Apidologie 33 (2002) 51–61

DOI: 10.1051/apido: 2001007

Original article

Reproduction of *Varroa destructor* in South African honey bees: does cell space influence *Varroa* male survivorship?

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(Received 18 May 2001; accepted 27 October 2001)

Abstract – The ability of *Varroa destructor* to reproduce in the African honey bee *Apis mellifera scutellata* was studied. In addition, the effects of space within the brood cell and short brood developmental time on mite reproduction, was investigated using *A. m. scutellata* cells parasitised by a *A. m. capensis* worker pseudo-clone. In *A. m. scutellata* worker cells *Varroa* produced 0.9 fertilised females per mother mite which is the same as found in susceptible European honey bees, but greater than the 0.4 produced in cells containing the pseudo-clone. Low mite reproductive success in cells containing pseudo-clone was mainly as a result of increased mite mortality. This was caused by male protonymphs and some mothers becoming trapped in the upper part of the cell due to the pseudo-clone being 8% larger than their host and not due to their short developmental time. Therefore, mite populations in South African *A. m. scutellata* and *A. m. capensis* honey bees are expected to increase to levels observed in Europe and USA.

Varroa destructor* / reproduction / cell size / mite mortality / *Apis mellifera scutellata

1. INTRODUCTION

The ectoparasitic mite *Varroa* sp. lives exclusively on cavity nesting honey bees and can either be found clinging to the underside of the adult bee (phoretic phase) or reproducing within the sealed honey bee brood cells (reviewed by Martin, 2001a). On the mites' original host, *Apis cerana* Fabr, several behavioral and physiological traits limit the population growth of the ectoparasite (Rath, 1999). However, on its new host, *A. mellifera* L., these limitations are lacking so the mite population is able to increase uncontrolled. Importantly, it is the mites' ability to transmit key bee viruses

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which eventually kills the honey bee colony (Martin, 2001b).

Although 18 haplotypes have so far been detected infesting *A. cerana* in Asia, only two, the Japan/Thailand and Korea haplotypes are able to reproduce in *A. mellifera* colonies (Anderson & Trueman, 2000). These two haplotypes along with the Sri Lanka, Nepal, China and Vietnam haplotypes are now collectively referred to as *Varroa destructor* Anderson & Trueman (Anderson & Trueman, 2000). During the past 50 years *V. destructor* has spread from Eastern Asia throughout the world causing the death of millions of colonies. Most of these can be attributed to the more widespread Korea haplotype which appears to be more virulent than the Japan/Thailand haplotype which is found predominantly in South America (Anderson, 2000).

Although 24 distinct taxonomic races of *A. mellifera* have been described (Ruttner, 1988) there is only one clear case where a race of *A. mellifera* exhibits natural tolerance towards *V. destructor* i.e. mite infested colonies can survive indefinitely without assistance from beekeepers. This is the Africanized bee (AHB) a hybrid of *A. m. scutellata* from South Africa and *A. mellifera* from Europe (Moritz, 1994) which now occurs throughout South and Central America. This tolerance by the AHB appears to be irrespective of mite haplotype, since early studies in Brazil (Moretto et al., 1991; De Jong, 1996) would have been on the Japan/Thailand haplotype which was the predominant haplotype in this region (Anderson & Trueman, 2000), while the *V. destructor* recently studied on AHB in Mexico (Medina & Martin, 1999) was confirmed as the Korea haplotype (Anderson, personal communication).

In addition to *A. m. scutellata,* the other South African honey bee is *A. m. capensis,* which is also suspected to be tolerant towards *V. destructor* due to the short developmental time of its sealed brood stage (Moritz and Hänel, 1984). Therefore, the possible effects of *V. destructor* on the South African bee population is the subject of great interest and debate among scientists (Allsopp et al., 1997) and beekeepers.

In February 1997 *V. destructor* was found at the Cape of Good Hope region of South Africa by Kryger and Moritz and later confirmed to be well established throughout the area (Allsopp et al., 1997; Allsopp, 1998) and of the Korea haplotype (Allsopp, 2000; Anderson & Trueman, 2000). Accidentally assisted by beekeepers, by 2000 the mite had spread from the Cape region occupied by *A. m. capensis* to the highveld regions around Pretoria occupied by *A. m. scutellata*. Colonies of *A. m. scutellata* in the highveld region are often invaded by imported *A. m. capensis* workers that initiate egg-laying, which despite being unfertilised, develop into more workers via thelytokous parthenogenesis. This is known as the 'capensis problem' (Allsopp, 1992) and recent genetic analysis indicates that the current invading *A. m. capensis* workers in the highveld region are all originally derived from a single worker and hence are referred to as a 'pseudo-clone' (Kryger, 2001; Kryger et al., 2002). The parasitic behaviour of the pseudo-clone results in their larvae being reared in cells not built by their sisters, a unique situation among non-manipulated honey bees. Beekman et al. (2000) found that *A. m. capensis* larvae are fed surplus brood food by nursing non-*capensis* workers and as a result they develop quicker and with more body-mass. This provides a rare opportunity to measure the effect of mite reproduction on two different sized honey bees reared in the same sized cells. This is important since space within the brood cell has a bearing on the mite's successful reproduction (Message and Gonçalves, 1995; Donzé and Guerin, 1997; Medina and Martin, 1999).

The aim of this study is to investigate the potential impact of *V. destructor* on the South African honey bees as well as

looking at the roles that space and short brood developmental time may have on the ability of mites to reproduce successfully.

2. MATERIALS AND METHODS

All observations were made during October 2000 in the Pretoria region of South Africa. The six *A. m. scutellata* colonies studied were naturally infested with *V. destructor* during the preceding year. Only mite infested *A. m. scutellata* colonies which where free from (n = 3) or invaded by (n = 3) very few pseudo-clones were used. Although this reduced the sample size of mites reproducing on the pseudo-clone, it helped rule out factors which may affect the mite's reproduction i.e. loss of humidity or temperature regulation. These changes in the colony are caused by usurpation of the host *A. m. scutellata* colony by invading pseudo-clones whose offspring rapidly replace the host worker population. This eventually leads to the death of the colony since the pseudo-clones do not forage so new brood cannot be reared (Martin et al., 2002).

The duration of the sealed brood stage of pseudo-clone and *A. m. scutellata* workers was determined by recording the time that individual cells were sealed and when these bees emerged, along with their weight at emergence. In addition the length of the fore wing and weight of adult pseudo-clones and *A. m. scutellata* workers were recorded to confirm the size differences between the two races of bees.

Frames of sealed brood were removed from the six study colonies and individual cells carefully opened. If mites were present they were removed and their sex and developmental stage determined. In addition all female deutonymphs were classified into five size groups using the photographs in Ifantidis (1983). This allows each mite family to be reconstructed (Martin, 1995a) in birth order and so the mortality rates of each offspring can be determined. The race, sex and developmental stage of the host honey bee were also recorded. The average number of eggs was calculated using cells capped longer than 200 hours and containing at three or more eggs. This allows more accurate comparisons to be made as it excludes the effects of mites that only produce males or no offspring. All infested cells sealed for longer than 200 hours were analyzed by placing the mother mites into one of the following six categories; (1) mother dead, (2) no offspring, (3) only male offspring, (4) fertilised female offspring i.e. live mature male and female offspring, (5) no fertilised female offspring due to premature death of the male, i.e. male dead, (6) no fertilised female offspring due to other causes, i.e. female offspring dead. Then the average number of mature females (unfertilised and fertilised) and fertilised female offspring produced per invading mother mite was calculated. The data obtained from the worker and drone cells of *A. m. scutellata* and worker cells occupied by the pseudo-clone were then compared with data from AHB (Medina and Martin, 1999) and European honey bees (EHB) studies (Martin, 1994, 1995b).

3. RESULTS

3.1. Duration time and size of pseudo-clones and *A. m. scutellata* workers

The mean duration time of the pseudo-clone sealed brood stage was 255 ± S.D. 9 h (n = 17) which is shorter than *A. m. scutellata* workers at 281 ± S.D. 9 h (n = 30). This is despite the pseudo-clones emerging 8% heavier ($\overline{X}$ = 0.097 ± 0.004 g, n = 23) than *A. m. scutellata* workers ($\overline{X}$ = 0.090 ± 0.004 g, n = 54), although they are being raised in cells of equal size in the same colony. Adult bees sampled from another 26 colonies also confirmed that the

Table I. Reproductive fate (%) of *V. destructor* invading brood cells from this (bold) and previous studies along with number of mature (unfertilised and fertilised) and fertilised females produced per invading mother mite. In this study only mites from cells sealed for 200 h or longer were used.

	Worker cells				Drone cells		
	Pseudo-clone n=87	***A. m. scutellata* n=118**	Africanised bees[1]	European bees[2]	***A. m. scutellata* n=98**	European bees[3]	*A. cerana*[4]
Mother dead	**15**	**6**	2.0	2	**6**	5	?
Fertilised female offspring	**30**	**51**	43	63	**59**	63	94–99
Unfertilised female offspring due to male death	**25**	**11**	19	12	**9**	10	1–2
Unfertilised female offspring due to other causes	**10**	**4**	13	4	**4**	5	0
Only male	**15**	**15**	11	9	**20**	14	0–2
No offspring	**5**	**13**	12	10	**2**	3	0–2
Mature females	**0.7**	**1.0**	0.9	1.0	**2.5**	2–2.2	4.5–4.6
Fertilised females	**0.4**	**0.9**	0.7	0.9	**2.2**	1.9–2.1	4.55

[1] Medina and Martin, 1999; [2] Recalculated from Martin 1994; [3] Martin, 1995b; [4] Boot et al., 1997.

pseudo-clones are consistently heavier ($\overline{X}$ = 0.097 g, n = 2096) than *A. m. scutellata* workers ($\overline{X}$ = 0.083 g, n = 7978). Measurements of the fore wing length again showed that pseudo-clones were 8% larger (9.2–9.3 mm) than *A. m. scutellata* workers (8.5–8.6 mm).

3.2. Reproduction of *V. destructor*

A total of 118 and 87 mite families were reconstructed from 1000 *A. m. scutellata* worker cells and 1700 cells containing the pseudo-clone, respectively. In addition, 98 mite families from 265 *A. m. scutellata* drone cells were reconstructed.

The reproductive ability of the mother mites invading brood cells in *A. m. scutellata* colonies is given in Table I. This shows that the number of mother mites which died within the cell, was low in cells containing *A. m. scutellata* workers and drones but high in the cells containing the pseudo-clone. The number of eggs laid by the surviving mothers was 4.5 ± 0.7 (n = 68) in cells containing *A. m. scutellata* workers compared to 3.9 ± 0.7 (n = 27) in those occupied by a pseudo-clone and increased to 4.9 ± 1.0 (n = 45) in *A. m. scutellata* drone cells. The average number of fertilised female offspring produced during one reproductive cycle per invading mother mite was 2.2 and 0.9 in cells containing *A. m. scutellata* drone and worker sealed brood respectively, which fell to 0.4 in cells containing the pseudo-clone. The main reason for the difference in the number of fertilised female offspring produced is the different levels of mother mite (Tab. I) and male mite offspring (Tab. II) mortality in each cell type, which is highest in the cells containing the pseudo-clone and lowest in the *A. m. scutellata* drone cells. In cells with the pseudo-clone most of the male mortality occurred during the protonymphal stage (Tab. III) and mother mites laying their first egg.

Table II. Percentages of *V. destructor* offspring mortality in this (bold) and previous studies along with the estimated survivorship of the five female offspring into mature (unfertilised and fertilised) or fertilised females. In this study only mites from cells sealed for 200 h or longer were used.

	Worker cells					Drone cells		
	Pseudo-clone	***A. m. scutellata***	Aficanised bees[1]	European bees[2]	European bees[3]	***A. m. scutellata***	European bees[4]	*A. cerana*[5]
Male	**48**	**28**	43	20	-	**16**	10	1–2
1st female	**24**	**4**	32	6	19	**6**	2	-
2nd female	**50**	**19**	57	62	51	**5**	7	-
3rd female	**83**	**85**	72	87	87	**6**	16	-
4th female	**100**	**100**	100	100	100	**15**	24	-
5th female	**100**	**100**	100	100	100	**33**	37	-
Estimated female survivorship	**1.43**	**1.92**	1.39	1.45	1.43	**4.35**	4.14	4.5–4.6
Estimated fertilised female survivorship	**0.74**	**1.4**	0.79	1.16	-	**3.65**	3.73	4.4–4.5

[1] Medina and Martin, 1999; [2] Martin, 1994; [3] Ifantidis et al., 1999; [4] Martin, 1995b; [5] Boot et al., 1997.

Table III. Developmental stage when *V. destructor* male mortality occurred given as percentages. Only cells which contained dead males and had been capped for > 150 h stage were analyzed.

	Worker cells				Drone cells	
	Pseudo-clone n=21	***A. m. scutellata* n=22**	Africanised bees[2] n=435	European bees[1] n=39	***A. m. scutellata* n=14**	European bees[3] n=242
Protonymph	**90**	**59**	33	46	**71**	71
Deutonymph	**10**	**23**	59	8	**0**	14
Adult	**0**	**18**	8	46	**29**	15

Calculated from the data collected during the following studies: [1] Martin, 1994; [2] Medina and Martin, 1999; [3] Martin, 1995b.

4. DISCUSSION

4.1. Comparison of *V. destructor* reproduction in *A. m. scutellata*, EHB and AHB

The reproductive ability of *V. destructor* in this study was compared with that from previous studies (Tab. I). The order in which the mites are able to reproduce successfully is: *A. cerana* drone >> *A. m. scutellata* drone = EHB drone >> *A. m. scutellata* worker = EHB worker > AHB worker >> pseudo-clone. Therefore, the Korea haplotype of *V. destructor* is able to reproduce within *A. m. scutellata* colonies at levels similar to that found in EHB (Tab. I) and the tolerance shown by AHB towards the mites (Medina and Martin, 1999) appears to be lacking in *A. m. scutellata*. There are several reasons why this appears to be the case. Firstly mite populations in AHB fluctuate during the year but their numbers rarely exceed several thousand (Medina and Martin, 1999; Vandame et al., 1999) while mite populations in both *A. m. scutellata* and *A. m. capensis* colonies have been reported to regularly exceed 10 000 (Allsopp, 1998; Allsopp et al., 1999; Allsopp, 2000). Secondly the number of fertilised female offspring produced in AHB is lower (0.7) than in *A. m. scutellata* (0.9) and EHB colonies (0.9), despite the

mite haplotype being the same (Korea) in all the studies.

The data presented in Table I encompass many factors which are acting on the mites' ability to produce fertilised mature females. Therefore, we compared levels of offspring mortality from this study with that from previous ones (Tab. II), particularly since increased levels of mite offspring mortality found in AHB is thought to contribute in part to its tolerance (Medina and Martin, 1999). The resulting reproductive success based solely on offspring mortality is in the following order: *A. cerana* drone >> EHB drone = *A. m. scutellata* drone >> *A. m. scutellata* worker > EHB worker > AHB worker > pseudo-clone. This order is very similar to that found when mite reproductive abilities are compared (Tab. I) and indicates the importance of offspring mortality in the ability of the mite to produce fertilised females, rather than other factors such as levels of mite non-reproduction or duration of the sealed brood stage which is similar for *A. m. scutellata* (281 h), AHB (278 h, Vandame, 1999) and EHB (279 h, Vandame, 1999).

4.2. Reproduction of *V. destructor* in the pseudo-clone and *A. m. capensis*

In the pseudo-clone very few (0.4) fertilised female mites are produced. This would result in very slow, if any, growth of the mite population. However, the host *A. m. scutellata* colony would collapse due the presence of the pseudo-clone long before any effect of mites was seen (Martin et al., 2002). This low reproductive success is due to the high levels of mother and male protonymph mite mortality and not the

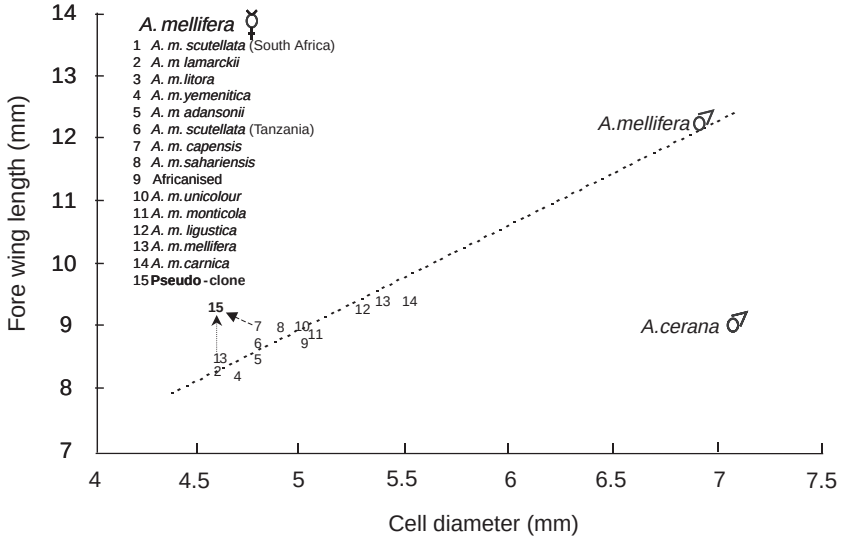

Figure 1. Relationship between the bee fore wing length and the diameter of the cell in which it was reared, in workers from 15 different races of *Apis mellifera*. Data was compiled from Ruttner (1988), Hepburn and Radloft (1998), Spivak et al. (1988), Buco et al. (1987) and this study. ♀ = worker, ♂ = male. The dashed line is the regression ($r^2 = 0.97$) of cell diameter on bee size across the 14 races of *A. mellifera* worker cells. The two dashed arrows indicate the relative position of the pseudo-clone to *A. m. capensis* and *A. m. scutellata* workers. Note that in *A. m. capensis* the space restrictions are not expected to occur since the relationship between the cell and bee size are similar to other races of *A. mellifera*. The position of *A. cerana* drones is given as a comparison.

number of female offspring produced by the surviving mothers which is comparable to that found in other races of honey bees (Tab. II). Although the pseudo-clone has the shortest sealed brood development time (255 h) of any race of *A. mellifera* studied, it does not prevent the production of adult female offspring, which was confirmed by the presence of up to two new female mites in some cells. Since the sealed brood development time of normal *A. m. capensis* workers i.e. reared by their own workers, is longer (264 h, Moritz and Jordan, 1992; 262 h, Beekman et al., 2000) than when reared by other workers, as in this study, it is therefore predicted that the relatively short capping time of will only slow down and not prevent mite populations from increasing in *A. m. capensis* colonies where the increased mite mortality due to limited space in the cell (see below) is not expected to occur (Fig. 1). This may help explain the dramatic increase in mite numbers (10 000+) in colonies in the Western Cape region of South Africa (Allsopp, 1998, 1999), an area mainly occupied by *A. m. capensis*.

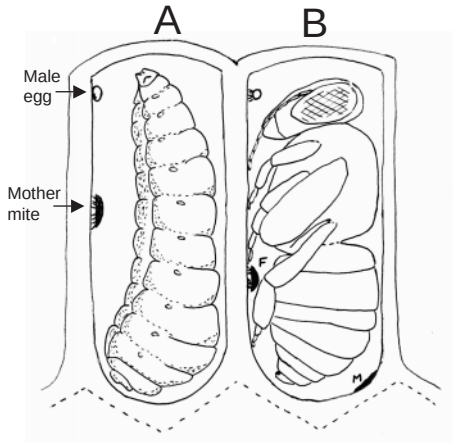

Figure 2. Changes in the available space before (A) and after (B) the developing honey bee pupates along with the position where the first (male) egg is laid, feeding site (F) and moulting site (M) adapted from Donzé and Guerin, 1997.

4.3. Effect of available space in the cell on mite reproduction

For ectoparasities which reproduce in enclosed cavities the amount of space can be an important constraint on their ability to reproduce successfully. Therefore, species like *Dichrocheles phalaenodectes* which breeds within the tympanic organ of moths (Treat, 1975) and *Varroa* sp., display traits such as lack of cannibalism, nest sanitation and space partitioning (Donzé and Guerin, 1997). One consequence of space partitioning in *Varroa* sp. is that the first (male) egg is laid near the cell cap. This increases the survival probability of the male mite since it is the only place in the cell not affected by the bee's molt (Fig. 2). However, the male mite must now pass the constriction caused by the bee's appendages to reach the feeding site which is established by the mother mite on the bee's abdomen (Fig. 2). Since only one male is produced per batch of eggs, its death will result in all the female offspring being unmated and so unable to produce offspring (Akimov and Yastrebtsov, 1984; Donzé et al., 1996; Martin et al., 1997; Harris and Harbo, 1999).

A survey of the literature revealed a close correlation ($r^2 = 0.97$) between fore wing length and brood cell diameter across 14 races of *A. mellifera* (Fig. 1), also fore wing length is closely correlated to bee head width ($r^2 = 0.97$ worker & drone) in *Apis* (calculated from data in Ruttner, 1988). Therefore, since the pseudo-clone which is among one of the larger *A. mellifera* races, is being reared in some of the smallest cells found in *A. mellifera*. (Fig. 1), there will be significantly less space between the bee pupae and cell wall in cells occupied by pseudo-clones than *A. m. scutellata* workers which may impede the movement of the mites. This may explain our frequent observations that dead male protonymphs

and some dead mother mites appeared to be trapped in the upper part of cells containing the pseudo-clone. This is illustrated by the high level of male protonymph mortality found in cells occupied by the pseudo-clone (48 × 0.90 = 43%) compared to those occupied by *A. m. scutellata* workers (28 × 0.59 = 16.5%). While in *A. cerana* drone cells, ancestral host of Varroidae, only 1–2% of the male offspring die (Tab. II). Interestedly this species builds the widest drone cells (7.1–7.2 mm) of any *Apis* sp. but rears the smallest *Apis* drones based on head width.

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 (Fig. 1).

ACKNOWLEDGMENTS

We wish to thank M. Beekman of Sydney University for her assistance in the field. We are especially grateful to R. Crewe and T. Wossler for providing laboratory facilities and bee colonies, at Pretoria University, and NERC for some financial support to SJM.

Résumé – Reproduction de *Varroa destructor* chez les abeilles d'Afrique du Sud: le volume de la cellule influence-t-il la survie de l'acarien mâle ?. On a étudié la capacité de *Varroa destructor* Anderson & Trueman à se reproduire sur l'abeille *Apis mellifera scutellata* en Afrique du Sud, pour deux raisons: (i) on soupçonne les abeilles africaines de présenter une tolérance naturelle vis-à-vis de l'acarien *V. destructor* semblable à celle des abeilles africanisées ; (ii) la présence d'un parasite intra-spécifique unique, le « pseudo-clone » représenté par l'ouvrière d'*A. m. capensis* qui, bien qu'élevée dans les cellules d'ouvrières d'*A. m. scutellata*, est 8 % plus grosse que les ouvrières de celle-ci. Cela permet d'étudier l'influence du volume à l'intérieur de la cellule et de la durée réduite de développement, deux facteurs majeurs limitant la reproduction de l'acarien.
Courant octobre 2000 dans la région de Prétoria, Afrique du Sud, 118 et 87 familles de *V. destructor* ont été respectivement reconstruites à partir de 1 000 cellules d'ouvrières d'*A. m. scutellata* et de 1 700 cellules renfermant le pseudo-clone. En outre 98 familles ont été reconstruites à partir de 265 cellules de mâles d'*A. m. scutellata*.
Dans les cellules d'*A. m. scutellata, V. destructor* a produit 0,9 femelles fécondées par mère d'acarien envahisseur, ce qui est semblable au chiffre trouvé chez les abeilles européennes sensibles (0,9) et supérieur à celui trouvé chez les abeilles africanisées tolérantes (0,7) ou chez les pseudo-clones élevés dans les cellules d'ouvrières d'*A. m. scutellata* (Tab. I). Les niveaux de mortalité de l'acarien variables selon le type de cellule (Tabs. I et II), plus forts dans les cellules renfermant le pseudo-clone et plus faibles dans les cellules de mâles d'*A. m. scutellata*, expliquent la différence quantitative dans la descendance femelle fécondée produite. Bien que la durée de développement du pseudo-clone (255 h) soit plus courte que celle de n'importe quelle autre race d'*A. mellifera*, il reste suffisamment de temps pour qu'au moins deux femelles fécondées d'acarien émergent, ce qui fut de fait observé au cours de l'étude. En conséquence on prédit que les populations d'acariens chez les deux races d'abeilles d'Afrique du Sud vont s'accroître jusqu'à la mort de la colonie, schéma rencontré en Europe et aux États-Unis.
L'influence du volume, ou son absence, entre le la cloison de la cellule et la nymphe d'abeille en développement (Fig. 2), sur la mortalité de la descendance mâle a été prouvée en comparant les taux de mortalité entre les cellules de couvain qui

renfermaient soit des ouvrières d'*A. m. scutellata* (28 %), soit des ouvrières d'*A. m. capensis* plus grosses (48 %) (Fig. 3). Chez *A. cerana*, hôte originel de l'acarien, seuls 1 à 2 % de la descendance mâle meurent dans les cellules de mâles qui ont, parmi les divers types de cellules d'*Apis*, le plus grand volume latéral libre (Fig. 1).

Varroa destructor* / reproduction / taille de la cellule / mortalité de l'acarien / *Apis mellifera scutellata

Zusammenfassung – Reproduktion von *Varroa destructor* in Südafrikanischen Honigbienen: gibt es einen Einfluss des Zellraums auf ein Überleben der Milbenmännchen. Die Reproduktionsfähigkeit von *Varroa destructor* Anderson und Trueman 2000 in Völkern von *Apis mellifera scutellata* wurde in Südafrika untersucht. Diese Frage ist deshalb interessant, weil bei den afrikanischen eine ähnliche natürliche Toleranz gegen *V. destructor* vermutet wird wie bei afrikanisierten Bienen. Außerdem kommt dort ein einzigartiger intraspezifischer Parasit der Honigbiene vor: Ein „Pseudo-Klon" von Arbeiterinnen der *A. m. capensis.* Diese sind trotz ihrer Aufzucht in Arbeiterinnenzellen von *A. m. scutellata* 8 % größer als *A. m. scutellata* Arbeiterinnen. Damit bot sich die Möglichkeit zwei wichtige begrenzende Faktoren für die Vermehrung der Milben zu untersuchen, den Effekt von Zwischenräumen innerhalb der Zelle und den von kurzer Verdeckelungszeit.
Im Oktober 2000 wurden in der Pretoria Region von Südafrika insgesamt 118 und 87 Milbenfamilien aus 1000 *A. m. scutellata* Zellen mit Arbeiterinnen derselben Rasse und aus 1700 Zellen mit Pseudo-Klon Arbeiterinnen rekonstruiert. Zusätzlich wurden 98 Milbenfamilien aus 265 *A. m. scutellata* Drohnenzellen rekonstruiert.
In *A. m. scutellata* Zellen mit normalen Arbeiterinnen wurden 0,9 begattete Weibchen pro Muttermilbe erzeugt. Das ist ein ähnlicher Wert wie bei den für Milben empfindlichen europäischen Bienen (0,9) und größer als bei den milbentoleranten afrikanisierten Honigbienen (0,7) oder den Pseudo-Klonen, die in *A. m. scutellata* Arbeiterinnenzellen aufgezogen wurden (0,4) (Tab. I). Der Hauptgrund für die Unterschiede in der Anzahl der begatteten Töchter ist die unterschiedliche Höhe in der Milbensterblichkeit in jedem Zelltyp (Tab. I und II). Die Sterblichkeit ist am höchsten in den Zellen mit Pseudo-Klonen und am niedrigsten in den Drohnenzellen von *A. m. scutellata*. Obwohl sich die Verdeckelungszeit der Brut in den Pseudo-Klonen (255 h) als die kürzeste von allen *A. mellifera* Rassen erwies, war immer noch genug Zeit für die Reifung von mindestens 2 begatteten Milbenweibchen, ein Ergebnis, das sich während dieser Untersuchung herausstellte. Aus diesem Grund sagen wir vorher, dass die Milbenpopulation in beiden südafrikanischen Rassen der Honigbienen nach dem gleichen Muster wie in Europa und den USA ansteigen wird, bis die Völker sterben.
Der Effekt der Zwischenräume zwischen Zellwand und der Bienenpuppe (Abb. 2), bzw. des Fehlens dieses Zwischenraums auf die Sterblichkeit der männlichen Nachkommen wurde aufgezeigt. Der Vergleich der Sterblichkeit der Männchen in den Brutzellen ergab, dass bei *A. m. scutellata* Arbeiterinnen 28 %, bei den größeren *A. m. capensis* Arbeiterinnen 48 % starben (Tab. III). In *A. cerana,* dem ursprünglichen Wirt von *Varroa destructor,* sterben nur 1–2 % der männlichen Nachkommen in den Drohnenzellen, die den größten seitlichen Zwischenraum zwischen Puppen und Zellwand innerhalb aller *Apis* Zelltypen aufweisen (Abb. 1).

Varroa destructor* / Reproduktion / Zellgröße / Milbensterblichkeit / *Apis mellifera scutellata

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