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Five years of bi-directional genetic selection for honey bees resistant and susceptible to *Varroa jacobsoni* *

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Summary — Two lines of honey bees *(Apis mellifera carnica)* were selectively propagated from an assembled parental stock through four generations. The resulting lines of bees diverged to be comparatively resistant and susceptible, respectively, to *Varroa jacobsoni*. Much of this phenotypic variation in honey bee response to *Varroa jacobsoni* has a genetic component. Since important portions of this genetic variation are additive, selective breeding shows good promise for providing the desired long-term solutions to *Varroa* mite difficulties.

***Apis mellifera* / *Varroa jacobsoni* / genetic selection / resistant line / heritability**

INTRODUCTION

The severity of *Varroa jacobsoni* Oud infestations in Europe has triggered research into a wide variety of control strategies (Dietz and Herman, 1988; Koeniger and Fuchs, 1988). Much of this research has focused on chemical controls and has produced knowledge of effective compounds and their use. In their review, Koeniger and Fuchs (1988) describe both the history of the development of chemical controls and the predictable long-term difficulties attending their use. Chief among the identified difficulties is the expectation that *V jacobsoni*, like other agriculturally important mites, will rapidly develop toxicant resistance. The combination of widespread use of compounds through much of the year and the multiple generations of mites each year make this a likely occurrence. Secondarily, concerns are often raised over the possible contamination of hive products. Fortunately, most of the

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control compounds in current use are lipophilic and are therefore most likely to be contaminants of wax rather than honey. Nonetheless, long-term use, widespread use, high dosage use, and the occasional presence of wax in honey products make the nonchemical control of *Varroa* a desirable goal.

The development of chemical controls for *Varroa* has taken first priority in the research community because of the need for rapid solutions to a devastating problem. However, nonchemical solutions requiring lengthy development time present interesting possibilities. One such approach is the development of strains of bees that are *Varroa* resistant or tolerant. As a contribution to this development, we report on the experimental production of lines of bees comparatively susceptible and resistant to *Varroa* mites.

MATERIALS AND METHODS

Throughout the experiment, we used honey-bee colonies of *Apis mellifera carnica* in standard Langstroth hives. The initial group of colonies and the subsequent generations derived from them were maintained in randomized locations at a single apiary site within a large wood lot. This location provided plentiful landmarks for worker bees which reduced to a minimum the chances of drift between colonies. However, at the same time, all colonies studied within each year were exposed to the same general milieu and consequently can be expected to have been subject to random and relatively similar *Varroa* reinfestation rates.

During the winter of 1984–1985, Yugoslavia suffered severe losses of honey bees colonies. The majority of these losses were a direct consequence of *Varroa* infestations. In each of three apiaries in widely separated areas of the country, only a single colony survived. These three colonies were collected and used as a base population for a bi-directional selection program.

Four daughter queens were reared from each of the three queens collected to form the base population and were open-mated during the early spring of 1985. Matings were conducted at the same time and in the same apiary. Drones were from *A m carnica* colonies located primarily in the experimental apiary and secondarily in the general area. Thus, all queens had access to similar mating opportunities. Eleven of the 12 queens survived introduction to full-sized (40 000–50 000 worker bees) colonies. These colonies were evaluated for their response to the naturally-occurring *Varroa* population present in the experimental apiary.

The evaluation process was based on the percentage of worker brood cells infested by reproducing mites (Kulinčević and Rinderer, 1988; Kulinčević *et al*, 1988, 1991). Twice monthly through the active beekeeping season, a comb containing sealed brood was removed from each colony and inspected. Inspection involved the removal of 100 worker pupae with dark eyes and light-brown abdominal chitin (16–17 d old). Examinations and classifications of indications of mite reproductive activity were made according to the procedures of Ifantidis (1984) except that samples were not frozen prior to inspection.

The average numbers of infested brood cells were calculated for all inspections of each colony. Comparisons of these averages were used to select the parents of the first generation. The two queens heading the colonies having the lowest average percentages of infestation were chosen to found the line selected for resistance to *V jacobsoni*. The two queens heading the colonies having the highest average percentages of infestation were chosen to found the line selected for susceptibility to *V jacobsoni*. In each of the lines, eight queens survived open-mating in the experimental apiary, introduction to field colonies and overwintering. Randomized colony locations and apiary conditions assured that all queens had similar access to the *A m carnica* drones of the immediate area and that colonies in the subsequent lines had reasonably equal likelihoods of infestation by *V jacobsoni* from colonies in the surrounding area. These colonies constitued the first selected generation.

The first generation was tested from June 23 to September 1, 1986. Colonies were examined every 2 wk (5 occasions) for the proportion of 100 worker brood cells infested by reproducing mites. Additionally, every 10 d (eight occasions) natural adult mite mortality was estimated. In order to evaluate a potential correlated response to selection based on rates of infestation of

cells, the numbers of dead mites that fell from the colony to screened paper inserts on the bottom boards of hives during 10 d were counted.

The second selected generation of resistant and susceptible stocks were produced by open-mating daughters of the two first-generation queens having progeny with the lowest rates of worker brood infestation. The second generation of susceptible stock was produced from the two queens of the first generation that showed the highest rates of infestation. Queens of both lines were produced, open-mated, and introduced to field colonies in autumn 1986.

Because of high mite populations in the experimental colonies during autumn 1986, each colony was treated by fumigation with 0.02 g of Amitraz. Winter losses were exceptionally heavy throughout Yugoslavia during the winter of 1986–1987. Ball (1988) found high titers of non-occluded virus particles, especially those of acute paralysis virus in dead and moribund bees from our experimental hives. This virus may have been spread to epizootic levels by *V jacobsoni* mites feeding on adults. In any event, losses among the untested second generation were severe. Two colonies from the resistant line and one from the susceptible line survived the epizootic. Similar and even greater levels of losses were common that winter throughout the country.

The active honey-bee season of 1987 was devoted to propagating the third generation of stock from survivors of the second generation. Twenty colonies, 10 derived from the survivors of the resistant stock and 10 derived from the survivors of the susceptible stock, were prepared for the 1987–1988 winter. These colonies were treated twice with fluvalinate fumigation (0.0025 g) (Kulinčević *et al,* 1991) during September 1987.

Colonies of the third generation were evaluated during the active beekeeping season of 1988. As before, average numbers of infested brood cells were periodically (7 occasions) determined for each colony of both lines. In addition, the numbers of dead mites resulting from fumigation of the colonies with fluvalinate (0.0025 g) were counted from paper inserts placed in screened bottom boards. These estimates of adult mite populations were made on four occasions.

The fourth generation was produced in 1988. Two parent colonies of each line were selected to produce fourth generation queens which were open-mated. These parents were chosen on the basis of general vigor as well as the percentage of cells infested with *V jacobsoni.* The average infestation rates of the parents was near the average of all the colonies of the stock the parents represented. Thus, selection was for maintenance rather than further separation of the stocks. Twenty colonies survived the winter, nine of the resistant line and 11 of the susceptible line. Colonies of fourth generation stock were treated twice with fluvalinate fumigation (0.0025 g) during the autumn of 1988. The fourth generation colonies were evaluated during the season of 1989. Brood infestation rates and the numbers of dead mites resulting from fumigation with fluvalinate were both evaluated on five occasions.

For comparisons of stock in the first, third and fourth generations, analyses of variance were performed on data normalized with square-root transformations. One-tailed tests evaluated line effects for hypotheses concerning comparative resistance and susceptibility.

RESULTS

The parental generation showed substantial variation in numbers of infested cells among colonies. Each colony was inspected six times; average infestation rates ranged from 3.8 to 32.5%. The entire parental generation had 11.6 ± 2.5% ($\bar{x}$ ± SEM) infestation rates. The parent colonies of the susceptible line averaged 14.8% of brood cells infested and the parent colonies of the resistant line averaged 5.6%.

The seasonal responses of the two lines in the first selected generation are markedly different ($P < 0.05$) (fig 1; table I). Both lines follow a pattern of hosting increasing numbers of parasites as the season progresses. However, the percentage of infested cells was uniformly less through the season in the resistant line.

The numbers of mites dying from natural mortality in the first generation colonies reflect the population trends apparent in

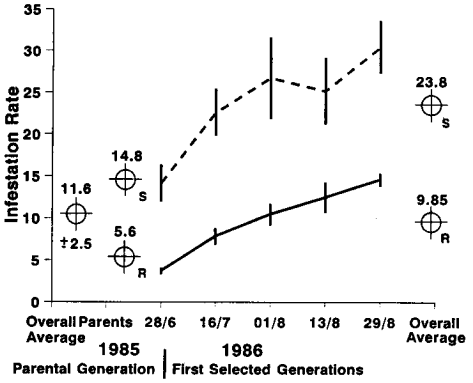

Fig 1. The average ($\bar{x}$ ± SEM) percentages of cells infested with *Varroa jacobsoni* for the parental and first selected generations in colonies of resistant (R and ———) and susceptible (S and ----------) lines. Inspection periods are indicated. For 1985, values for the overall average of the 11 colonies that comprised the parental generation and the average of the parents selected to found the resistant and susceptible stocks are shown. For 1986, average infestation rates of the eight resistant and the eight susceptible colonies for five inspection dates and the overall averages for all inspection dates are shown.

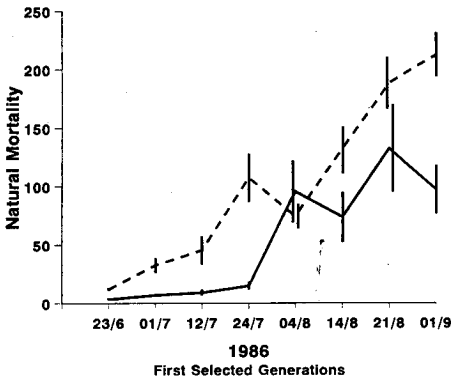

Fig 2. The average ($\bar{x}$ ± SEM) natural mortality of *Varroa jacobsoni* in eight colonies each of the first generation of resistant (———) and susceptible (--------) lines for eight inspection dates.

the percentage of infested cells (fig 2). The overall tendency is for the colonies of the susceptible line to have higher numbers of mites dying ($P < 0.07$) (table II).

The second generation of both selected lines suffered severe winter mortality. The remaining colonies of the second generation were used as sources of germplasm to propagate the third generation. Also, we decided that the project could not continue without some use of acaricide. Due to this treatment, data from the third and fourth generations cannot be compared directly to each other or to data from the first generation and were analyzed separately.

Results of the third generation indicate continued differences between the two selected lines of bees. The treatments with fluvalinate reduced the overall numbers of mites in the colonies. Nonetheless, resistant colonies had about half the number of infested cells as the susceptible colonies (fig 3; table I; $P < 0.004$).

As with the first generation, the numbers of dead mites resulting from fumigation with fluvalinate reflected the observed infestation rates of the third generation. Numbers increased through the active season with colonies of the susceptible line having larger populations of mites than colonies of the resistant line (fig 4; table II; $P < 0.044$).

Fourth generation data were consistent with earlier trends. Because of treatment with fluvalinate, the infestation rates were generally low. Nonetheless, resistant colonies had less than half the numbers of infesting mites that were found in colonies of the susceptible line (fig 3; table I; $P < 0.002$). As in other generations, the numbers of dead mites found after fumigation with fluvalinate reflected the infestation

Table I. Analyses of variance for numbers of infested cells in 3 generations of lines of bees sharing a common parental base and bred for comparative resistance and susceptibility to infestation by *Varroa jacobsoni.*

		Analyses of variance			
	Source	df	MS	F	P
Generation 1					
	L	1	46.7	3.3	0.046
S = 8	C(L)	13	14.2		
R = 8	D	4	7.8	6.9	0.000 2
0 = 5	L x D	4	0.1	0.1	0.98
	Error	52	1.1		
Generation 3					
	L	1	12.7	9.1	0.004
S = 9	C(L)	18	1.4		
R = 10	D	6	19.0	48.2	0.0001
O = 7	L x D	6	0.6	1.5	0.2
	Error	106	0.4		
Generation 4					
	L	1	13.3	12.9	0.002
S = 11	C(L)	18	1.0		
R = 9	D	4	10.4	20.5	0.0001
O = 5	L x D	4	0.5	1.1	0.4
	Error	71	0.5		

For each generation the number of susceptible line colonies (S), the number of resistant line colonies (R) and the number of observation dates (O) are indicated. The analyses provide degrees of freedom *(df)*, mean square *(MS)* *F* values *(F)*, and the probabilities of the chance occurrence of larger *F* values *(P)* for variation arising from lines (L), colonies nested in lines (C(L)), dates of observation (D), line by date interactions (L x D), and error. Analyses are of square-root transformed data. Line differences are evaluated by 1-tailed tests (see figs 1, 3).

levels observed. Overall, less than half the number of mites were killed in colonies of the resistant line compared to those killed in colonies of the susceptible line (fig 4; table II; $P < 0.04$).

DISCUSSION

This research documents the development of stocks of honey bees which are comparatively resistant and susceptible to *Varroa jacobsoni.* The employment of classical selection techniques reveals two important characteristics in honey-bee response to *V jacobsoni.* First, there is clear intercolonial variation in measurements of proportions of cells infested with *V jacobsoni.* Secondly, differential infestation rates are at least partially genetic in origin since selection produced significant bi-directional differences between lines in a single generation which was maintained in the lines in subsequent generations despite the colony maintenance difficulties encountered with the second generation. It is important to

Table II. Analyses of variance for dead *Varroa jacobsoni* mites from colonies in 3 generations of lines of bees sharing a common parental base and bred for resistance and susceptibility to infestation by *V jacobsoni*.

			Analyses of variance		
	Source	df	MS	F	P
Generation 1					
	L	1	350.3	2.3	0.07
S = 8	C(L)	14	149.8		
R = 8	D	7	161.2	14.7	0.000 1
0 = 7	L x D	7	11.9	1.1	0.37
	Error	98	10.9		
Generation 3					
	L	1	183.9	3.2	0.044
S = 9	C(L)	18	57.0		
R = 10	D	3	1 086.9	70.6	0.0001
O = 4	L x D	3	12.2	0.8	0.5
	Error	54	15.4		
Generation 4					
	L	1	267.2	3.3	0.043
S = 11	C(L)	18	80.9		
R = 9	D	4	42.2	4.6	0.002 2
0 = 5	L x D	4	2.9	0.3	0.86
	Error	72	9.2		

For the first generation, dead mites resulted from natural mortality. For the third and fourth generations, dead mites resulted from fumigation of hives with fluvalinate. For each generation, the number of susceptible line colonies (S), the number of resistance line colonies (R), and the number of observation dates (O) are indicated. The analyses provide degrees of freedom *(df)*, mean squares *(MS)*, *F* values *(F)*, and the probabilities of the chance occurrence of large *F* values *(P)* for variation arising from lines (L), colonies nested in lines (C(L)), dates of observation (D), line by date interactions (L x D), and error. Analyses are of square-root transformed data. Line differences are evaluated by 1-tailed tests (see figs 2–4).

emphasize that year by year, under comparable environmental conditions, the lines were consistently different in the predicted directions of resistance and susceptibility. This is true for both the selected characteristic of the proportion of infested cells and the coincident characteristic of dead mites collected from the colonies. Such responses can only occur in a common environment when the stocks differ genetically. Additional selection has a high likelihood of producing lines that are still more divergent from base populations.

Realized heritabilities suggest that to some degree the selected trait has a polygenic determination. The approach of Moran (1984) to calculate heritability ($h^2 = R/S$ x 3/2) adjusts for the use of open mating in selection programs. Using this approach, the realized heritabilities are 0.3 for increased resistance and 4.2 for decreased resistance for the first generation

TABLE 2. Results of tests for homogeneity of variances testing for differences between inbreeding levels for males and females in *Apis mellifera*. Bartlett's test and one-tailed *F*-tests were used for experiments 1 and 2 respectively. The values given are the probability that the observed differences in asymmetry values among levels of inbreeding are due to chance.

Sample	Character 1	Character 2	Character 3	Character 4	Character 5
Experiment 1					
MR males	0.3653	0.8109	0.0258	0.0030	0.7485
MR females	0.0298	0.0888	0.0017	0.4997	0.6272
SR females	0.9660	0.0042	0.9878	0.7454	0.5843
Experiment 2					
$F = 0.75$ vs $F = 0.0$	0.8211	0.8005	0.8815	0.5000	0.2219

MR = Material Reared; SR = Standard Reared.

any association between inbreeding level and asymmetry (Steel and Torrie, 1960). For these analyses individual replicate colony data were not pooled thus giving multiple estimates of asymmetry for each inbreeding level within each sex.

RESULTS

Asymmetry values for pooled replicate colony data are given in Table 1. Significant differences in asymmetry values among inbreeding levels were observed in a number of cases (Table 2). Of these cases, none showed any significant relationship with inbreeding level as revealed by regression analyses (Table 3). An examination of the variance values for these cases shows that in all instances the level of asymmetry is lower in at least one sample with a higher inbreeding value than in samples less inbred.

For experiment 2, there were no significant differences between $F = 0.75$ and $F = 0.0$ females (Table 2). In fact, for four of the five characters the asymmetry value was lower in the inbred sample than the outbred control.

In no cases was there a significant relationship between asymmetry and inbreeding level (Table 3). An examination of the sign of the regression lines indicates that within each sex both positive and negative regressions were observed.

Males displayed greater levels of asymmetry than females in 87% of cases (Table 1) of which 62% were significant (Table 4). Females were never observed to be significantly more asymmetric than males.

Of 20 comparisons between MR and SR females, MR females displayed higher levels of asymmetry in 50% of cases of which 2 cases were significant. SR females were significantly more asymmetric than MR females in a single case (Table 4).

DISCUSSION

The results show that inbreeding has no effect on developmental stability in *A. mellifera* as measured by fluctuating asymmetry. Increasing the level of homozygosity in the diploid part of the genome (females) up to levels at which 75% of the genome was homozygous resulted in no significant change in the level of fluctuating asymmetry from that observed in outbred material.

For this haplo-diploid system, the general level of genomic heterozygosity does not appear to be an important factor for the maintenance of developmental stability. This result is perhaps not surprising, as haploid males, which are effectively 100% homozygous, still need to possess a sufficient level

TABLE 3. Results of regression analyses testing for relationship between inbreeding level and asymmetry for each character. Values given are the probabilities that the slopes of the regression differ from zero due to chance. Signs in parentheses indicate negative or positive regression.

Sample	Character 1	Character 2	Character 3	Character 4	Character 5
MR males	(−) 0.4712	(+) 0.8083	(+) 0.4676	(−) 0.1304	(−) 0.8599
MR females	(+) 0.1406	(+) 0.0638	(+) 0.2511	(+) 0.5482	(−) 0.5582
SR females	(+) 0.8501	(−) 0.3940	(+) 0.7969	(+) 0.6183	(+) 0.8773

MR = Maternal reared; SR = Standard Reared.

in the selected lines, thereby increased the ability of the measures to discriminate between the lines, and reduced the h^2 for the trait within the selected lines. Regardless of the causes, these clear differences in repeated generations provide additional information supporting the conclusion that variation in response to *V jacobsoni* among honey bees has a genetic additive variance component.

The precise nature of the mechanism for increased resistance is yet to be identified. The measurement "percentage of brood cells infested" was chosen because it is presumed to cover several possible mechanisms of resistance. Attractiveness of brood to parasites; feeding cues; and developmental characteristics of immature honey bees, including rates of development and the timing of developmental events, are only a few examples of the possible mechanisms of resistance that would be included in a selection program based on the proportion of infested cells through a beekeeping season. Further work may better describe the mechanisms of resistance now that resistant is documented.

This research demonstrates that the potential exists for man to select *Apis mellifera* that are more resistant or tolerant to *V jacobsoni*. Natural selection may also be producing such lines. Kosarev (1987) reports on the resurgence of feral colony numbers in Russian forests in the late 1970s. Perhaps this change is further evidence of the potential for the development of lines of Western honey bees resistant to *Varroa jacobsoni*.

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Résumé — Cinq années de sélection génétique bidirectionnelle de colonies d'abeilles sensibles et résistantes à *Varroa jacobsoni*. La population de base a été constituée à partir de 3 reines fécondées après un hiver ayant causé de grosses pertes dans les colonies. L'infestation par *V jacobsoni* avait contribué à ces pertes et l'on a estimé que les colonies survivantes pouvaient présenter un certain degré de résistance. À partir de cette population de base, on a obtenu par élevage une génération parentale de 11 colonies. L'évaluation de ces 11 colonies a été faite par des examens bimensuels, pendant la saison apicole, du pourcentage de cellules de couvain d'ouvrières infestées par des acariens capables de se reproduire. Les parents choisis à partir de ce groupe de 11 colonies ont été utilisés pour produire une première génération sélectionnée de lignées résistantes et sensibles. Ces lignées étaient très différentes du point de vue des taux d'infestation (fig 1; tableau I) et peu différentes en ce qui concerne la mortalité naturelle des populations d'acariens infestants (fig 2; tableau II). La seconde génération a subi une mortalité hivernale sévère et n'a pas été testée. Néanmoins, les colonies survivantes de cette génération ont été utilisées pour produire une 3^{e} génération sélectionnée puis, à la suite, une 4^{e} génération sélectionnée. Les 2 lignées des 3^{e} et 4^{e} générations présentaient une nette différence à la fois dans le taux d'infestation (fig 3; tableau I) et dans le nombre d'acariens morts après fumigation de fluvalinate (fig 4; tableau II).

Les héritabilités obtenues suggèrent que le caractère sélectionné est dans une certaine mesure déterminé par plusieurs gènes. On a calculé pour la 1re génération

sélectionnée une héritabilité de 0,3 pour la résistance accrue et de 4,2 pour la résistance réduite. Les différences d'environnement entre la génération parentale et la 1re génération sélectionnée ont décalé toutes les réponses vers des niveaux plus élevés et gonflé les estimations de h^2 pour la résistance accrue. Bien qu'il n'y ait pas eu de différence de sélection au sein des lignées dans la sélection des parents de la 4e génération, celle-ci a continué à présenter des différences dans la résistance et la susceptibilité à *V jacobsoni.*

Cette recherche atteste le développement de lignées d'abeilles qui sont relativement résistantes ou sensibles à *V jacobsoni.* Il en ressort clairement 2 conclusions importantes. Premièrement, la variabilité phénotypique vis-à-vis de *V jacobsoni* a une composante génétique. Deuxièmement, une grande partie de cette variabilité a des bases génétiques qui répondent aux programmes classiques de sélection. De tels programmes fourniront vraisemblablement les solutions à long terme aux problèmes causés par *V jacobsoni.*

***Apis mellifera* / *Varroa jacobsoni* / sélection / lignée résistante / héritabilité**

Zusammenfassung — Fünf Jahre einer genetischen Zweiweg-Selektion von resistenten und empfänglichen Bienenvölkern für *Varroa jacobsoni.* Es wurden zwei Linien von Honigbienen *(Apis mellifera carnica)* vier Jahre lang unter Selektion gezüchtet. Die daraus entstandenen Linien waren gegen *Varroa jacobsoni* relativ resistent, beziehunsgweise empfänglich.

Die Ausgangspopulation aus drei begatteten Königinnen wurde nach einem Winter mit verbreiteten Völkerverlusten zusammengestellt. Zum Teil war der Befall mit *Varroa jacobsoni* für diese Verluste verantwortlich und es wurde angenommen, daß die überlebenden Völker einen gewissen Grad an Resistenz haben könnten. Aus dieser Ausgangspopulation wurden die Königinnen für 11 Völker gezüchtet, welche die Parentalgeneration bildeten. Diese Völker wurden durch monatlich zweimalige Untersuchungen bewertet, indem während der aktiven Bienensaison der Prozentsatz der Arbeiterbrutzellen mit fortpflanzungsfähigen Milben registriert wurde.

Aus dieser Gruppe von 11 Völkern wurden die Elterntiere ausgewählt, um eine erste selektierte Generation der resistenten und empfänglichen Linien zu erzeugen. Diese Linien unterschieden sich stark in der Befallsrate (Abbildung 1, Tabelle I), aber nur schwach in der natürlichen Mortalität der befallenden Milbenpopulationen (Abbildung 2, Tabelle II). Die zweite Generation erlitt schwere Winterverluste und wurde nicht geprüft. Die überlebenden Völker dieser Generation wurden jedoch zur Begründung einer dritten selektierten Generation und, in der Folge, auch einer vierten selektierten Generation benutzt. Die zwei Linien sowohl der dritten wie der vierten selektierten Generation waren deutlich verschieden, sowohl nach der Befallsrate (Abbildung 3, Tabelle I) wie nach der Anzahl toter Milben, die nach Beräucherung mit Fluvalinat gefunden wurden (Abbildung 4, Tabelle II).

Die vorhandene Heritabilität weist darauf hin, daß das selektierte Merkmal zum Teil polygen (durch mehrere Erbanlagen) bestimmt ist. In der ersten Generation der Selektion wurde eine Heritabilität von 0.3 für erhöhte Resistenz und eine solche von 4.2 für verminderte Resistenz berechnet. Umweltunterschiede zwischen der Eltern- und der ersten selektierten Generation verschoben alle Reaktionen auf ein höheres Niveau und blähten die Heritablitäts-Schätzungen für erhöhte Empfänglichkeit auf. Es ist wichtig festzustellen, daß diese Umwelteinflüsse die Schätzungen für erhöhte Resistenz nicht ausschalteten.

Obwohl für die Auswahl der Eltern der vierten Generation innerhalb der Linien kein Selektionsunterschied bestand, zeigte die vierte Generation weiterhin Unterschiede in der Resistenz und Empfänglichkeit für *Varroa jacobsoni.*

Diese Untersuchung dokumentiert die Entwicklung von Linien der Honigbiene, die gegenüber *Varroa jacobsoni* relativ resistent, bzw empfänglich sind. Zwei Schlußfolgerungen sind offensichtlich: Erstens, die phänotypische Variabilität gegenüber *V jacobsoni* besitzt eine genetische Komponente. Zweitens, viel von dieser Variation stammt von genetischen Grundlagen, die sich durch klassische Selektionsprogramme erfassen lassen. Solche Programme werden wahrscheinlich die erwünschte Langzeit-Lösung für die Schwierigkeiten mit der Milbe *V jacobsoni* liefern.

***Varroa jacobsoni* / Resistenz / Selektion / Heritabilität**

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