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Original article

Population growth of *Varroa jacobsoni* Oud in Mediterranean climates of California

B Kraus *, RE Page Jr

Department of Entomology, UC Davis, Davis, CA 95616, USA

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Summary — In April and October mite-free honey-bee colonies were artificially infested with 50 individuals of *Varroa jacobsoni* each and treated with the pesticide Apistan® after a period of 24 weeks. Population growth was studied in 24 colonies from April to October and in 6 colonies from October to April. The proportion of *Varroa jacobsoni* that invaded the test colonies after the initial inoculation was monitored in colonies that were constantly treated with Apistan®. Conservative calculations suggested that the initial mite population in a honey-bee colony increases on average about 300-fold during 1 year in central California. This result excludes the contribution of additional mites that invaded the colonies. The result of the present study demonstrates the high virulence of *Varroa jacobsoni* in California, where beekeepers are forced to treat infested colonies twice a year.

***Varroa jacobsoni* / population dynamics / virulence / Mediterranean climate / California**

INTRODUCTION

The population growth and virulence of the honey-bee parasite *Varroa jacobsoni* depend on numerous factors. The most obvious ones are race and strain of the bee (Moritz and Hänel, 1984; Büchler, 1990; Rosenkranz, 1990; Fuchs, 1991; Moretto *et al,* 1991; Otten, 1991; Kulincevic *et al,* 1992, *etc*), climate (De Jong *et al,* 1984; Ritter and De Jong, 1984; Moretto *et al,* 1991, *etc*) and possibly *Varroa* biotype (Delfinado-Baker and Houck, 1989). In cold and temperate climates, the number of mites increases about 10-fold per year and infested colonies collapse after about 4 years (Ritter, 1984; Fries *et al,* 1991; Korpela *et al,* 1992). In tropical climates the parasite seems to be less virulent (Ritter and De Jong, 1984; Engels *et al,* 1986; Rosenkranz, 1990). From countries with Mediterranean climates, high population growths and increased virulence of *V jacobsoni* have been reported (Lubinevski *et al,* 1988; Frilli, 1989). In particular, the question whether we are always dealing with the same mite

* Present address: Universiteit Utrecht, Vakgroep Vergelijkende Fysiologie Projectgroep Ethologie en Socio-oecologie, Centrumgebouw Noord 2 Padualaan 14, De Uithof, Postbus 80086, NL-3508 TB Utrecht, The Netherlands.

biotype has not yet been answered. The parasite was most likely imported into South America in 1971 from Japan (De Jong *et al,* 1982). The results of a study conducted by Delfinado-Baker and Houck (1989) suggest that *V jacobsoni* spread from South America to the USA where it was detected in 1987. An alternative hypothesis is that is was imported illegally from Europe by beekeepers. Delfinado-Baker and Houck (1989) suggested a lower virulence of mites from North America compared to mites from Europe on the basis of the hypothesis of a South American origin of mites in the USA.

The objective of the present study was to determine population growth of *V jacobsoni* in Mediterranean climates of California 1 year after the massive Varroa-induced losses of commercial and feral honey-bee colonies started to occur.

MATERIALS AND METHODS

Study conducted from April to October 1993

Tests were conducted with *Apis mellifera* L and with *Varroa* mites collected from this species. Tests were conducted for a 24-week period from April to October 1993. Colonies were compared for the number of *Varroa* mites, the number of bees, the size of the brood area and the amount of pollen and honey.

Production of colonies with similar *Varroa* mite infestation levels

Twenty-four packages of bees (1 kg bees per package) were established with naturally mated sister queens. Each package was treated with one Apistan® strip (10% fluvalinate) on April 14 1993 (Herbert *et al,* 1989). After 5 d, the Apistan® strips were removed and the packages were installed into single chamber Langstroth-hives containing comb foundation. Two weeks later, each colony was inoculated with 50 female *Varroa* mites. Fifty young workers were removed from a brood comb and kept in a queen cage. *Varroa* mites sampled from a highly infested colony were removed from their host bees with a paint brush and transferred through the mesh wire of the queen cage to workers. The inoculation of the bees was conducted at 32°C and 55% relative humidity. The bees and the 50 mites were returned to their colony in queen cages, with sugar.

The bees were treated in a package to prevent contact of the Apistan® strips with wax. Residues of fluvalinate in wax might kill the *Varroa* mites after the initial inoculation (Moosbeckhofer, 1991). The period of 2 weeks between Apistan® treatment and inoculation was chosen to prevent the same effect caused by traces of fluvalinate on bees.

Test groups, management of colonies and colony estimates

Colonies were positioned in groups of 4. The groups were separated by 5 colonies permanently treated with Apistan® that served as monitor colonies to document the transfer of *Varroa* mites between colonies. The entrances of all colonies were reduced to a width of 5–7 cm to prevent a mass transfer of *Varroa* mites by robbing (Sakofski *et al,* 1990). Ten colonies were treated with vegetable shortening patties (mixture of powdered sugar, drivert sugar (consisting of 92% sucrose + 8% invert sugar), sugar and Crisco® shortening) to test the effect of vegetable oil on population growth of *V jacobsoni.* Eleven colonies were maintained without vegetable shortening patties. Data obtained from treated colonies were used in the present study because vegetable shortening patties had no clear influence upon population growth of the parasite (Kraus and Page, 1995).

After becoming established in the middle of April, the colonies were fed continuously until the start of the nectar flow at the end of May. Colonies were maintained in a single story with a standard depth of 24.4 cm. Colonies were checked weekly for eggs and larvae to detect broodless periods, because *Varroa* mites only reproduce in brood cells. During the nectar flow, honey was extracted from broodless combs, if necessary, to provide space for brood rearing.

From 8–11 October, the number of bees, the amount of brood, the amount of pollen, and the

amount of honey per colony were estimated following the method described by Gerig (1983).

Varroa mite counts

The hives were provided with a removable bottom board. In monitor colonies and artificially infested colonies, the number of dead mites was counted weekly. After 20 weeks (September 13, 1993; March 10, 1994) the test colonies were treated with Apistan® for 28 d and the number of dead *Varroa* mites was counted.

Calculation of population growth

Given a population size N_0 of 50 mites and a population size N_t at the time t, determined by counting dead mites after treatment with fluvalinate, the intrinsic rate of population increase r is determined as follows (Carey, 1993).

$$r = \ln (N_t / N_0)$$

$$\text{increase } R = e^r$$

To estimate the impact of invading mites on population growth, the average number of mites N_i that invaded the monitor colonies during period p_i was added to the calculated number of mites before adding period $p_i + 1$ in the calculation. The number of *Varroa* mites N_t at a time t (with t consisting of n periods with a length of time p) and with an average number of mites NI_i invading the monitor colonies during period p_i was calculated as:

$$N_t = \sum_{i=1}^{n} N_{i-1} \times r_p + NI_i$$

N_i is the total number of *Varroa* mites in a colony at the end of period p_i. The factor r was determined by iterative comparison of results of calculations using different values of r with the value of N_t actually found.

Study conducted from October 1993 to April 1994

Population growth of *V jacobsoni* was studied in 6 colonies from October to April. In 4 colonies, the combs that had direct contact with Apistan® strips during the previous treatment were removed and replaced by new combs prior to inoculation. In 2 colonies the combs that had direct contact with the pesticide were not removed prior to inoculation. Fifteen days after finishing the final Apistan® treatment during the study conducted from April to October 1993, 6 colonies were inoculated again with 50 mites each on October 22, as described above. Colonies were positioned in a row. To monitor invasion levels, data were used from all 5 monitor colonies located within the apiary. The entrances of the colonies remained reduced to a width of 5–7 cm. Colonies were maintained in a single story with a standard depth of 24.4 cm. Stored honey was not extracted and the colonies were not provided with additional food. Besides differences mentioned above, the study was conducted as described in part one.

RESULTS

Mite populations at test end and levels of mite invasion measured in monitor colonies

At the end of the study conducted from May 1st to October 7, test colonies contained an average number of 1 614 ± 485 SE (range = 690–2 867, $n = 21$) mites. At the end of the study conducted from October 22 1993 to April 7 1994, colonies contained an average number of 1 268 ± 316 SE (range = 854–1 620, $n = 4$). Data obtained from 2 colonies with combs that had direct contact with Apistan® strips prior to reinoculation with mites, were not included since mite populations in those colonies were found to be clearly lower than in other test colonies.

Calculation of population growth

The study conducted from May 1st to October 7 1993 resulted in an intrinsic rate of increase per week of $r_7 = 1.16$. The study conducted from October 22 1993 to April 7 1994 resulted in an intrinsic rate of increase

per week of $r_7 = 1.14$. Given these intrinsic rates of increase the mite population would increase within 1 year 2 248-fold and 910-fold, respectively. Given an intrinsic rate of increase of $r_7 = 1.14$ during the winter 6 months and a intrinsic rate of increase of $r_7 = 1.16$ during the summer 6 months, the mite population increases 1 430-fold within 1 year.

During the 24 weeks period between artifical inoculation of the colonies with mites and Apistan® treatment on average 186 (summer) and 219 (winter) *Varroa* mites entered the monitor colonies (fig 1). To take these mites in account, we calculated population growth based on the assumption that all mites that invaded monitor colonies or artificially infested colonies originated from colonies not participating in the study. The study conducted from May 1st to October 7 1993 resulted in an intrinsic rate of increase per week of $r_7 = 1.13$. The study conducted from October 22 1993 to April 7 1994 resulted in an intrinsic rate of increase per week of $r_7 = 1.10$ (fig 2). Given these rates of increase, the mite population increased within 1 year by 576-fold and 42-fold, respectively. Given an intrinsic rate of increase of $r_7 = 1.13$ during the summer 6 months and an intrinsic rate of increase of $r_7 = 1.10$ during the winter 6 months the mite population increases 286-fold within 1 year.

Comparison of natural death rate and calculated population size

Natural death rate during the first 4 months of the study suggests slower population growth than the calculation based on r_7. During the fifth month of the study natural death rate indicates a faster population growth than the calculation based on r_7 (fig 2).

Effect of Apistan® residues in wax on V jacobsoni

At the end of the study conducted from September 1993 to April 1994, colonies that contained combs with direct contact with Apistan® prior to reinnoculation with mites contained an average of 403 ± 50 mites (range = 352–453, $n = 2$). Colonies without combs exposed to Apistan® contained an average number of 1 268 ± 316 SE mites (range= 854–1 620, $n = 4$). Colonies exposed to combs containing residues of fluvalinate (active compound of Apistan®)

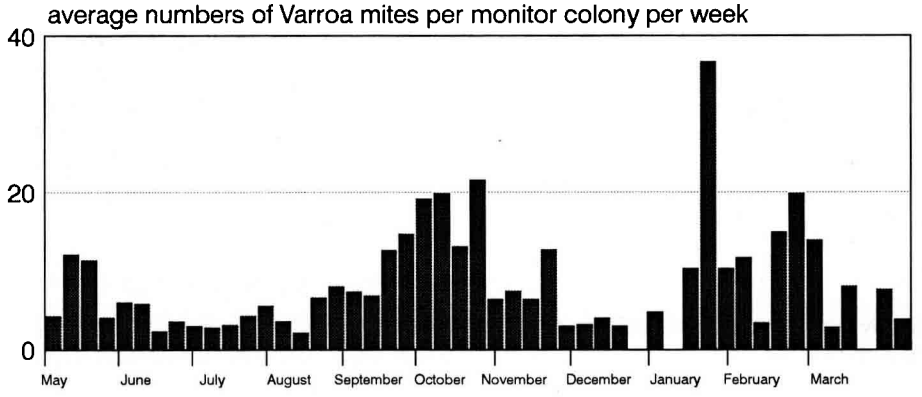

Fig 1. Numbers of *Varroa* mites invading 5 monitor colonies placed among artifically inoculated test colonies. Monitor period: start inoculation May 1 1993 (summer); end Apistan® treatment April 7 1994 (winter).

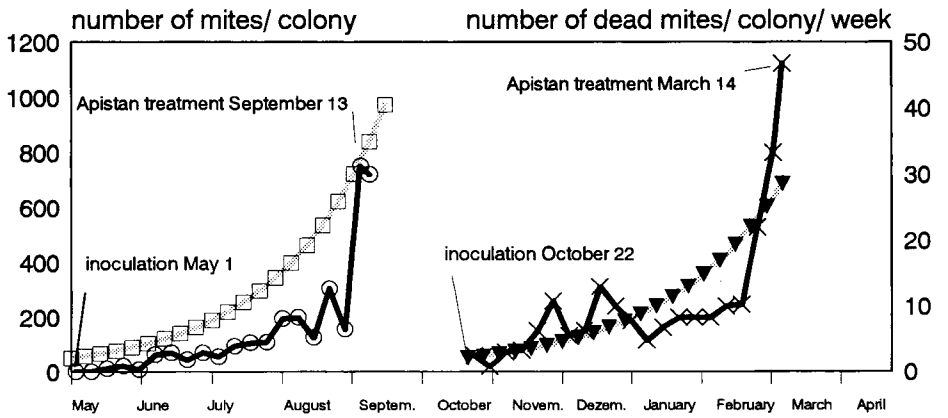

Fig 2. Natural *Varroa* death rate in colonies inoculated with 50 mites each and *Varroa* population size calculated on the basis of constant reproduction of mites. Series 1: (circle, solid line, ordinate 2): average number of dead *Varroa* mites per colony per week ($n = 21$). Series 2 : (square, broken line, ordinate 1) : average number of *Varroa* mites per colony calculated based on 1.16-fold increase of the mite population within 7 d. Invading mites are not taken in account. Series 3: (cross, solid line, ordinate 2): average number of dead *Varroa* mites per colony per week ($n = 4$). Series 4: (wedge, broken line, ordinate 1): average number of *Varroa* mites per colony calculated based on 1.14-fold increase of the mite population within 7 d. Invading mites are not taken in account.

contained on average 68% fewer *V jacobsoni* than colonies that did not contain contaminated combs.

Effect of colony strength

No clear correlation between number of bees, amount of brood, ratio of bees per brood, amount of honey, amount of pollen and levels of *Varroa* mite infestation was found (Spearman rank correlation coefficient: $r_S = 0.199, 0.216, 0.028, 0.060, 0.292$; $\alpha > 0.5$).

DISCUSSION

The data presented show that population size of *V jacobsoni* in infested honey-bee colonies increases in California at least 30 times faster than previously reported from countries with more temperate climates (Ritter, 1984). It is likely that this is rather an underestimate. The reproduction of *V jacobsoni* was underestimated as the calculations were based on the assumption that all mites invading colonies contribute to size of the *Varroa* population. However, this assumption is only true if all the mites that invaded monitor colonies are mites imported from colonies other than the test colonies. Probably a substantial portion of mites that invaded the monitor colonies originated from test colonies and, therefore, did not add to total population growth within test colonies. Reproduction of *V jacobsoni* was further underestimated because a high proportion of mites was killed at the beginning of the final Apistan® treatment and, therefore, excluded from reproduction for the duration of the 4 treatment weeks. Reproduction of *V jacobsoni* was slightly overestimated by adding the number of mites that invaded monitor colonies within a 7-d period to the mite population only at the end of this period. Reproduction of the immigrant mites was not considered during that period.

Even in cold climates, the numbers of mites can increase in an infested colony up to 100-fold within one summer (Fries *et al,* 1991). In temperate and cold climates, broodless periods interrupt the mites' reproduction and the mite population declines during winter (Ritter, 1984; Fries *et al,* 1991; Korpela *et al,* 1992). We also found high reproduction rates during the winter in California. Fast population growth of the parasite in Mediterranean climates is, therefore, obviously not caused by fast population growth during summer. The main factor causing rapid population growth of the *Varroa* population in honey-bee colonies located in Mediterranean climates is probably the nearly constant presence of brood. It is unlikely that the high virulence of *V jacobsoni* in California might be related to its recent introduction with no time for host–parasite adaptation. Even in European countries where *V jacobsoni* was detected in the 1970s, no signs of adaptation of either host or parasite towards a more balanced relationship have developed. Delfinado-Baker and Houck (1989) suggested a lower virulence of mites from North America compared to mites from Europe, based on the probable South American origin of mites in the USA. However, this has been proven wrong by the present study. The population growth of the parasite forces Californian beekeepers to apply measures of *Varroa* control colonies in the fall and the spring. Beekeepers located in countries with more temperate or cold climates usually only treat colonies with pesticides in the fall. In Israel, with a Mediterranean climate, 1 treatment per year also proved to be insufficient (Lubinevski *et al,* 1988).

A calculation of population growth of *Varroa* mite populations in infested colonies conducted by Calatayud and Verdu (1993) by means of natural death rate led to results comparable to results of the present study ($r = 0.027$ per day compared to $r = 0.021$ per day during summer in the present study). However, population growth calculated on the basis of the assumption of constant reproduction and population growth indicated by natural death rate is not highly correlated in the present study. This might be caused by seasonal differences in reproduction rate, seasonal deviations in natural death rate and other factors which make it difficult to calculate the size of *Varroa* populations based on natural death rate (Fuchs and Koeniger, 1984; Liebig *et al,* 1984; Maul, 1984; Rademacher, 1985). In previous studies, reproduction of *V jacobsoni* was found to be influenced by the total number of brood cells per colony and by the number of brood cells per bee (Otten, 1991). In the present study no significant correlation was found. Colony estimates were only conducted in October and correlations between the size of the mite population and the number of brood cells per colony and the number of brood cells per bee may be more pronounced during the summer or early fall.

The previously described effect of Apistan® upon *V jacobsoni* occurring after termination of the treatment (Moosbeckhofer, 1991) was confirmed. Mites in such situations are obviously constantly exposed to considerable amounts of fluvalinate residues in wax and are, therefore, constantly selected for pesticide resistance.

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Résumé — La dynamique des populations de *Varroa jacobsoni* Oud sous le climat méditerranéen de Californie. Le climat influe sur la croissance des popula-

tions de *Varroa jacobsoni,* parasite de l'abeille mellifère (Ritter et De Jong, 1984 ; De Jong *et al,* 1984 ; Moretto *et al,* 1991 ; *etc*). Dans les régions à climat méditerranéen, une croissance rapide des populations, ainsi qu'une virulence élevée, ont été mises en évidence (Frilli, 1989 ; Lubinevski *et al,* 1988) mais n'a jamais été précisément quantifiée. Notre étude vise à déterminer la dynamique des populations de *V jacobsoni* en Californie centrale (climat méditerranéen), un an après le début de pertes massives de colonies causées par le parasite. Pour cela des colonies d'abeilles *(Apis mellifera ligustica)* traitées à l'Apistan® ont été infestées le 1er mai 1993 (21 colonies) et le 22 octobre 1993 (6 colonies) avec 50 varroas chacune. La mortalité naturelle et l'invasion des acariens dans 5 colonies traitées continuellement à l'Apistan® ont été relevées chaque semaine. Vingt-quatre sem plus tard (13 septembre 1993 et 10 mars 1994) les populations de varroas présentes dans les colonies infestées ont été déterminées par un traitement à l'Apistan®. À la fin de l'expérimentation faite en été il y avait en moyenne 1 614 ± 485 acariens dans les colonies (écart = 690–2867, $n = 21$), et 1 268 ± 316 (écart = 854–1620, $n = 4$) à la fin de celle d'hiver. Cela correspond à une augmentation de la population R_7 de 1,16 fois en été et de 1,14 fois en hiver. On a essayé d'évaluer l'impact du transfert de nouveaux varroas sur la croissance de la population. Si on admet pour le calcul de R_7 que tous les transferts d'acariens se sont faits à partir de colonies non prises en compte dans l'étude, on obtient un facteur R_7 de 1,13 en été et de 1,10 en hiver. Selon ce calcul de R_7 la population de varroas dans les colonies infestées augmente de 286 fois par an. En climat tempéré la population n'est multipliée que par 10 chaque année. La croissance rapide du parasite en climat méditerranéen n'est pas due à un taux de reproduction plus élevé mais à la possibilité de se reproduire continuellement dans le couvain qui est présent presque toute l'année. En revanche, en climat tempéré et en climat froid, la reproduction de *V jacobsoni* s'interrompt pendant les périodes où il n'y a pas de couvain (Ritter, 1984 ; Fries *et al,* 1991 ; Korpela *et al,* 1992). Aucune corrélation significative n'a été trouvée entre le nombre d'abeilles, la surface de couvain, le rapport abeilles/couvain ou les quantités de miel et de pollen avec le niveau d'infestation par *V jacobsoni.* Avant l'infestation provoquée en octobre 1993 les rayons de 4 colonies, qui avaient été en contact avec des lanières d'Apistan®, ont été remplacés par des rayons dépourvus de résidus. Dans 2 colonies, où ils n'avaient pas été remplacés, les varroas étaient 68,2% moins nombreux à la fin de l'expérience que dans les colonies qui ne renfermaient que des rayons dépourvus de résidus. Ce résultat confirme celui de Moosbeckhofer (1991) : les résidus de fluvalinate dans la cire exercent une action sur *V jacobsoni.* Selon Delfinado-Baker et Houck (1989) *V jacobsoni* a pu être importé d'Amérique du Sud en Amérique du Nord par des abeilles africanisées et serait en conséquence moins virulent aux États-Unis qu'en Europe. Notre étude infirme cet espoir. Les apiculteurs californiens sont contraints par la croissance rapide des populations de *V jacobsoni* à traiter leurs ruches 2 fois par an avec une méthode efficace. En climat froid ou tempéré un traitement à l'automne suffit.

***Varroa jacobsoni* / dynamique population / virulence / climat méditerranéen / Californie**

Zusammenfassung — Das Populationswachstum von *Varroa jacobsoni* im mediterranen Klima von Kalifornien. Das Populationswachstum des Bienenparasiten *Varroa jacobsoni* Oud wird von Klimafaktoren beeinflußt (Ritter und De Jong, 1984; De Jong *et al,* 1984, Moretto *et al,* 1991). In Ländern mit mediterranem Klima wurde

ein schnelles Populationswachstum und damit eine hohe Virulenz des Parasiten festgestellt (Lubinevski *et al,* 1988; Frilli, 1989), jedoch nicht näher quantifiziert. In der vorliegenden Studie sollte die Frage nach dem Populationswachstum von *V jacobsoni* im mediterranen Klima Zentralkaliforniens ein Jahr nach dem ersten Auftreten von durch den Parasiten verursachter Völkerzusammenbrüchen beantwortet werden. Hierzu wurden mit dem Varroazid Apistan® behandelte Bienenvölker *(Apis mellifera ligustica)* am 1. Mai 1993 (21 Völker) sowie am 22. Oktober 1993 (6 Völker) mit jeweils 50 Milben infiziert. Es erfolgte eine wöchentliche Kontrolle des natürlichen Totenfalles sowie der Milbeninvasion in fünf permanent mit Apistan® behandelten Monitorvölkern. Ab dem 13.September 1993 sowie dem 10. März 1994 wurde die in den infizierten Völkern befindliche Varroapopulation durch eine Apistan® behandlung bestimmt. Am Ende der während des Sommerhalbjahres durchgeführten Studie befanden sich im Durchschnitt 1614 ± 485 SE (Spanne = 690–2867, $n = 21$) Milben in den Völkern, am Ende der während des Winterhalbjahres durchgeführten Studie im Durchschnitt 1268 ± 316 SE (Spanne = 854–1620, $n = 4$) Milben. Daraus ergibt sich eine wöchentliche Zunahme der Population r_7 um das 1,16-fache im Sommer und 1,14-fache im Winter. Es wurde versucht, den Einfluß der Invasion durch zusätzliche Milben abzuschätzen. Geht man bei der Berechnung von r_7 von der Annahme aus, daß der Milbentransfer ausschließlich von nicht in den Versuch integrierten Völkern in Versuchsvölker hinein erfolgte, so ergibt sich ein Faktor r_7 von 1,13 in Sommer und 1,10 im Winter. Diese sehr konservative Berechnung von r_7 ergibt eine Zunahme der *Varroa*population in infizierten Völkern um das 286-fache pro Jahr. In gemäßigten Klimaten nimmt die *Varroa*population lediglich um das etwa 10-fache pro Jahr zu (Ritter, 1984). Das schnelle Populationswachstum des Parasiten in mediterranen Ländern wird nicht durch eine höhere Reproduktionsrate verursacht, sondern durch die ständige Möglichkeit zur Reproduktion in der fast permanent vorhandenen Bienenbrut. In temperaten und kalten Klimaten hingegen wird die Reproduktion von *V jacobsoni* durch brutlose Perioden unterbrochen (Ritter, 1984; Fries *et al,* 1991; Korpela *et al,* 1992). In der vorliegenden Studie waren bei einer im Oktober 1993 durchgeführten Schätzung der Anzahl Bienen, der Brutfläche, der Honigmenge und der Pollenmenge weder einer dieser Parameter noch der Koeffizient *Anzahl Bienen/ Brutfläche* signifikant mit der Anzahl Milben im Volk korreliert. Vor der im Oktober 1993 durchgeführten Infektion mit *V jacobsoni* wurden bei vier Völkern Waben, die zuvor Kontakt mit Apistan® streifen hatten, gegen rückstandsfreie Waben ausgetauscht. Bei zwei Völkern erfolgte kein Austausch von Waben. In diesen Völkern befanden sich zu Versuchsende 68,2% weniger Milben als in den Völkern, die ausschließlich rückstandsfreie Waben enthielten. Dieses Ergebnis bestätigt den von Moosbeckhofer (1991) beschriebenen Effekt von im Wachs befindlichen Fluvalinatrückständen auf *V jacobsoni.* Delfinado-Baker und Houck (1989) beschrieben die Möglichkeit, daß *V jacobsoni* durch afrikanisierte Bienen von Südamerika aus nach Nordamerika importiert wurde und daher in den USA weniger virulent sei als in Europa. Die vorliegende Studie zeigt, daß diese Hoffnung sich nicht erfüllt hat. Kalifornische Imker sind durch das schnelle Populationswachstum von *V jacobsoni* gezwungen, ihre Völker zweimal pro Jahr mit einer effektiven Methode zu behandeln. In temperaten oder kalten Klimaten ist eine Behandlung im Herbst im allgemeinen ausreichend.

***Varroa jacobsoni* / Populationswachstum / mediterranes Klima / Virulenz / Kalifornien**

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