, and then down to 0.50 with 7 mothers).

3.5.4. Male abundance – population level

Number of mother mites (Wald = 201.361, $P < 0.001$), time (Wald = 43.313, $P < 0.001$), colony (Wald = 9.815, $P = 0.02$), the interaction between number of mothers and time (Wald = 50.061, $P < 0.001$) and the interaction between number of mothers and colony (Wald = 16.472, $P = 0.001$) were all significant predictors of the abundance of male mites. The number of male mites in cells first increased and then decreased with an increase in the number of mother mites (from 0.58 ± 0.028 with 1 mother, to 2.62 ± 0.223 with 5 mothers, and then down to 1 ± 1.000 with 7 mothers) and increased across time (from 0.09 ± 0.017 to 0.66 ± 0.054). When the data were split into two sets, one with one mother mite and the other with more than one mother mite, the only significant result was for the probability of having a male mite in cells with one mother, which increased over time (Wald = 16.771, $P = 0.002$).

Similar results were seen when data were analysed at the cell level, with only the number of mother mites and time being significant predictors of reproduction by *Varroa destructor* (analyses not shown).

4. DISCUSSION

Brood-cell size had no effect on the growth of the varroa mite population as measured by the abundance of mother mites and female & male offspring mites. While the small-cell comb did have a slightly higher probability of being infested, mirroring the results of Berry et al. (2010), there was no cell-size effect on the intensity of the mites within cells. In contrast, while in three out of four colonies mother mites were less abundant in the smaller cells, this was not reflected in the abundance of female offspring. So, for both prevalence and abundance, any potential impact of cell size disappears when the population biology of the mite is assessed. Together with the results of Berry et al. (2010) these data suggest that reducing cell size is unlikely to be a useful defence against *V. destructor*

infestation in the native European honey bee, *A. mellifera mellifera*.

In a previous attempt to test the small cell size hypothesis, Taylor et al. (2008) found that Italian honeybees (*A. mellifera ligustica*) failed to draw out the foundation comb into correspondingly sized cells, making it difficult for them to test whether cell size affected the likelihood of mites infesting cells. In contrast, in this study *A. m. mellifera*, the Northern European dark bee, which as a native subspecies is the subject of current conservation effort (Prichard, 2006), had no problem in drawing out the different cell sizes. Similar results were found by McMullan and Brown (2006) who further demonstrated that small cell size resulted in a reduction in bee size (head width, radial cell length and body mass) that was proportionately much less than the reduction in cell size.

The first factor in determining *V. destructor* population growth is the invasion of brood cells. In worker cells, cell size and colony size (Boot et al., 1993) have been suggested as important discriminatory factors. Picirillio and de Jong (2003) reported that in Africanised brood, the largest cells (5.33 mm) were approximately 38% more infested than medium cells (5.15 mm), which in turn were 13% more infested than small cells (4.8 mm). Similarly, Message and Gonçalves (1995) reported that *V. destructor* mites preferred the larger cells (~5.1 mm) to the smaller cells (~4.6 mm). In contrast, our findings and those of Taylor et al. (2008) and Berry et al. (2010) suggest that more small cells were infested than the standard cells. This apparent preference for smaller cells may be related to the 'trapping' phenomenon suggested by Ifantidis (1988). Trapping is the temporary immobilisation of female varroa mites at the bottom of the open brood cells on older bee larvae, thus preventing them from leaving with the nurse bee, which effectively increases the reproductive potential of the mite. Ifantidis (1988) suggested that using larger worker comb cells would reduce the trapping effect and hence reduce the potential reproductive output of the mite.

Notwithstanding the evidence of increased prevalence of mites in the small-cell combs, the key determinant of population growth is the mite abundance. It was clearly demonstrated in this experiment that cell size had no effect on the number of mother mites or the number of female mite offspring that were produced. Similarly, Berry et al. (2010) found no effect of cell size on *V. destructor* population size at the end of their experiment, although the number of mites on adult bees was significantly higher. Furthermore, in our experiment, cell size did not influence whether males would be available to mate with the female offspring or the abundance of those males in the cells.

The major factors driving mite populations in our experiment were season and colony. The mite population of the test colonies (as measured by mite drop, prevalence, intensity and abundance) exhibited a seasonal pattern, as has previously been described (Sakofski et al., 1990; Pettis and Shimanki, 1999; Ellis et al., 2001). Low mite populations were recorded in the early season, before an increase and then steady maintenance during late summer and early autumn. These dynamics, and the mechanisms behind them, were examined in greater detail by reconstructing mite families in older brood (⩾210 post capping). At the population level, both the number of female and the number of male offspring increased as the season progressed, and this was presumably driven by the increase in prevalence of mother mites (and vice versa). Interestingly, both female and male offspring increased in number with an initial increase of mother mites within cells, but then decreased as the number of mother mites reached its peak. It is likely that this is a function of competition for space (Martin, 1995) and exhibits how mite reproduction may plateau as infestation increases.

While non-chemical and integrated control are important for the future control of *V. destructor* in honeybees, our results suggest that reduced brood-cell size is unlikely to have any value as a control strategy in *A. m. mellifera* under European conditions.

ACKNOWLEDGEMENTS

The authors would like to thank the Department of Agriculture and Food for funding for this

research. We are grateful to Danny Keogh for his assistance in the field and Teagasc for the use of bee colonies at the Crop Research Centre, Carlow. Also, thanks to members of Fingal North Dublin BKA for access to colonies. Two reviewers and Yves Le Conte made helpful comments that improved the manuscript.

La taille des cellules du couvain n'a pas d'influence sur la dynamique des populations de *Varroa destructor* chez l'abeille occidentale, *Apis mellifera mellifera*.

***Apis mellifera* / *Varroa destructor* / taille de la cellule / prévalence / méthode de lutte sanitaire**

Zusammenfassung – Die Größe der Brutzellen hat keinen Einfluss auf die Populationsdynamik der Milbe *Varroa destructor* bei der westlichen Honigbiene *Apis mellifera mellifera*. Die Varroa-Milbe (*Varroa destructor)* ist ein Ektoparasit der europäischen Honigbiene *Apis mellifera*, die sich in Arbeiterinnen- und Drohnenbrutzellen fortpflanzt. Ohne chemische Bekämpfung werden Bienenvölker im Allgemeinen durch die Varroa-Milbe getötet. Der Reproduktionserfolg der Milben soll durch das Platzangebot innerhalb der Brutzelle beeinflusst werden und es gibt zahlreiche Behauptungen, dass die Verwendung von kleinen Arbeiterinnenbrutzellen vorteilhaft ist und als Bekämpfungsmethode eingesetzt werden kann (Message and Gonçalves, 1995; Martin and Kryger, 2002; Piccirillo and de Jong, 2003; Borrill, 2007). Die Populationsdynamik des Parasiten wird allerdings durch zahlreiche Faktoren beeinflusst einschließlich des Anteils nicht reproduzierender Muttermilben sowie der Überlebensraten der Männchen und der Nachkommen. Das Ziel der vorliegenden Arbeit war es, den Effekt von kleinen Zellgrößen auf den Reproduktionserfolg der Milben zu erfassen und festzustellen, ob der Einsatz von Waben mit kleineren Zellgrößen bei der nordeuropäischen Honigbiene *Apis mellifera mellifera* Vorteile bringt.
Um Nebeneffekte durch den Stockduft der Bienenvölker auszuschließen, wurden nur Mittelwände von einem Hersteller verwendet mit 4,9 mm (klein) bzw. 5,4 mm (Standard) Zellgröße, die alle von einem einzigen Bienenvolk ausgebaut wurden. Temperaturschwankungen, Feuchtigkeit und die Aktivität der Bienen wurden standardisiert, indem im Brutmagazin jeweils Waben mit kleinen Zellen abwechselnd mit Standardwaben eingehängt wurden. Vor Beginn der Versuche wurden alle Bienenvölker mit Varroa-Milben von einem Volk infiziert, um einen hohen und einheitlichen Befall der Versuchsvölker sicher zu stellen. In 3-wöchigen Abständen wurden gegenüberliegende Wabenstücke einer Wabengasse (8 × 8 cm) mit 18–20 Tage alter Brut gesammelt. Dabei wurden insgesamt 2229 Brutzellen geöffnet und die Varroa-Familien bestimmt. Der natürliche Milbenfall zeigte, dass bei allen Versuchsvölkern die Milbenpopulation im Verlauf der Saison anstieg (Abb. 1). Überraschenderweise war bei kleineren Brutzellen der Prozentsatz an infizierten Brutzellen (im Verhältnis zu den ausgewerteten Brutzellen) höher als bei den Standardbrutzellen (Tab. Ia), während sich die Befallshäufigkeit (= Anzahl aller Milbenstadien im Verhältnis zur Anzahl ausgewerteter Brutzellen, Tab. Ib) und Befallsintensität (= durchschnittliche Anzahl aller Milbenstadien pro befallene Brutzelle, Tab. Ic) bei den beiden Zellgrößen nicht unterschied. Aufgrund dieser Ergebnisse gibt es keinen Hinweis darauf, dass kleine Zellgrößen den Varroa-Befall in Bienenvölkern reduzieren und die Verwendung von Waben mit kleinen Zellen wird daher nicht als Bekämpfungsmaßnahme empfohlen.

***Apis mellifera* / *Varroa destructor* / Zellgröße / Natürlicher Milbenfall / Prävalenz**

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