Apidologie 31 (2000) 689–699

Original article

Changes in reproduction of *Varroa destructor* after honey bee queens were exchanged between resistant and susceptible colonies

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(Received 6 February 2000; revised 29 June 2000; accepted 27 July 2000)

Abstract – This study examines changes in reproduction and mortality of *Varroa destructor* when queens from stocks of honey bees (*Apis mellifera* L.) that differ in susceptibility to the mites were exchanged between colonies. Queens were selected for suppression of mite reproduction (SMRD). In two experiments uniform colonies of bees were established; half the colonies were given queens selected for SMRD, and half were given unselected queens. Queens were exchanged after 7 (experiment 1) and 13 weeks (experiment 2). The percentage of mites that had no progeny was determined for each colony at 5 times (2 before and 3 after exchanging queens). Mites that had no progeny included live and dead mites. Results showed (1) that reproduction of mites is suppressed by adding a queen selected for SMRD, and (2) that a mite population recovers its reproduction when a SMRD queen is replaced by an unselected queen. Selection of the SMRD trait can be reduced to counting only live mites that laid no eggs and dead mites.

***Apis mellifera* / *Varroa destructor* / resistance to pests / suppression of mite reproduction (SMRD)**

1. INTRODUCTION

Long-term solutions to the parasitism of honey bees by the mite, *Varroa destructor* Anderson and Trueman [1] (formerly called *Varroa jacobsoni* Oudemans) are sought because of a desire to avoid using pesticides in a bee colony and because of acaricide resistance by the mite [14, 18–21, 26]. One solution is the selective breeding of honey bees to produce bees that suppress mite reproduction [8, 11, 12].

Although an immediate suppression of mite reproduction would be desirable, the trait that we have selected has a delayed effect (suppression of mite reproduction delayed, SMRD). This is a heritable

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character in bees [9], and we have enhanced its expression to high levels in the last few years [10, 13]. The reproduction of mites is unchanged in the first brood cycle after installing a queen selected for the SMRD trait, but after 5–6 weeks the mean number of progeny produced by mites in worker brood is reduced [10, 13]. The causes of this delayed effect on mite reproduction are unclear.

Reduced numbers of progeny from mites may result from factors associated with immature bees [4, 6, 24, 25], with adult bees [3, 5, 6, 25], or an interaction between the adults and immatures. Rozenkrantz and Bartalszky [22] found that fewer mites lay eggs in colonies of bees after a long broodless period. There is also evidence that the absence of egg production is associated with mites that have insufficient spermatozoa in the seminal receptacles [13].

This study examines the reproduction of mites in colonies of bees where queens with the SMRD trait were exchanged with queens without the SMRD trait. By examining mite reproduction at various points before and after exchange of the two types of queens, we measured changes in mite reproduction and the time-course associated with these changes. Mite reproduction in worker brood was suppressed in colonies of bees headed by queens selected for the SMRD trait, and mite reproduction increased when the SMRD queens were removed.

2. MATERIALS AND METHODS

These experiments were field tests that examined mite reproduction in colonies of bees. Two general groups of mites were identified, mites that had produced progeny and those that did not lay eggs. The first group included normally reproductive mites and mites that produced nonviable offspring (mites that only produced a son, those that produced progeny that died, and those that had progeny too young to mature before the host bee emerged from the brood cell). The second group included dead and live mites that had not laid eggs. The counting and analysis of this second group of mites was the focus of this paper because absolute non-reproduction of mites is the main characteristic of SMRD bees [13].

Colonies were formed by subdividing a large mixture of mite-infested bees (ca. 25 kg of bees) into equal test populations as per [7]. Bees and mites were collected from 15–20 colonies of bees. Each test colony began with a test queen and two 500 g packages of bees that were scooped from a large, mixed population.

For installation, the 2 cages of bees, a caged queen and combs with only worker-sized cells were placed into a standard Langstroth deep hive. No drone combs were allowed in the colonies and no drones were produced during the test period. The worker bees were immediately released from their cages, but the hive entrances remained closed (screen over entrances). Entrance screens were removed after dark on the following day (after 30 h). Queens were released after an additional 24 h.

We measured mite reproduction in mite-infested cells by examining capped worker brood cells from each colony on each of the 5 inspection days. We searched for mites in cells of worker brood that were 210 ± 10 h postcapping (bee pupae with tan coloration). Only foundress mites from singly infested cells with this age of host pupae were evaluated because the mites produce all of their eggs by this point in the honey bee's development cycle [15]. Cells with multiple foundress mites were excluded from the analysis because the average progeny per mite is reduced in multiply infested cells [16]. To determine the number of foundress mites in a brood cell, the number of shed female skins was subtracted from the number of adult female mites in the cell.

In both experiments, 30 mites per colony were evaluated during the first 1–2 measurements, but it became more difficult to

find mites in brood cells near the end of a test. During the middle to late sampling dates, we evaluated as many mites as could be found in a total of 500 brood cells (range 10–25 mites).

When adult foundress mites died in a cell, they were either free in the cell next to the pupa or sandwiched between the cell wall and the cocoon, 'entrapped by the cocoon' [13]. Because an entrapped mite is not removed by nest-cleaning bees, the overall frequency of this phenomenon will increase on a brood comb over time. Entrapped mites are covered by the cocoons of subsequent bees that are reared in the brood cell. Careful separation of the layers of cocoons away from the entrapped mite was necessary to decide if the mite was entrapped by the bee that was in the cell or if the entrapment occurred in an earlier cycle. Entrapped mites that lay beneath multiple cocoons were not counted. None of the dead foundress mites in this study produced progeny before dying in the cell.

2.1. Experiment 1: Exchange of queens after 32 days of egg laying

Twenty test colonies were formed on 30 June 1998. Each colony was formed using a caged queen, 1 kg of bees, 610 mites and no brood. The queens were released 2 d later (day 0). Ten colonies began the experiment with queens having the SMRD trait, and 10 began with a queens from colonies that did not suppress mite reproduction (sus).

About midway in the experiment we established a 16-day period of no brood production by caging all queens on day 32. Queens remained in their respective colonies until day 45 when each queen with the SMRD trait was exchanged with queens that lacked the trait (sus queen). All queens were released on day 48. Therefore, all mites had at least 4 days when there was no brood available to invade, but some had as long as 16 days. This procedure provided a broodless period at the time of queen exchange that was comparable to the broodless period that all colonies experienced at the beginning of the experiment. This timing limited the mites to a maximum of 3 reproductive cycles on brood from the first queen. The percentage of mites that had no progeny were measured twice before exchanging queens (on days 19 and 47) and three times after exchanging queens (on days 66, 82 and 103).

2.2. Experiment 2: Exchange of queens after 105 days of egg laying

Ten test colonies were formed on 12 May 1998. Each colony began with 0.9 kg of bees, 614 mites and no brood. The queens were released two days later (day 0). Five colonies began with a SMRD queen, and 5 began with a susceptible queen. SMRD and susceptible queens were caged and exchanged on day 105, and all queens were released from their cages 2 d later. This interrupted egg-laying for 2 d, which subsequently produced a 2 d period (days 112–114) in which there was no brood available for mites to invade. The percentage of mites that had no progeny was measured twice before exchanging queens (on days 55 and 86) and three times after exchanging queens (on days 124, 140 and 167).

Statistical analyses: Both experiments consisted of two treatments determined by the order in which the two types of queens (SMRD or susceptible) were given to test colonies. The first treatment was a SMRD queen followed by a susceptible queen (designated as 'SMRD–sus'). The second treatment was a susceptible queen followed by a SMRD queen (designated as 'sus–SMRD'). The variable analyzed was the percentage of mites that had not produced progeny (which included dead mites and live mites that did not lay eggs). A repeated measures analysis of variance was used to test for statistical significance from three sources of

variation: (1) the effects of the two treatments, (2) changes related to time or sampling date, and (3) the interaction of treatment and time. Because the number of mites examined was not equal in each colony at each of the 5 sampling dates, the analysis was weighted by the number of mites (range 10–30). To keep the repeated measures analysis strictly conservative, the unstructured variance-covariance matrix option was used in the ANOVA (Proc Mixed, [23]).

The significance of the treatment × time interaction is more informative than the treatment term in the ANOVA. Since this study involved placing two types of queens into each test colony at different times, all mite populations had experienced brood and bees from both types of queens. As a result, the absence of a treatment effect was not surprising or important. However, the significant interaction term reflects that a variable changes differently between treatments through time. The variable measured is high in one treatment group while low in the other. This is expected if mite reproduction is affected by the genetics of the bees in the colony, which was manipulated by switching the type of queen bee in each test colony at a set time.

3. RESULTS

The percentage of foundress mites that had no progeny was the main variable analyzed. In both experiments, only time and the treatment × time interaction were significant sources of variation in the repeated measures ANOVA (Tab. I). The significant treatment × time term shows that the percentage of mites that had no progeny was different between the two treatment groups through time. Generally, the time-course of the percentage of mites that had no progeny in the 'SMRD then Sus' group was opposite the plot for the 'Sus then SMRD' group (the two plots appear to be mirror images in Fig. 1). Initially both treatment groups had the same low percentage of mites that had no progeny on day 19 in experiment 1 (Fig. 1 and Tab. II). This variable was initially low (ca. 15%) in both treatments because both groups were established with bees and mites from colonies that were not selected for the SMRD trait. The lack of any difference between the two treatments suggests that the original mite population was not affected by the genetics of either the capped worker brood (which had been in the colony for 8–12 d) or the newly-emerged worker bees (which had been in the colony

Table I. Summary of the repeated measures analysis of variance for the percentage of mites that had no progeny in experiments 1 and 2 (see text). In both experiments the variable had a significant treatment × time interaction, which suggests that the two treatment groups behaved differently through time. In general, non egg-laying by mites followed the introduction of a queen selected for the SMRD trait (Fig. 1 and Tabs. II and III). These results suggest a strong genetic effect of the host bees on mite reproduction.

Experiment	Source	NDF	DDF	F statistic	Pr > F
1	Treatment	1	18	1.55	0.2296
	Time	4	18	4.71	0.0089
	Treatment × time	4	18	5.99	0.0030
2	Treatment	1	8	3.96	0.0819
	Time	4	8	5.05	0.0250
	Treatment × time	4	8	8.51	0.0056

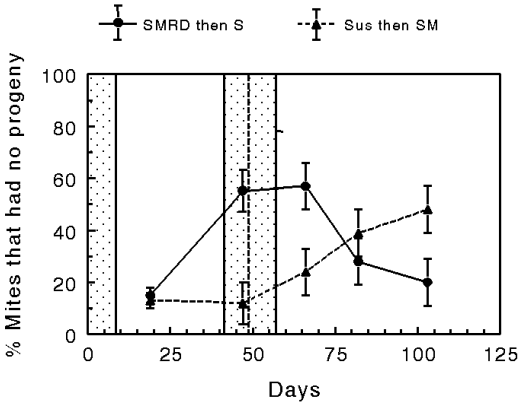

Figure 1. Changes in the percentage of mites that had no progeny (mean ± SE) for experiment 1 (see Materials and Methods for description). The two shaded areas represent periods when there was no brood available for mite invasion. The first period was caused by forming colonies from packages; the second was caused by caging queens for 16 days prior to the exchange of queens (queens were caged on day 32, exchanged, and released on day 48). This second broodless period forced mites into a phoretic period on adult bees that ranged from 4–16 days. The second queen began laying on day 48, which is indicated by the vertical dotted line. The categories of mites that had no progeny are listed in Table II.

Table II. Changes in the percentages (mean ± SE) of 3 categories of mites that had no progeny throughout experiment 1 (see text and Fig. 1). Each colony was formed with package bees, and the 1st queen began laying eggs on day 0. Ten colonies were started with queens that had been selected for resistance to *V. destructor* mites because of the SMRD trait, and 10 colonies were started with an unselected queen (sus) that produced bees that did not have the SMRD trait. The second queen began laying in the colony on day 48.

Treatment (1st queen–2nd queen)	Days	Mites that had no progeny[a] (%)			Total mites[d]
		Live mites that did not lay eggs	Mites that were dead next to pupa[b]	Mites that were entrapped by cocoon[c]	
SMRD–sus	19	11 ± 2	1 ± 1	3 ± 1	300
	47	38 ± 5	0 ± 1	16 ± 4	236
	66	35 ± 7	2 ± 1	20 ± 5	267
	82	18 ± 9	1 ± 1	9 ± 4	135
	103	14 ± 6	2 ± 3	4 ± 4	190
sus–SMRD	19	9 ± 2	1 ± 1	4 ± 1	300
	47	10 ± 5	2 ± 1	2 ± 4	296
	66	15 ± 7	2 ± 1	7 ± 5	302
	82	32 ± 9	2 ± 1	5 ± 4	230
	103	27 ± 6	7 ± 3	14 ± 4	194

[a] Mites were examined from bee pupae that were in worker brood cells at 190–220 h postcapping. Only singly infested cells were examined. Mites that had no progeny included (1) live mites that laid no eggs, and (2) dead mites that laid no eggs.

[b] These dead mites were found within the bee's cocoon next to pupa, suggesting that they died after the larva had spun its cocoon.

[c] Entrapped mites were found between the wax wall of the cell and the silk cocoon that had been spun by the host bee larva prior to pupation. Because these dead mites are not removed from the cells by nest cleaning bees after the host bee has emerged, the numbers of entrapped mites in a comb will be build up over time; therefore, only mites beneath the uppermost layer of silk cocoon were counted.

[d] The total number of mites sampled from the 10 colonies in each treatment group. We examined 30 singly infested cells per colony. When infestations were low, we examined 500 cells and used fewer than 30 observations.

for 0–7 days) produced by the first test queens.

The treatment groups diverged by day 47 in experiment 1 when the percentage of mites that had no progeny significantly increased to ca. 50% for the 'SMRD then Sus' treatment group (Fig. 1 and Tab. II). The two treatments remained divergent up to 20 days after the queens had been exchanged (the second queen began laying in each colony on day 48) (Fig. 1 and Tab. II). The two plots cross during the fourth measurement, and diverge in opposite directions by the last measurement, indicating that the reproductive potential of mite populations was being affected by the second test queen during the interval from 66–103 days.

The treatment groups were already different by day 55 when we made the initial measurements for experiment 2 (Tab. III). In this experiment, the first queen of each treatment was allowed to lay eggs through day 105, which is more than three times the period that had been allowed in experiment 1. As a consequence, the percentage of mites that had no progeny was very high for the SMRD–sus group during the entire test (Tab. III). In experiment 1, this percentage for the SMRD–sus group began to decrease 34 d after inserting a susceptible queen (day 82) (Fig. 1 and Tab. II); however, in experiment 2, percent mites that had no progeny remained high 33 d after inserting the susceptible queen (day 140) (Tab. III).

The percentage of mites that had no progeny in the sus–SMRD group of experiment 2 followed a pattern similar to the same group in experiment 1 (compare the sus–SMRD group between the figure and Tab. III). The trend was that there were fewer mites that had no progeny when the susceptible queen was present and significantly higher percentages of them within 30 d of installing the SMRD queen.

In either test, when the percentage of mites that had no progeny was high, about 32–58% of the mites were live mites that did not lay eggs and 7–16% were dead mites that were entrapped by the cocoon (Tabs. II and III).

Table III. Changes in overall percentage of mites that had no progeny and in the 3 categories of mites that had no progeny throughout experiment 2 (mean ± SE) (see text). Each colony was formed with package bees, and the 1st queen began laying eggs on day 0. Five colonies were started with queens that had been selected for the SMRD trait, and 5 colonies were started with an unselected queen (sus) that produced bees known not having the SMRD trait. The second queen began laying in the colony on day 107. See Table II for a description of column headings.

Treatment (1st queen–2nd queen)	Days	Mites that had no progeny (%)	Mites that had no progeny (%)			Total mites
			Live mites that did not lay eggs	Mites that were dead next to pupa	Mites that were entrapped by cocoon	
SMRD–sus	55	55 ± 10	50 ± 9	2 ± 1	4 ± 1	139
	86	75 ± 7	65 ± 7	3 ± 1	8 ± 2	114
	124	66 ± 13	36 ± 7	1 ± 1	29 ± 8	74
	140	85 ± 27	57 ± 27	3 ± 3	25 ± 7	49
	167	56 ± 11	35 ± 8	6 ± 3	16 ± 9	46
sus–SMRD	55	14 ± 10	14 ± 9	0 ± 1	0 ± 1	147
	86	17 ± 7	16 ± 7	1 ± 1	1 ± 2	160
	124	40 ± 13	23 ± 7	3 ± 1	14 ± 8	146
	140	83 ± 27	64 ± 27	6 ± 3	12 ± 7	68
	167	67 ± 12	47 ± 9	1 ± 3	19 ± 9	30

4. DISCUSSION

The genotype of the host bees had a strong effect on the percentage of foundress mites that had no progeny. Replacing a susceptible queen with one that had been bred for suppression of mite reproduction (SMRD) led to significant and predictable reductions in this variable. About 5–6 weeks were necessary before the percentage of mites that had no progeny increased to > 50% in colonies of bees having a SMRD queen. Changes in the opposite direction, from > 50% to lower values (ca. 20%), also required a few weeks after susceptible queens replaced SMRD queens. This delayed effect is similar to other tests [2, 6, 11, 17].

Explanations of the delayed effect on mite reproduction that occurs when genetically different queens are exchanged should consider two factors: (1) which mites are affected, the original mite population that began a test or mites that were raised in colonies after exchanging queens, and (2) which host bees, the adults or the immatures, cause the diminished reproduction. At least two explanations can be offered, and these ideas can explain changes in mite reproduction for both directions in the reciprocal exchange of queens in this study.

In one scenario, differences in mite reproduction are produced by changes in the genotype of the adult bees. Several weeks are needed to build up a critical mass of adult bees that affect enough mites to produce a measurable difference between treatment groups. The treatment groups for experiment 1 were identical on day 19, which suggests that the different genotypes of the immature bees produced by the two types of queens did not have a direct effect on mite reproduction (Fig. 1). Also, the adult bee populations were identical because both groups began with the same heterogeneous mix of adult bees that did not have the SMRD trait, and there were no adult bees produced from the test queens until day 20–21. Differences in mite reproduction were apparent on day 47, and these differences could be related to the different genotypes of adult bees produced by the two types of queens. The differences could be related to the genotypes of nurse bees because the nursing of that brood would have been on days 34–39, when most nurse bees were young bees that had been produced by the resident queens. Alternatively, differences in mite reproduction might be related to the phoretic experience of the mites on other adult bees produced by the resident queens.

The second interpretation is that changes in mite reproduction reflect changes in the demographics of the mite population. The mite population that existed in a colony prior to an exchange of queens will retain its characteristic level of reproduction, while the new mites raised within the colony will have a reproductive potential determined by the genotype of bees (adults and/or immatures) from the new queen. Changes in the composition of the mite population might explain changes in the percentage of mites that had no progeny because the reproductive ability of individual mites seems fixed. Martin et al. [16] found mites that reproduce normally in one cycle tend to reproduce normally in subsequent cycles, while mites with abnormal reproduction tend to remain abnormal. In this scenario, as the original mites are lost through mortality, they are replaced by new mites having a different reproductive potential. Hence, the change in percentage of mites that had no progeny reflects a change in demographics and not a change in the reproductive potential of individual mites.

Although the current experiments cannot exclude either of the two explanations, we favor the second explanation because the diminished mite reproduction in the 'SMRD then Sus' group was slower to recover if the SMRD queen remained in the colony for a longer period of time. In experiment 2, the percentage of mites that had no

progeny remained high in the 'SMRD then Sus' treatment group up to 60 days after the second queen had been installed, which was much longer than the time needed (34 d) for the same treatment group in experiment 1 (compare Fig. 1 and Tab. III). If diminished mite reproduction was caused by the genotype of adult bees from the SMRD queen, an increased reproductive potential of mites would have been expected sooner in experiment 2 as adult bees from susceptible queen became a larger proportion of the entire bee population.

However, if individual mites exposed to brood or adults bees having the SMRD trait are permanently affected, a change in the percentage of mites that had no progeny would not be apparent until new mites were raised on the brood and/or bees from the queens that did not have the SMRD trait. Since up to 75% of all mites could not lay eggs just prior to the exchange of queens (Tab. III), the increased reproductive potential of mites raised on the susceptible queen would not be apparent until after a much longer period of time when compared to experiment 1. In other words, the demographics of the mite population in the 'SMRD then Sus' group were slower to change in experiment 2 (versus experiment 1) because fewer mites could produced daughters immediately after the exchange of queens.

Mites affected by the SMRD trait are characterized by an increase in the numbers of live mites that did not lay eggs and mites that died in the cell (entrapped by the cocoon). Normally only about 10–15% of the live foundress mites do not lay eggs [13, 22] and about 1–2% of the foundress mites are found dead in an infested cell [15]. When SMRD queens are present, up to 65% of the mites were live mites that had not laid eggs. We believe this reflects a poor mating event in the brood cell because we found greatly reduced sperm counts for live mites that did not lay eggs from another study using the same type of bees [13]. Because the disrupted mating event occurs in the brood cell, it seems likely that the immature bees are the likely source of the inhibition of mite reproduction. However, we cannot definitively exclude the idea that the genetics of the adult bee population affected mite reproduction in the brood cell.

We know that the abnormally high level of mortality of mites in colonies with the SMRD trait occurs early (before the bee larva spins its cocoon) because dead mites are found between the cell wall and the cocoon. These mites had entered the cells, and they were either unfit or something in the cell was killing them. Since this mortality level does not occur in these colonies during the first brood cycle, it appears that dead mites are the result of unfit mites entering cells, a situation parallel to the entry of live mites that do not reproduce. Perhaps the mites that were found dead and those reported to lay no eggs are unfit in a similar way. The two characteristics may be related. Those that die may simply be older, unlucky, or slightly less fit than those that survive but lay no eggs.

These findings suggest that selecting for the SMRD trait may simply involve counting entrapped mites and live mites that produce no eggs, thus avoiding the time-consuming analysis of the number, age, and sex of the mite progeny from all singly-infested brood cells.

ACKNOWLEDGMENTS

Daniel Winfrey assisted with the field and laboratory work. Deborah Boykin (USDA-ARS, Stoneville, MS) designed the statistical analyses. This research was supported in part by a grant from the Michigan Department of Agriculture and was conducted in cooperation with the Louisiana Agricultural Experiment Station.

Résumé – Modification de la reproduction de *Varroa destructor* après échange de reines d'abeilles entre colonies résistantes et sensibles. Cette étude examine les modifications de la reproduction et de la mortalité de l'acarien *V. destructor* lorsque

des reines de lignées d'abeilles (*Apis mellifera* L.) ayant une susceptibilité différente aux acariens sont échangées entre colonies. Les reines ont été sélectionnées pour la suppression de la reproduction de l'acarien (SMRD), caractère héréditaire qui augmente le pourcentage d'acariens ne pondant pas d'œufs.

Ces expériences ont été menées en champ. Les colonies ont été constituées en subdivisant un grand mélange d'abeille infestées (environ 25 kg), prélevées dans 15–20 colonies, en populations tests de même taille, comprenant chacune une reine test et deux paquets d'abeilles de 500. On n'a laissé aucun couvain de mâle durant tout le test.

Au début de chaque test la moitié des colonies ont reçu une reine sélectionnée pour le caractère SMRD et l'autre moitié , une reine non sélectionnée. Les reines ont été échangées sept semaines (expérience 1) et 13 semaines (expérience 2) plus tard. On a mesuré la reproduction des acariens dans des cellules mono-infestées en examinant les cellules de couvain operculé 210 ± 10 h après l'operculation. Les cellules possédant de multiples fondatrices d'acariens ont été exclues de l'étude. Trente acariens par colonie ou autant d'acariens possibles trouvés dans 500 cellules ont été examinés à chaque date.

On a déterminé une variable, le pourcentage d'acariens sans descendance, pour chaque colonies à cinq périodes différentes (deux avant et trois après l'échange de reines). Étaient comptés les acariens vivants et les acariens morts n'ayant pas pondu. Lorsque des fondatrices d'acariens mouraient dans une cellule, elles étaient soit libres dans la cellule à côté de la nymphe, soit prises en sandwich entre la paroi de la cellule et le cocon (" piégées par le cocon "). Parce qu'un acarien piégé n'est pas éliminé par les abeilles nettoyeuses, la fréquence totale de ce phénomène sur un rayon augmente avec le temps. Les acariens piégés sont recouverts par les cocons des abeilles suivantes élevées dans la cellule ; c'est pourquoi les acariens situés sous de multiples cocons n'ont pas été comptés.

Les résultats montrent que (i) la reproduction des acariens peut être supprimée en ajoutant une reine sélectionnée pour le caractère SMRD, et (ii) qu'une population d'acariens peut recouvrer sa reproduction lorsqu'une reine SMRD est remplacée par une reine non sélectionnée. Le génotype des abeilles adultes, comme des immatures, produites par des reines SMRD provoque une augmentation du pourcentage d'acariens sans descendance. La suppression de la reproduction des acariens a été caractérisée par une augmentation du pourcentage d'acariens vivants n'ayant pas pondu (jusqu'à 60 %) et d'acariens qui sont morts piégés par le cocon (jusqu'à 16 %) durant les 30–50 jours de présence d'une reine SMRD (Fig. 1, Tabs. I et II). Ces deux pourcentages ont diminué (10–15 % et 2–5 % respectivement) quand des reines non sélectionnées ont remplacé les reines SMRD. Lorsqu'on sélectionne le caractère SMRD, il peut être plus efficace de ne compter que ces acariens plutôt que d'essayer de prédire le succès reproducteur de tous les acariens échantillonnés dans la colonie.

***Apis mellifera* / *Varroa destructor* / résistance aux parasites / suppression de la reproduction de l'acarien**

Zusammenfassung – Änderungen der Vermehrung von *Varroa destructor* nach dem Tausch von Königinnen zwischen resistenten und nichtresistenten Bienenvölkern. Diese Studie untersucht die Änderung der Reproduktion und Mortalität von Varroamilben (*Varroa destructor* Anderson and Trueman) nach dem Tausch von Königinnen unterschiedlich varroaempfindlicher Zuchtlinien zwischen den Völkern. Die Königinnen waren auf dise Unterdrückung der Reproduktion der Milben hin selektiert worden, diese erbliche Eigenschaft (SMRD) steigert den Anteil der Milben, die keine Eier legen.

Die Experimente untersuchten die Milbenvermehrung in Bienenvölkern im Freiland.

Die Völker wurden durch Aufteilung einer Mischung milbenbefallener Bienen aus 15–20 Bienenvölkern gebildet (ca. 25 kg Bienen). Jedes Testvolk wurde aus 500 g Bienen aus dieser Mischung gebildet und mit einer Testkönigin versehen. Die Bildung von Drohnenbrut wurde während der ganzen Versuchszeit verhindert. Die Hälfte der Völker wurde mit SMRD-Königinnen versehen, die andere Hälfte mit unselektierten Königinnen. Nach 7 (Experiment 1) bzw. 13 (Experiment 2) Wochen wurden die Königinnen ausgetauscht. Wir untersuchten die Milbenreproduktion in von nur einer Milbe befallenen Arbeiterinnenzellen mit Puppen 210 h nach der Verdeckelung. Von mehreren Milbenweibchen befallene Zellen wurden von der Analyse ausgeschlossen. Zu jedem Untersuchungszeitpunkt wurden 30 Milben untersucht, oder so viele wie bei der Untersuchung von 500 Zellen gefunden wurden.

In jedem der Völker wurde an 5 verschiedenen Zeitpunkten (zweimal vor und dreimal nach dem Tausch der Königinnen) der Prozentsatz von Milben ohne Nachkommen bestimmt. Diese Untersuchungsvariable schloss sowohl lebende als auch tote Milben ein, die keine Eier abgelegt hatten. Die in den Zellen gestorbenen Weibchen befanden sich entweder frei in den Zellen oder eingesperrt zwischen der Zellwand und dem Kokon. Weil solche eingesperrten Milben von den zellputzenden Arbeiterinnen nicht entfernt werden, nimmt die Anzahl eingesperrter Milben in einer Brutwabe im Laufe der Zeit zu. Die eingesperrten Milben werden dabei von den Kokons der später in den Zellen aufgezogenen Bienen bedeckt, von mehreren Kokonlagen bedeckte Milben wurden daher nicht gezählt.

Die Ergebnisse zeigten, dass (1) die Reproduktion der Milben durch Zusetzen einer auf SMRD selektierten Königin unterdrückt werden kann, und (2) dass eine Milbenpopulation ihre Reproduktion wieder aufnehmen kann, wenn eine selektierte Königin durch eine unselektierte Königin ersetzt wird.

Der höhere Anteil von Milben ohne Nachkommen wird entweder durch den Genotyp der von den SMRD-Königinnen Larven und Puppen oder erst durch den der Arbeiterinnen verursacht. Die Unterdrückung der Milbenreproduktion war einerseits durch eine innerhalb von 30–50 Tagen nach Einsetzen der SMRD-Königinnen auftretende Steigerung des Anteils lebender Milben ohne Eilage (bis zu 60 %) und andererseits durch einen höheren Anteil von zwischen Zellwand und Kokon eingeschlossenen toten Milben (bis zu 16 %) zurückzuführen (Abb. 1 und Tab. II und III). Beide Anteile fielen auf niedrige Werte (10–15 % bzw. 2–5 %) zurück, wenn die selektierten Königinnen durch unselektierte ersetzt wurden. Bei einer Selektion auf die SMRD Eigenschaft ist der Aufwand am geringsten wenn nur diese Milben gezählt werden statt dass der Reproduktionserfolg aller gefundenen Milben bestimmt wird.

***Apis mellifera* / *Varroa destructor* / Resistenz gegen Milben / Unterdrückung der Milbenvermehrung (SMRD)**

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