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Original article

Possible host-parasite adaptations in honey bees infested by *Varroa destructor* mites*

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Abstract – We investigated *Varroa destructor* mite population growth in a line of honey bee (*Apis mellifera*) colonies hat have survived mite infestation for seven years without treatment (Bond colonies), and in a line of colonies that had been treated to control the mites (Controls). We investigated if the source of mites affected mite population growth. The results showed that the overall mite population growth rate was reduced by 82% in Bond colonies compared to Control colonies, irrespective of the mite source (mites from Bond or Control colonies). Two traits may partly explain the difference seen in mite population growth. First, Bond colonies produced less worker and drone brood compared to Control colonies. Second, Control colonies had a larger proportion of the mites in the sealed brood compared to Bond colonies. Reduced brood production and traits leading to differences in mite distribution could be interpreted as adaptive responses to mite pressure, although a causal relationship was not demonstrated.

***Varroa destructor* / population dynamics / *Apis mellifera* / natural selection / co-adaptation / Europe**

1. INTRODUCTION

The parasitic external mite *Varroa destructor* Anderson & Trueman has become the main obstacle to profitable beekeeping since the adaptation of the parasite to the European honey bee, *Apis mellifera* L., although it appears that the honey bee colonies also succumb to virus infestations triggered and vectored by the mite (Martin, 2001). To avoid losses of colonies, beekeepers in most parts of the world treat their colonies using various methods to control the mites. These control methods are problematic for at least four reasons. First, some methods are effective (acaricides) but leave residues in the hive products, thereby jeopardizing product quality (Bogdanov et al., 1998; Wallner, 1999). Second, highly effective acaricides often lead to the mites evolving resistance to the applied drugs (Sammataro et al., 2005). Third, some control methods are less problematic from a residue point of view but are often less effective, more laborious, or damage the bees to varying degrees (Imdorf et al., 1990, 1999; Charrière and Imdorf, 2001). Fourth, the control of mites by beekeepers removes the selective pressure on both the host and the parasite (and viruses) that could produce host-parasite co-evolution with long term survival of both (Fries and Camazine, 2001).

Over several decades, it has become obvious that the Africanized honey bees in South America withstand *V. destructor* mite infestations without being seriously damaged. The process leading up to this co-existence between the host and the parasite has not been documented, but several factors are probably involved (see review in Rosenkranz, 1999). It is now also evident that honey bees are likely to co-adapt with the *V. destructor* mite – virus complex, and secure survival of both the host and the parasite, not only in Africanized bees in South-America, but also in Europe (Fries et al., 2006) and in North America (Seeley, 2007).

A small honey bee population on the island Gotland in the Baltic Sea artificially infested

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by *V. destructor*, has survived mite infestations for over seven years without mite control in a project entitled the "Bond project" ("Live and let die") (Fries et al., 2006; Fries, 2007). Queens and colonies from this population of bees are hereafter referred to as "Bond queens" and "Bond colonies" respectively. Up to this date, the reasons for survival of the honey bee colonies remain unknown. We do not know if the survival of the colonies depends on traits associated with the mites, with the bees, or both.

It could be hypothesized that the adaptive process leading up to co-existence should be faster in the mite population compared to the honey bee population, because of the shorter generation interval of the mite, not to mention the adaptive capacity of viruses, in particular the single stranded RNA-viruses we find in honey bees (Morse, 1994). In South-America, it appears that the mite tolerance is associated with honey bee characteristics (Rosenkranz, 1999), but data from Europe (Milani et al., 1999) and North America (Seeley, 2007) suggest that reduced mite virulence is important for explaining colony survival where mite control is not practised.

In a factorial experiment, we compared mite population growth and bee reproduction in colonies that had not been treated to control mites and colonies that had been treated (Bond and Control bee colonies, respectively), containing mites from both types of colonies (Bond and Control mites). We demonstrated that the source of bees was important, but that the source of mites was not, in explaining the difference in mite population growth observed between Bond colonies and Control colonies.

2. MATERIALS AND METHODS

Twenty queens (Bond queens) were produced from two of the original colonies that had survived without *V. destructor* control since 1999. The queens were mated within the same population of honey bees (N = 13). The breeders were chosen from the two best colonies in the spring 2005. Thus, the strongest Bond colonies in 2005 were overrepresented in the experimental population in the experiment presented here. Another 20 queens (Control queens) were produced from two different breeder queens by a local queen breeder rearing honey bees resembling *A. mellifera ligustica*. This queen breeder had earlier supplied approximately 20% of the breeding material for the colonies not exposed to mite control for seven years (see Fries et al., 2006 for details). However, the genetic relationship between the Bond bees and the Control bees are unknown today since the Bond bees have reproduced and changed queens without interference since 1999. On June 20, 2005, each queen was marked with paint on the thorax and was introduced into 1.2 kg of bees and placed into a 10 frame hive body of the Swedish standard frame 366×222 mm. The bees originated from 15 colonies where Apistan strips had been in place for 8 weeks prior to harvesting the adult bees. A sample of 100–200 adult bees to be analysed for *V. destructor* mites was taken from each of the 40 hives directly after queen introduction. None of these 40 samples contained any mites.

The colonies were divided into two apiaries, A an B, isolated from one another and from other known honey bee colonies, with 20 colonies in each apiary. In apiary A, approximately 3 dL of adult bees from mite-infested colonies that had been subjected to mite control (Control mites) were added into all colonies. A separate sample of 3 dL of adult bees was investigated to estimate how many mites that were added into each colony. This sample contained 40 female mites (Control mites).

In apiary B, approximately 2 dL adult bees collected from the original Bond colonies that had survived without mite control since 1999, were added into all of the colonies. A separate sample of 2 dL of adult bees was investigated to estimate how many mites that were added into each colony. This sample contained 105 female mites (Bond mites).

All colonies were managed as normal colonies and were fed sugar solution for winter during August 2005. Because of the obvious risk of mixing mites among bee colonies, only one mite provenance could be used in each apiary. Therefore, the design did not allow for a separation of the possible effects of apiary from those of mite origin, but this is not a problem if the apiary effect is non-significant.

In early May 2006, based on wintering results (four dead colonies), presence of unmarked queens (two colonies), drone laying queens (4 colonies) and the general colony conditions (three colonies deemed to weak for further comparisons), it was decided to use a total of 27 colonies for comparing mite and bee population growth during the breeding

season. These colonies had the following distribution: Apiary A with Control mites contained five colonies with Bond queens and seven colonies with Control queens; Apiary B with Bond mites contained seven colonies with Bond queens and eight colonies with Control queens. Beginning in early May, the number of bees and number of brood cells (worker brood and drone brood separately) were estimated on approximately a monthly basis using the Liebefeld method (Imdorf et al., 1987). This method required lifting each from a colony and estimating the number of bees and sealed brood cells of each cast, on each comb side. When the same person is responsible for all the estimates, as in this experiment, the accuracy in comparative work is high (Imdorf et al., 1987). At the same time samples of approximately 200 worker brood cells and, if available, approximately 100 drone cells were sampled. Approximately 200 adult worker bees were also shaken off brood combs and collected. All samples were investigated in the laboratory for the number of adult *V. destructor* females. Samples were collected on May 9, June 7, July 6, August 1, September 3, and September 29 when only little brood production remained. On November 1, samples of approximately 200 adult bees were collected from the 25 colonies wintered (two colonies were not wintered because of late queen failure), and investigated for *V. destructor* mites.

Based on the observed number of bees and brood in each colony, and the number of mites in each bee and brood sample, the total number of mites per colony was estimated. Based on the same data, the distribution of mites among adult bees and among brood cells within each colony was also calculated by multiplying the measured infestation rate of bees and two types of brood by the estimated total number of bees and brood cells.

2.1. Statistics

We used linear repeated measures mixed-effects models to test the importance of the source of mites and the source of bees, drone and worker brood production, *V. destructor* population size and mite infestation level on adult bees. Mite population size was log-transformed [$\log_{10}(x)$] prior to the analysis. Because mite population size increased logarithmically over time, we could perform analysis of covariance for this variable. For the other dependent variables, sampling occasion was assumed as a fixed factor. All other factors included in the model, i.e. mite origin and queen origin, were considered as fixed effects.

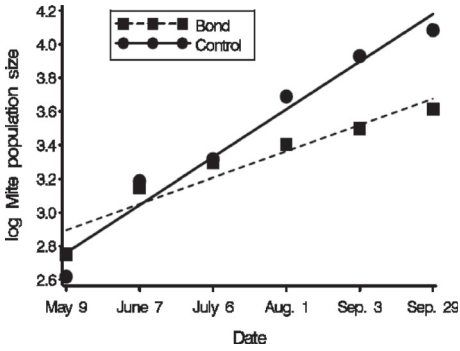

Figure 1. Average mite population size (log10-transformed) over the season, in Bond (N = 12) and Control queen colonies (N = 15). The differing regression line slopes demonstrate the significant 'Time × Queen origin' effect for Mite population size in Table I. Because mite population growth rate did not differ between apiaries (i.e. n.s. 'Time × Mite origin' interaction for Mite population size in Tab. I) data from apiaries were pooled in the figure.

In each colony multiple measurements were taken over time. As measurements from a colony were likely to co-vary over time, each measurement could not be considered as an independent observation. Thus, we analysed data with a repeated measures approach (Little et al 1996). Using Aikaike's information criteria (AIC) we tested, for each dependent variable, which covariance structure to assume given the data (Littell et al., 1996). We tested compound symmetric, autoregressive order 1, and unstructured covariance structures, and chose the one that gave the best (lowest) AIC value in each case (Littell et al., 1996).

We started by analysing a full model including all possible interactions. Non-significant factors were sequentially excluded from the model starting with the higher order interactions. Factors that were part of significant interactions were kept in the model (Crawley, 2002). We used Proc Mixed in SAS 9 for Linux for all statistical analyses (SAS, 1999).

3. RESULTS

In both apiaries with different mite sources, the mite populations increased more rapidly in the Control colonies compared to the Bond colonies (Tab. I, Fig. 1). There was no

Table I. Final linear mixed-effects models describing the effects of mite and queen origin (Bond or Control) as well as their interactions from 27 colonies. Non-significant factors that were part of significant interactions were not removed.

	Covariance structure[†]	d.f.	F	*P*
Mite population size	ar(1)			
Mite origin		1.24	4.8	0.04
Queen origin		1.24	4.1	0.05
Time[††]		1.128	150.9	<0.0001
Time × Queen origin		1.128	12.3	0.0006
Worker brood quantity	cs			
Mite origin		1.24	1.6	0.22
Queen origin		1.24	7.4	0.01
Time		5.121	64.4	<0.0001
Mite origin × Time		5.121	3.7	0.003
Drone brood quantity	un			
Mite origin		1.24	2.3	0.14
Queen origin		1.24	4.5	0.04
Time		5.24	17.4	<0.0001
Queen origin × Time		5.24	4.2	0.007
Mite origin × Time		5.24	3.4	0.02
Proportion of mites on bees	cs			
Queen origin		1.25	17.2	0.0003
Time		5.116	7.5	<0.0001
Queen origin × Time		5.116	2.8	0.02
Bee population size	cs			
Mite origin		1.24	0.60	0.45
Queen origin		1.24	0.17	0.68
Time		5.117	61.3	<0.0001
Queen origin × Time		5.117	2.5	0.03
Mite origin × Time		5.117	4.6	0.0007

[††] Covariance structure used based on Akaike's information criteria; autoregressive order 1 ar(1), unstructured (un) or compound symmetric (cs).

[†] Time was set to continuous for the analysis of *Varroa* population size.

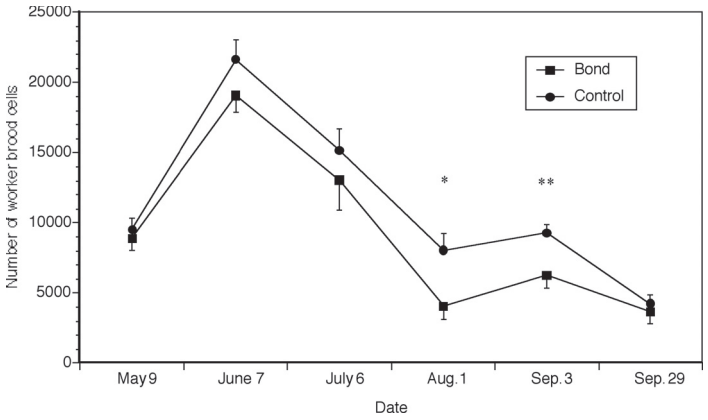

Figure 2. Total number of worker brood cells estimated in colonies with Bond queens (N = 12) and with Control queens (N = 15). Errors bars are – SE for Bond colonies and + SE for Control colonies. * $P < 0.05$, ** $P < 0.01$, *t*-tests.

significant difference in growth rate depending on mite source, but there was a difference in mite infestation level between apiaries, which was due to the difference in the initial inoculated mite levels (see Methods). Thus, the slower mite population growth in the Bond colonies appeared to be linked to the honey bee source, rather than to the source of mites. Toward the end of the season (September 29), the mite population was approximately three times higher in the control colonies compared to Bond colonies (Fig. 1). The mite infestation rate of adult bees in broodless colonies on November 1 was 0.42 ± 0.06 and 1.0 ± 0.16 in Bond colonies and Control colonies respectively.

Bee provenance determined the amount of worker brood, with a larger overall amount of worker brood in Control colonies compared to Bond colonies (Fig. 2, Tab. I). Overall production of drone brood was not significantly different in Bond compared to Control colonies (Fig. 3, Tab. I), but the production was higher in Control colonies on two occasions. The significant Mite origin × Time factor (Tab. I) was because the apiaries differed in brood production on the third observation occasion only. On all other dates the difference was not significant. The overall level of brood production did not differ between apiaries infested by mites of different origin (Tab. I).

The overall colony sizes (adult bee populations) did not differ significantly between apiaries (Tab. I), nor was there an overall significant difference in colony size between Bond colonies and Control colonies (Tab. I). However, Bond colonies were significantly smaller ($P < 0.05$) on two measuring occasions, June 7 and August 1.

The analysis of the distribution of mites among brood cells and among adult bees demonstrated that the mites were differentially distributed in Bond colonies compared to the Control colonies. During the last three sampling occasions, a larger proportion of the mites were present on adult bees in the Bond colonies compared to control colonies (Fig. 4, Tab. I).

4. DISCUSSION

The presented data suggest that the natural selection pressure to which Bond colonies have been exposed from mite infestations may have resulted in adaptations that result in slower population growth of the mites. Furthermore, the results clearly show that the main reasons for this development are due to the bees and not with the mites. This contradicts the only two studies investigating colonies that have survived mite infestations in Europe or North America (Milani

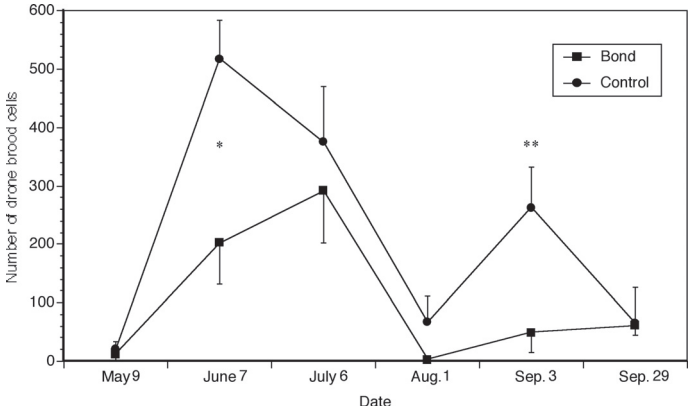

Figure 3. Total number of drone brood cells estimated in colonies with Bond queens (N = 12) and with Control queens (N = 15). Errors bars are – SE for Bond colonies and + SE for Control colonies. * $P < 0.05$, ** $P < 0.01$, *t*-tests.

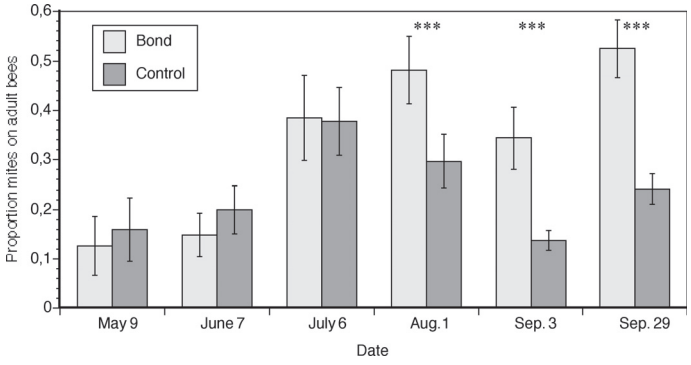

Figure 4. The proportion of mites located on adult bees as estimated from bee and brood samples. Errors bars are ± SE. *** $P < 0.001$, *t*-tests.

et al., 1999; Seeley, 2007). Both studies concluded that less virulent mites were of major importance. The study by Seeley (2007) demonstrated that colonies with queens from a feral population of bees, that now re-colonized the Arnot forest in Northeastern USA, indeed have a similar mite population growth compared to colonies with commercial Carniolan bees. The conclusion was that survival of the feral population most likely was dependent on avirulent mites (Seeley, 2007). However, a complete transfer experiment of the host and the parasite was not performed, demonstrating avirulence in the mites. Together with the current study, we now have independent studies suggesting that adaptations that lead to host-parasite co-existence can occur both in the bee and probably also in the mite populations. This scenario may evolve provided the beekeepers do not interfere in the host-parasite coevolution by controlling the mites. However, it should be emphasised relying on a natural selection strategy to overcome problems with *V. destructor* mites is likely to cause massive bee losses and to be totally unacceptable to apiculture, agriculture and horticulture, not to mention the ecological consequences with reduced pollination.

The *V. destructor* mite population growth was significantly slower in colonies with Bond queens compared to Control queens (Fig. 1, Tab. I), leading to a mite population size that was on average three times higher in the Control colonies at the end of the breeding season (Fig. 1). The infestation rate of adult bees in broodless colonies in early winter

(November 1) was also significantly higher in Control colonies compared to Bond colonies. However, it should be noted that the mite population levels (Fig. 1) and adult bee mite infestation levels in early winter (0.42 ± 0.06 mites/bee) were high also for the Bond bees. These mite levels suggest that Bond bees may become severely damaged by the mite infestations, although some colonies may survive. Thus, we emphasize that what we demonstrate in the Bond bees is only a relative mite tolerance, yielding a slower mite population build up compared to colonies where mite control has been practised.

This study does not explain the mechanisms leading to the relative mite tolerance in Bond bees compared to Control bees. Modelling the mite population dynamics demonstrates that the total amount of brood produced is a critical parameter that influences both how the mites distribute themselves between brood and adult bees, as well as the total production of mites (Fries et al., 1994; Calis et al., 1999). The brood measurements demonstrate lower overall worker brood production in the Bond bees (Fig. 2). For drone brood, the relative difference in brood production was even greater between Bond colonies and Control bees on two occasions (Fig. 3). The difference in drone brood production should have influenced the mite population growth more than the difference in worker brood production since the reproductive success of the mites and mite population growth rates are higher when more drone brood is available (Schulz, 1984). Therefore, the differences observed in brood production between Bond colonies and Control colonies were probably one factor responsible for the differences in mite population growth rates. Reducing the total amount of brood produced could be an adaptive response to mite infestation pressure, although we cannot rule out that other factors may have selected for reduced brood rearing in the Bond bee population, irrespective of mite pressure.

The overall reduced amount of worker brood in Bond colonies (Fig. 2, Tab. I) did not result in an overall significantly smaller colony size (Tab. I), although Control colonies were significantly larger on two measuring occasions ($P < 0.05$, t-test). Greater worker brood production could be expected to produce larger colonies. Although the difference in worker brood production was significant (Tab. I), the difference was not huge (Fig. 2). It is difficult to determine if this result reflects low precision in the estimates of colony size or differences in adult bee longevity between the groups. What is obvious is that the total brood production in Bond colonies was significantly less (Figs. 2, 3, Tab. I) but that colony sizes did not differ dramatically (Tab. I).

Mite distribution among the adult bees and among the brood differed between Bond and Control bees. During the last three observation occasions, the Bond bees had an increasing and significantly larger proportion of the mites located on the adult bees. Again, and not surprising, modelling the mite population growth demonstrated that the distribution pattern between adult bees and brood is important for determining the mite population growth (Fries et al., 1994; Calis et al., 1999). It could be argued that with larger amounts of brood a higher proportion of mites would be expected in the Control bees, simply because the bee/brood ratio is important for determining the mite invasion rate into the brood (Boot et al., 1995). However, on the last observation occasion, on September 29, there was no significant difference in the amount of brood between the groups compared, neither for worker brood nor for drone brood. On August 1, the difference was small and occurred only for worker brood (Figs. 2 and 3). From this we conclude that the mites did distribute themselves differently between Bond bees and Control bees, which in part could explain the slower mite population increase on Bond bees. The reasons for differences in distribution pattern remain unknown, but it has been suggested that variations in inherent brood attractiveness for the adult female mites may influence the mite distribution and mite population growth (Guzman-Novoa et al., 1999; Vandame et al., 1995). Alternatively, the Bond bees may have been removing mite-infested brood from the colony through hygienic behaviour (Spivak and Reuter, 2001). It is striking that there was an increased proportion of the mites in the brood with increased mite load in the Control bees, but that this effect was

not seen in the Bond bees (Fig. 4). Density dependent effects from mites have been registered on mite population growth in Africanized bees, but not to the same extent on bees of European origin (Vandame et al., 1995). Our results suggest that this parameter (density dependent distribution of mites between brood and adult bees) needs further study.

In conclusion, the natural selection pressure to which Bond colonies have been exposed to from mite infestations, may have resulted in adaptations that result in slower population growth of the mites, although the direct causal relationship between mite pressure and changes in brood production or mite distribution pattern was not demonstrated. The reduced mite population growth in Bond colonies was found irrespective of mite source, suggesting that traits associated with the bees and not with the mites were responsible for this reduced growth rate. The reduced mite population growth may partly be explained by a lower total production of worker and drone brood in the Bond colonies. Furthermore, the distribution of mites between brood and adult bees differed between Bond colonies and Control colonies. A lower proportion of mites in the sealed brood in Bond colonies may also in part explain the reduced mite population growth in these colonies.

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Adaptations possibles de l'hôte au parasite chez les abeilles domestiques infestées par les acariens *Varroa destructor*.

***Varroa destructor* / *Apis mellifera* / dynamique population / sélection naturelle / co-adaptation / Europe**

Zusammenfassung – Mögliche Parasit-Wirt-Anpassungen bei Honigbienen, die von Varroa Milben befallen sind. Wir untersuchten, ob sich die *Varroa*-Populationsdynamik zwischen Honigbienenvölkern, die über 7 Jahre ohne jegliche *Varroa*-Behandlung überlebten (so genannte Bond-Völker) und Bienenvölkern, in denen regelmäßige *Varroa*-Behandlungen durchgeführt wurden (Kontrollvölker), unterscheidet. Zusätzlich untersuchten wir, ob die Herkunft der Milben das *Varroa*-Populationswachstum beeinflusst.

Von zwei Bienenvölkern, die seit 1999 ohne Varroa-Behandlung überlebten, wurden 20 Königinnen produziert (Bond-Königinnen) und innerhalb dieser Bond-Population begattet. Weitere 20 Königinnen (Kontrollköniginnen) wurden von einem lokalen Züchter auf der Basis von *A. mellifera ligustica* produziert. Diese Königinnen wurden in milbenfreie Völker eingeweiselt.

Die Völker aus beiden Versuchsgruppen wurden auf zwei isolierte Bienenstände (A + B) mit je 20 Bienenvölkern aufgeteilt. Am Bienenstand A wurden jedem Bienenvolk ca. 40 weibliche Milben aus Völkern mit Varroa-Behandlung zugegeben. Am Bienenstand B wurden jedem Bienenvolk ca. 105 Milben aus den originalen Bond-Völkern, die seit 1999 ohne Behandlung überlebt hatten, zugegeben.

Die Bienenpopulation wurde monatlich erfasst, indem der Brutumfang sowie die Anzahl der Bienen abgeschätzt wurden. Gleichzeitig wurden jeweils Brut- und Bienenproben entnommen und auf Varroa-Befall hin untersucht.

Die Ergebnisse lassen vermuten, dass der natürliche Selektionsdruck bei den Bond-Völkern zu einer Anpassung geführt hat, die sich in einem geringeren Populationswachstum der *Varroa*-Milben in den Bond-Versuchsvölkern ausdrückt. Da dieser Effekt unabhängig von der Herkunft der Milben ist, scheinen für das geringere Populationswachstum in erster Linie Eigenschaften der Bienen und nicht Eigenschaften der Milben verantwortlich zu sein. Bei den Auswertungen fielen zwei Eigenschaften auf, die zumindest teilweise die Unterschiede in der Zunahme der Milbenpopulation zwischen Bond- und Kontrollvölkern erklären könnten. Erstens produzieren Bond-Völker weniger Brut (sowohl Drohnen- als auch Arbeiterinnenbrut) als die Kontroll-Völker. Zweitens unterscheidet sich die Verteilung der Milben innerhalb des Bienenvolkes zwischen den Bond- und Kontrollvölkern: In den Kontroll-Völkern befand sich ein größerer Anteil an Milben innerhalb der verdeckelten Brut.

Eine Reduzierung des Brutumfangs mit einer Beeinflussung der Verteilung der Milben zwischen Bienen und Brut könnte eine adaptive Antwort auf einen langfristigen Infektionsdruck

durch *Varroa*-Milben sein. Allerdings können wir nicht ausschließen, dass unabhängig vom Infektionsdruck auch andere Faktoren bei der Bond-Bienenpopulation eine Selektion auf reduziertes Brutaufkommen bzw. auf eine spezifische Verteilung der Milben begünstigt haben.

***Varroa destructor* / Populationsdynamik / *Apis mellifera* / natürliche Selektion / Co-Adaptation / Europa**

REFERENCES

Bogdanov S., Kilchenmann V., Imdorf A. (1998) Acaricide residues in some bee products, J. Apic. Res. 37, 57–67.

Boot W.J., Schoenmaker J., Calis J.N.M., Beetsma J. (1995) Invasion of *Varroa jacobsoni* into drone brood cells of the honey bee, *Apis mellifera*, Apidologie 26, 109–118.

Calis J.N.M., Fries I., Ryrie S. (1999) Population modelling of *Varroa jacobsoni* Oud., Apidologie 30, 111–124.

Charrière J.D., Imdorf A. (2001) Träufelbehandlung mit Oxalsäure, Schweiz. Bienenztg. 121, 18–22.

Crawley M.J. (2002) Statistical Computing: An Introduction to Data Analysis Using S-Plus. Wiley, Chichester, UK.

Fries I. (2007) Varroaangripna bin som överlever utan behandling i ett nordiskt klimat, Bitidningen 105, 14–16.

Fries I., Camazine S. (2001) Implications of horizontal and vertical pathogen transmission for honey bee epidemiology, Apidologie 32, 199–214.

Fries I., Camazine S., Sneyd J. (1994) Population dynamics of *Varroa jacobsoni*: a model and a review, Bee World 75, 5–28.

Fries I., Imdorf A., Rosenkranz P. (2006) Survival of mite (*Varroa destructor*) infested honey bee (*Apis mellifera*) colonies in a Nordic climate, Apidologie 37, 564–570.

Fries I., Hansen H., Imdorf A., Rosenkranz P. (2003) Swarming in honey bees (*Apis mellifera*) and *Varroa* mite (*Varroa destructor*) population development in Sweden, Apidologie 34, 1–9.

Guzman-Novoa E., Sanchez A., Page R.E., Garcia T. (1999) Susceptibility of European and Africanized honeybees (*Apis mellifera* L.) and their hybrids to *Varroa jacobsoni* Oud., Apidologie 27, 93–103.

Harris J.W., Harbo J.R. (2004) Selective breeding for honey bees with a low percentage of varroa mites in capped brood [abstract], Am. Bee J. 144, 405.

Imdorf A., Bühlmann G., Gerig L., Kilchenmann V., Wille H. (1987) Überprüfung der Schätzmethode zur Ermittlung der Brutfläche und der Anzahl Arbeiterinnen in freifliegenden Bienenvölkern, Apidologie 18, 137–146.

Imdorf A., Bogdanov S., Ibáñez Ochoa R., Calderone N.W. (1999) Use of essential oils for the control of *Varroa jacobsoni* in honey bee colonies, Apidologie 30, 209–228.

Imdorf A., Kilchenmann V., Maquelin C. (1990) Optimale Ameisensäureanwendung, Schweiz. Bienenztg. 113, 378–385.

Littell R.C., Milliken G.A., Stroup W.W., Wolfinger R.D. (1996) SAS system for mixed models, SAS Publishing, Cary, NC, USA.

Martin S.-J. (2001) The role of Varroa and viral pathogens in the collapse of honeybee colonies: A modelling approach, J. Appl. Ecol. 38, 1082–1093.

Milani N., Pechhacker H., Della Vedova G. (1999) Reduced fertility in a European population of *Varroa jacobsoni* Oud., Apidologie 30, 435–436.

Morse S.S. (Ed.) (1994) The evolutionary biology of viruses, Raven Press, New York, USA.

Rosenkranz P. (1999) Honey bee (*Apis mellifera* L.) tolerance to *Varroa jacobsoni* Oud. in South America, Apidologie 30, 159–172.

Sammataro D., Untalan P., Guerrero F., Finley J. (2005) The resistance of varroa mites (Acari: Varroidae) to acaricides and the presence of esterase, Int. J. Acarol. 31, 67–74.

SAS (1999) SAS Institute, Cary, NC, USA.

Schulz A.E. (1984) Reproduktion und Populationsentwicklung der parasitischen Milbe *Varroa jacobsoni* Oud. in Abhängigkeit vom Brutzyklus ihres Wirtes *Apis mellifera* L., Apidologie 15, 401–420.

Seeley T.D. (2007) Honey bees of the Arnot Forest: a population of feral colonies persisting with *Varroa destructor* in the northeastern United States, Apidologie 38, 19–29.

Spivak M., Reuter Gary S. (2001) *Varroa destructor* infestation in untreated honey bee (Hymenoptera: Apidae) colonies selected for hygienic behavior, J. Econ. Entomol. 94, 326–331.

Vandame R., Otero-Colina G., Colin M. (1995) Dinámica comparativa de las poplaciones de *Varroa jacobsoni* en colmenas de abejas europeas y africanizadas en Córdoba, Ver. In IX Seminario Americano de Apicultura, 1995, Colmina, Mexico, pp. 61–62.

Wallner K. (1999) Varroacides and their residues in bee products, Apidologie 30, 235–248.