

Review article

**Honey bee (*Apis mellifera* L.)
tolerance to *Varroa jacobsoni* Oud. in South America**

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Abstract – The study of *Apis mellifera* colonies in South America that are tolerant to *Varroa jacobsoni* may help us to understand the general requirements for *V. jacobsoni* tolerance. The situations in Brazil, Uruguay and Argentina are described. There are clearly different modes and levels of *V. jacobsoni* tolerance in these countries. The Africanized honey bee in tropical Brazil has extremely low infestation rates, and reduced *V. jacobsoni* fertility in worker brood is a striking tolerance factor. In Uruguay, long-term survival of untreated and presumably non-Africanized honey bee colonies was confirmed. Striking tolerance factors, however, were not evident in Uruguay and infestation levels are higher than in Brazil. In the non-tropical regions of Argentina honey bee colonies cannot survive without *V. jacobsoni* treatment. The actual data cannot answer the question whether the observed *V. jacobsoni* tolerance is a trait of the host or is due to lower virulence of the parasite. The ecological conditions which may have favoured natural selection in Brazil and Uruguay are discussed.
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***Varroa jacobsoni* / host–parasite relationship / tolerance / Brazil / Uruguay**

1. INTRODUCTION

Tolerance¹ to varroosis is defined as the capacity of a honey bee colony to coexist with an infestation of the parasitic mite, *Varroa jacobsoni* Oud. (Acari: Varroidae), without the need for treatments applied by the

beekeeper. We do not have any reports of such tolerant *Apis mellifera* stocks within the United States and Europe, and annual treatments of colonies in these continents are still necessary for colonies to survive. Ten and twenty years of coexistence of the bees and mites in the US and Europe,

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¹ Some authors use the term 'resistance' for the phenomenon of long-term survival of *Varroa*-infested honey bee colonies.

respectively, have not led to a balanced host–parasite relationship. A stable relationship is urgently needed because of increasing problems with residues from chemical treatments in bee products, and resistance of mites to acaricides [66].

Intensive breeding work in Europe and the United States [10, 15, 31, 34] demonstrates the feasibility of selecting for certain tolerance factors of the host, such as hygienic behaviour [6]. Recently, some promising results demonstrated a slower increase of the *V. jacobsoni* population in pre-selected colonies [31, 61]. But there is no reliable information from the United States or Europe that, under non-experimental conditions, colonies can survive for extended periods without treatment. Reports of *V. jacobsoni*-tolerant stocks by a commercial queen breeder [65] could not be verified by objective performance tests [11, 35]. No serious predictions have been made for the time required to establish *V. jacobsoni* tolerance through selective breeding. Tolerance to *V. jacobsoni* is a multifactorial phenomenon. The study of already balanced host–parasite relationships between the mite and *A. mellifera* may help i) to evaluate the important host factors, and ii) to understand the ecological prerequisites for the development of *V. jacobsoni* tolerance.

The highly tolerant original host species, *A. cerana*, is only of limited value in understanding the relationship between the mites and *A. mellifera*. First, the commercial bee-keeping practices with *A. mellifera* in the western hemisphere differ considerably from the management practices of *A. cerana* in Asia. Second, the lack of mite reproduction in worker brood is the most striking tolerance factor in *A. cerana*; yet it seems to be a species-specific phenomenon. In *A. mellifera* colonies, female mites can generally reproduce in both worker and drone brood; a few recent and exceptional cases have

been reported from Indonesia in which mites did not reproduce in some *A. mellifera* colonies [2].

Substantial reports of tolerant *A. mellifera* populations are restricted to North Africa [51] and South America only. Long-term studies of the Africanized honey bee in Brazil are available. Meanwhile, research activities have also focused on tolerance in *A. mellifera* in other parts of Central and South America, where the climatic conditions and the honey bee races are more similar to those in subtropical and temperate latitudes.

In this review, *V. jacobsoni* tolerance of *A. mellifera* in two regions of South America is evaluated:

- tropical South America (Brazil);
- subtropical (temperate) South America (Uruguay, Argentina).

Possible tolerance factors, and the ecological conditions which may have favoured the establishment of tolerance, are discussed. Published data and as yet unpublished results of our research group² are presented and discussed.

2. *V. JACOBSONI* TOLERANCE IN BRAZIL

2.1. Situation

The first *V. jacobsoni* mites arrived in Brazil in 1979, introduced via Paraguay from Japan [28]. To date, acaricides against *V. jacobsoni* are not registered in Brazil and treatment against *V. jacobsoni* is generally not practised [18]. The common race of honey bee is the Africanized bee, a hybrid of European races and the introduced *A. m. scutellata* [47]. The mechanism of ‘Africanization’ is still discussed controversially (hybridization versus spread of a pure African gene pool) but the actual interpre-

² Data are contributed by P. Aumeier, M. Husemann, R. Kirsch, Z. Paulino-Simões, M. Stürmer.

tation of mtDNA frequencies [47] and the clear existence of hybridization areas in Mexico, Uruguay and Argentina [6, 12, 47] strongly support the spread of hybrid populations which are formed by natural selection. The ecological consequences are quite clear: during the last 40 years this honey bee has occupied most of tropical and subtropical South America and has recently reached the USA [33]. Requeening of Africanized colonies with European queens occurs but beekeepers generally prefer Africanized bees [18]. Exact data on the levels of *V. jacobsoni* infestation are rare, because there is no economic need to monitor mite population dynamics. Losses of Africanized honey bee colonies due to varroosis are not reported and possible negative effects on honey production seem to be negligible.

Average infestation rates of adult bees in Africanized colonies are mainly below 5%; higher values were detected only during the first years after the occurrence of the mite in Brazil ([18], De Jong, pers. comm.). In a 3-year study (1986–1988) in Brazil, Moretto et al. [41, 43] found variation in infestation rates according to climate, although they only published the variation in infestation on adult bees which depends on the amount of bee brood. Accordingly, adult bee infestations above 10% were reported only from a cold mountain area in the state of Santa Catarina during periods with little brood; in tropical and subtropical areas (with brood year round) the average adult bee infestation rate remained below 5%. Interestingly, in further investigations in Santa Catarina during 1991 and 1993, Moretto et al. [45] found a significant reduction in adult bee infestation from 2.3 to 1.7%. Unfortunately, corresponding data on brood infestation rates are not published.

A few data indicate that infestation rates may be race-specific; higher infestation rates were observed in European honey bees [24, 43]. A comparison between Africanized and European honey bees, however, is difficult

because under tropical climatic conditions, the better adapted Africanized honey bees have competitive advantages. If there is no competition with Africanized honey bees for resources, European honey bee colonies also can survive mite infestation without acaricide treatment. This was demonstrated by a long-term survey on an isolated and honey-bee-free tropical island in northeast Brazil, where 20 pure *A. m. ligustica* colonies, infested with mites, were introduced in 1984. The colonies have survived to date, multiplying by swarming, and confirm that European honey bee races also have the potential of *V. jacobsoni* tolerance, at least under tropical climatic conditions [20].

Information on the *V. jacobsoni* situation is sparse from Brazil's neighbouring tropical countries. In Paraguay, the level of *V. jacobsoni* tolerance seems to be comparable to that of Brazil [43, 49]. In Colombia, however, losses of colonies were reported after the spread of the mites [63]. Unlike Brazil, the use of acaricides is recommended for beekeepers and has been used already at an early stage of *V. jacobsoni* infestation. One can speculate that this treatment strategy had some influence on the development of tolerance, but with the little data available, this view is rather speculative.

2.2. Tolerance factors of Africanized honey bees in Brazil

The most obvious tolerance factor in Brazil is the low fertility of female mites in worker brood of the Africanized honey bee: only about half of the mites which invade worker brood cells lay eggs; in contrast, in drone brood about 90% of the mites are able to reproduce. It is very important to define 'fertility' strictly: all *V. jacobsoni* females which lay at least one egg are counted as fertile (cf. Harbo and Harris [32]). Ritter and De Jong [50] reported that only about 50% of *V. jacobsoni* females are able to reproduce in worker brood of Africanized bees. Periodical investigations

later on confirmed these findings ([13, 39, 42, 53, 56], see *table I*). The average number of eggs laid by reproducing mites in Africanized honey bees ranges from 3.3 to 4.0 [39, 56]. Surprisingly, similar values are reported from other honey bee races with higher percentages of fertile mites [29, 53, 57]. Some seasonal and colony-specific variation exists, but in all investigations on Brazilian Africanized bees the average percentages of fertile mites only ranged between 37 and 57%. From that we can emphasize two points:

– the reported percentage of mites that are infertile in worker brood is substantially higher compared to the average 15 % in European honey bee races in Europe and USA (reviewed in [26, 37, 56], *table I*) and could be sufficient to prevent an increase in the mite population [26], independently of other adaptations of the Africanized honey bee;

– the low mite fertility remained surprisingly stable over a 15-year period. One would expect a greater fitness of mites which are able to reproduce in both drone and worker brood.

The latter point may indicate that reduced mite fertility is more a host trait than a parasite trait. This view is supported by comparative experiments with Africanized and European honey bees at the same study site in Brazil, where about 80 % of the mites reproduced in worker brood of Italian or Carniolan honey bees ([13, 53, 56], *table I*), significantly more than in Africanized bees. Therefore, mites derived from the same source population of bees (Africanized) showed a significant difference in fertility depending on host type.

Unfortunately, we do not know the physiological reasons for non-reproduction of *V. jacobsoni* in worker brood. It is likely that the mechanisms differ from that in *A. cerana*, where the mite cannot reproduce in worker brood at all [1, 8, 55]; selection of a non-reproducing ‘*cerana* mite’ is discussed by Boot et al. [7]. In Brazil, the total lack

Table I. Percentages of infertile (= non-egg laying) *V. jacobsoni* females in singly infested worker brood cells in Brazil from 1981 to 1997 (number of cells analysed are given in parenthesis; reference is given in square brackets).

	Year of examination [reference]								
	1981–1983 [49]	1985 [13]	1986 [55]	1986–1988 [41] ¹	1991/1992 [42]	1992 [39]	1995 [4]	1996 ²	1997 ²
Africanized									
Worker brood	57 (186)	51 (337)	43 (361)	47 (1 658)	44 (1 050)	44 (373)	49 (358)	47 (509)	37 (265)
Drone brood	28 (14)	13 (?)						16 (238)	
European									
Worker brood	53 (45) ³	25 (368) ⁴	19 (152) ⁵	36 (2 098) ⁶			17 (238) ⁵	20 (392) ⁵	6 (149) ⁴

¹ Calculated from Masters thesis; ² unpublished data of our research group; publication of data in preparation; methods described in [55]; ³ *Apis mellifera ligustica*, one colony only; ⁴ *Apis mellifera ligustica*; ⁵ *Apis mellifera carnica*; ⁶ *A. m. ligustica* × Africanized hybrids.

of mite reproduction in worker brood has never been observed. The hypotheses that the non-reproducing mites are unmated [38] or that non-reproduction is a trait solely of the mite [27] are unlikely. Experiments with different brood types within the same colony [13] and artificial introduction of mites from Africanized colonies into European brood cells (Stürmer and Rosenkranz, unpublished data) clearly demonstrate an effect of the origin of the brood. A comparison of the haemolymph of Africanized and European honey bee larvae, the only nutritional resource for *V. jacobsoni* females during oogenesis and reproduction, did not reveal any differences in the content of juvenile hormone [53], proteins [40] or carbohydrates (unpublished data). Additionally, the micro-climatic conditions within the sealed brood cells are independent of honey bee race and external environmental conditions [52]. The triggering of vitellogenesis and oogenesis in *V. jacobsoni* females remains one of the important open questions for the understanding of this host–parasite relationship. Further research should focus on the initiation and course of oogenesis in the mite [62]. Additionally, we have to analyse the influence of the phoretic phase of the mite on adult bees as suggested by Rosenkranz and Stürmer [54] and Rosenkranz and Bartalszky [58] which could resolve some of the disagreements in the discussion of *V. jacobsoni* infertility. Finally, the influence of mite genetics on fertility should be considered (see Conclusions).

Grooming and removal (hygienic) behaviour of the bees is considered to be an additional important tolerance mechanism to the mite [6]. Moretto et al. [44] found Africanized honey bees were more effective in grooming mites from adult bees than were Italian bees in experiments using observation hives (38 versus 5 % of *V. jacobsoni* were removed by Africanized and *A. m. ligustica* bees, respectively). Thus, grooming may contribute to the high level of *V. jacobsoni* tolerance of Africanized honey bees in Brazil. There is evidence of a correlation

between infestation rate and grooming behaviour, but even Africanized colonies with a very low grooming efficacy have infestation rates below 5 % [46]. An exact quantitative analysis of the value of this behavioural trait remains difficult because of methodological problems [6].

Comparative studies on removal behaviour of mite-infested brood are rare. Córrea-Marques and De Jong [14] confirmed the prevalence of a specific removal behaviour in Africanized honey bees in Brazil. Aumeier et al. [4], however, could not detect any difference in the removal rate of *V. jacobsoni*-infested worker brood cells between Africanized and European (*A. m. carnica*) honey bees in Brazil.

Africanized honey bees are known to have a shorter postcapping period, which could limit the successful development of *V. jacobsoni* offspring. Rosenkranz and Engels [57] confirmed an average 8-h difference in the postcapping period between Carniolan and Africanized honey bees at the same tropical study site. The effect of these differences on mite population dynamics still has to be quantified [26]. Martin [37] assumed that a reduction in the post-capping period would only delay the build-up of a mite population within a colony.

Several studies in Mexico have confirmed the lower attractivity of Africanized honey bee worker brood compared to European brood: when brood of different origins was offered simultaneously within the same colony, European brood was twice as infested as Africanized brood [30]. In contrast to Camazine [13], recent experiments in Brazil revealed similar results with a two- to six-fold lower attractivity of Africanized worker brood compared to *A. m. carnica* brood [4]. Lower brood attractivity would prolong the phoretic phase of the mites and could, therefore, reduce the number of their reproductive cycles. These differences in brood infestation rates could depend on race-specific behaviour of the adult bee during brood care, differences in duration of the

attractive period to *V. jacobsoni* females, or differences in the attractiveness (odours) of the larva itself. The latter point could be disproven in Brazil by use of a laboratory bioassay with dated worker brood of *A. m. carnica* and Africanized bees: no race-specific differences in larval attractivity could be found [5].

Finally, the ratio of worker to drone brood and seasonal patterns of swarming and brood rearing in Africanized honey bees could limit the rate of *V. jacobsoni* reproduction [26, 37]. However, because of the defensive behaviour of the Africanized honey bee, exact and regular evaluation of the population dynamics are rare [21].

2.3. Ecological conditions which may favour *V. jacobsoni* tolerance

An important prerequisite for the rapid and obviously permanent establishment of *V. jacobsoni* tolerance was the enormous number of feral colonies of Africanized honey bees in Brazil. Even in natural rainforest ecosystems without any beekeeping activities, the honey bee is the predominant pollinator [67]. The most common means for Brazilian beekeepers to obtain honey bee colonies is to trap them using bait hives [18]. Obviously, the colonies managed by beekeepers represent only a small percentage of Brazil's large honey bee population. Therefore, the feral honey bee population is permanently exposed to selection pressure from the mite, and the total renunciation of mite treatments in Brazil may lead to a continuous input of heritable traits from feral population, favouring the process of selection for mite resistance.

3. *V. JACOBSONI* TOLERANCE IN URUGUAY AND ARGENTINA

3.1. Situation

Compared to Brazil, exact data on the *V. jacobsoni* situation in Uruguay and

Argentina during the past 20 years are rare and limited to publications in local journals. In Uruguay, the mites were first detected in 1979, with high infestation rates and losses of colonies during the first years [59]. However, reports on *V. jacobsoni* damage to colonies and the extent of treatments are contradictory. During the first years, suitable acaricides were hardly available and treatments, therefore, were rare. Within a few years the situation became more stable with respect to colony losses due to *V. jacobsoni* [59], which is supported by a report of Toscano [64], who analysed 24 788 samples of adult bees from all over the country over a 10-year period (1985–1995). The average infestation rate increased from about 6 % in 1985 to 9 % in 1992. Since then the infestation level has remained stable, with some regional variation.

Interestingly, 80 % of the 1995 samples had infestation rates below 15 %, which was considered a threshold for damage [64]. However, this long-term study did not distinguish between colonies treated and untreated with acaricides. Meanwhile, an increasing percentage of beekeepers treat their colonies because they are afraid of reduced honey yields due to high infestation rates; the actual percentage of beekeepers who do not use acaricides is estimated at 25 % (Toscano, pers. comm.).

In March 1997 we checked brood and adult bee samples from 54 colonies that had never been treated (non-treatment was confirmed by analysing wax samples for residues of the common acaricides and through long-term co-operation with these beekeepers) in the provinces of Rio Negro and Montevideo, and found average infestation rates of about 10 % in worker brood and 4 % on adult bees, with significantly lower infestation rates in the region of Montevideo. The absolute number of mites per colony confirmed by Bayvarol® treatments of 12 of these colonies ranged from 179 to 2 381 (unpublished data). For non-treated colonies and in comparison to German con-

ditions [35], these relative and absolute infestation rates are remarkably low. This preliminary result was confirmed by a 1-year study during 1998 (unpublished data): the infestation rates increased during the season with some regional variations, but there existed mechanisms to reduce the number of mites during the 'winter', when there was lower breeding activity. Summarizing, commercial beekeeping without treatment for *V. jacobsoni* is possible in Uruguay, but infestation rates are higher compared to Brazil.

The degree of Africanization of the honey bees in Uruguay is still controversial. It is assumed that Uruguay is crossed by the southern limit of Africanization, approximately at 33–34°S [12, 60]. By the use of morphometrical methods, Ruttner et al. [59] did not find evidence of Africanization of bees in the region of Maldonado. Burgett et al. [12], however, stated a 2:3:5 relation of European to Africanized to hybrid colonies when using mtDNA analysis. The bees of our test hives were morphometrically different from Brazilian Africanized bee samples (unpublished data). Without doubt, the defence and swarming behaviour of the 'Uruguay bee' is significantly different from Africanized honey bees in Brazil (unpublished data).

In Argentina, the first *V. jacobsoni* mites were detected in 1976 [22]. In the tropical northern region (with Africanized bees) reports of colony losses to *V. jacobsoni* are not known ([19]; Bedascarrasbure, 1998, pers. comm.) but statistical data are not available because beekeeping in the tropical north is on a small scale and beekeeping management and treatments for mites are minimal. Massive colony mortality during the first years of varroosis were reported from the province of Buenos Aires, the region with high developed commercial beekeeping activities [9, 19]. The damage from *V. jacobsoni* in most provinces of Argentina leads to intensive use of acaricides; today the most common treatment is the use of wooden

strips ('tablitas') coated with fluvalinate ([9]; Bedascarrasbure, 1998, pers. comm.).

The tropical northern part of Argentina is clearly dominated by the Africanized honey bee [60], while in the central and southern regions *A. m. ligustica* and the so-called 'Criolla' honey bee, a locally adapted strain, are used. The long-term survival of untreated colonies in the subtropical and temperate part of the country has never been demonstrated. This is striking because the province of Buenos Aires, for instance, is located close to southern Uruguay, where honey bee colonies have survived about 15 years without any mite treatment (see above). However, signs of *V. jacobsoni* tolerance are reported from some stocks of the Criolla bee in the province of Buenos Aires [23]. Some of these colonies showed a surprisingly high infertility of female mites in worker brood, with significant seasonal variations [22, 23, 36]. Unfortunately, at this time, these colonies containing mites with low reproductive rates are no longer available (Mancangeli, 1997, pers. comm.).

3.2. Tolerance factors in Uruguay

Since the publication of Ruttner et al. [59], the 'Uruguay bee' has been a hopeful example of a honey bee that is tolerant of *V. jacobsoni* in non-tropical regions with a low (or even no) level of Africanization ([12]; unpublished data). In a 3-year study, they found extremely low *V. jacobsoni* fertility in worker brood which even decreased during the test period. However, they did not measure 'infertility' but rather calculated successful reproduction (= number of adult daughters per mother mite) from their data (Ruttner, pers. comm.). A comparison of this calculation with other data is, therefore, difficult. In our studies (unpublished data), we found a low average percentage (11.5 %) of infertile mites in worker brood (table II), which was within the range of infertility in non-tolerant European honey bees ([58], table I). Noticeable was the vari-

Table II. Percentages of infertile (= non-egg laying) *V. jacobsoni* females in singly infested worker brood and natural mortality of adult female mites in worker brood cells of 54 honey bee colonies in two provinces of Uruguay (unpublished data).

	1997			1998		
	X	Range	n	X	Range	n
Infertility						
Rio Negro	10	0-45	628	7	5-24	3 235
Canelones ¹	14	0-33	368	15	11-22	2 355
Mortality						
Rio Negro	6	0-25	881	12	4-28	4 241
Canelones ¹	7	0-43	545	9	6-15	2 745

¹ The 1997 data includes some samples from the province of Flores.

ation in fertility and small but consistent differences between bees from Rio Negro and Canelones (*table II*). Although these data merit further evaluation, they indicate that reduced fertility of the mite cannot be responsible for the tolerance to varroosis of the 'Uruguay bee'. Our recent data do not indicate any striking tolerance factor in bees from Uruguay. There appears to be a comparatively high mite mortality of 6-12 %, on average, within worker brood cells (*table II*) and a higher percentage of unsuccessful reproduction (no production of viable adult offspring) of egg-laying mites. This may explain in part the decrease in mite population during 'winter'.

3.3. Ecological conditions which may favour *V. jacobsoni* tolerance in Uruguay

Beekeeping in Uruguay is mostly commercial or semi-commercial with beekeepers having from 100 to several thousand colonies. The use of feral colonies by beekeepers is less common than in Brazil. The colonies kept by beekeepers show a surprisingly low swarming tendency (unpublished data). Therefore, regular input of natural swarms into apiaries which may exhibit some natural tolerance to *V. jacobsoni* can-

not sufficiently explain the actual situation. The establishment of tolerance in Uruguayan bees may have been favoured by the fact that a substantial portion of beekeepers did not treat their colonies (in contrast, in Argentina, outside its tropical regions, regular acaricidal treatments of colonies are recommended and commonly practised).

The lack of queen breeding activities of the Uruguayan beekeepers means that up to 30 % of the colonies requeen themselves naturally during a year and controlled mating is not common (unpublished data). Managed honey bees in Uruguay are therefore presumably under similar selective pressure as feral honey bee populations. Data on the biology of feral swarms (and their number in relation to the managed colonies) in Uruguay are hardly available. The infestation levels of feral colonies should be recorded in further research projects.

4. CONCLUSIONS

Tolerance toward *V. jacobsoni* is clearly observed and documented in some parts of South America. However, the degree of tolerance is highly variable in different parts of South America.

– Non-tolerant honey bees exist in temperate and subtropical Argentina.

– Tolerant honey bee colonies exist in Uruguay with a relatively high mite infestation. Colony mortality is rare but economic losses can occur.

– Highly tolerant honey bees exist in tropical and subtropical Brazil. *V. jacobsoni* infestation levels are extremely low and colony losses are unknown.

According to the different infestation rates across South America, the factors that contribute to *V. jacobsoni* tolerance are not uniform. The low fertility of *V. jacobsoni* females in worker brood is the main tolerance factor of the Africanized honey bee in Brazil, obviously supported by other factors such as increased grooming and hygienic behaviour of the bees or a lower attractivity of the bee brood.

In Uruguay, a striking tolerance factor has not yet been detected and, at least, reduced fertility of mites like that in Brazil could not be confirmed (*tables I and II*). Probably, an additive effect of several traits prevents an unlimited increase of mite populations in tolerant colonies of Uruguay. Our recent studies (unpublished data) indicate a higher mite mortality in brood, a slightly reduced *V. jacobsoni* fertility in some colonies, and a higher rate of unsuccessful reproduction of fertile mites, compared to the same traits of European bees in Europe or United States. Therefore, we assume a multifactorial mechanism of tolerance of Uruguayan bees to *V. jacobsoni*, with each tolerance trait contributing a small amount to whole colony tolerance. A similar level of *V. jacobsoni* tolerance without striking tolerance factors has recently been reported from Mexico [30].

4.1. Is tolerance a trait of the honey bee or of the *V. jacobsoni* mite?

A general question is whether tolerance is a trait of the honey bee or the expression of lower virulence of the mite. The following two facts support a mite-biased selection.

1) The shorter generation time of *V. jacobsoni* versus honey bees should favour the more rapid adaptation of *V. jacobsoni* to selection pressure.

2) By use of genetic methods, three different geographically isolated mite populations could be distinguished in America [16, 17]. These groups may represent populations with different virulence (or perhaps tolerance levels of the host). Recently, the different reproductive ability of two genetically distinct *V. jacobsoni* populations from Germany and Papua New Guinea, respectively, has been demonstrated [3]. For Brazil, a Japanese origin of the mites was determined. The mites from Argentina and Uruguay, with higher virulence, have not yet been analysed. However, it is unlikely that the origin of these mites differs from that of the Brazilian ones. Further study in this field is urgently needed.

In the case of the *V. jacobsoni*–honey bee relationship, even a non-benign strategy could be advantageous for the mite: if environmental conditions favour the distribution of mites into neighbouring colonies from dying colonies through robbing or drifting bees. In general, it depends on environmental conditions, parasite and host density and gene flow within the parasite population whether a virulent or a benign strategy of the parasite is more adaptive [25]. For *V. jacobsoni*, this question remains open.

A host-dependent tolerance to *V. jacobsoni* is supported by comparative studies with Africanized and European honey bees in Brazil, which clearly reveal an influence of honey bee race [4, 43, 56]. The recent results from Uruguay demonstrate that *V. jacobsoni* tolerance is not limited to Africanized bees within a tropical climate.

Unfortunately, we have to face the fact that *V. jacobsoni* tolerance is influenced by multiple factors of the host, possibly by genetically determined virulence of the parasite, and additionally triggered by environmental conditions. This combination of

factors could create different modes and levels of tolerance depending on honey bee race, origin of the mite and climatic conditions.

Therefore, it is difficult to transpose the results from South America to the conditions in the United States and Europe. The example of Uruguay demonstrates that there are certain limitations to selective breeding activities: the evaluation and selection of numerous tolerance factors are difficult in practice and methods for measuring of small differences in particular traits are not yet available.

Nevertheless, the experience in Uruguay and the island experiment in Brazil [20] are promising, and demonstrate that with different bee races and under different climatic conditions, *V. jacobsoni* tolerance can arise. Probably we have to accept that natural selection rather than selective breeding is necessary for this. Under natural conditions, the number of swarms and drones produced by a colony will depend on the infestation level. This is supported by observations of Pechhacker [48], who revealed a five-fold lower flight activity of drones parasitized by *V. jacobsoni*. Therefore, even under sublethal infestation levels, there exists a strong selection pressure on the honey bee colony for *V. jacobsoni* tolerance. This means that more information is needed on host–parasite relationships under natural selective conditions. In temperate climates with expected high colony losses, this will be difficult. ‘Island experiments’, such as that of De Jong and Soares [20], should be performed under different climatic conditions to produce a European honey bee tolerant to *V. jacobsoni* in a temperate climate.

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Résumé – Tolérance de l’abeille mellifère, *Apis mellifera* L., à *Varroa jacobsoni* Oud. en Amérique du Sud. La tolérance à *Varroa jacobsoni* ; définie comme étant la capacité d’une colonie d’abeilles à coexister avec l’acarien sans traitements, n’a été mentionnée de façon importante que pour l’hôte d’origine, *Apis cerana* Fabr., et les populations d’*Apis mellifera* d’Afrique du Nord et d’Amérique du Sud. L’étude en Amérique du Sud des colonies d’*A. mellifera* tolérantes à *V. jacobsoni* peut aider à comprendre les conditions générales requises pour la tolérance. La situation de l’acarien au Brésil, en Uruguay et en Argentine est décrite. Les abeilles africanisées de la zone tropicale du Brésil ont des taux d’infestation extrêmement bas. L’infestation des adultes reste en général en dessous de 5 % et les apiculteurs n’effectuent pas de traitement contre *V. jacobsoni*. La fertilité réduite de *V. jacobsoni* sur le couvain d’ouvrières (en moyenne 50 % d’acariens fertiles contre plus de 80 % chez les abeilles européennes) constitue le facteur de tolérance le plus marquant (tableau 1). Quelques autres facteurs, comme le comportement hygiénique et l’attractivité du couvain, peuvent contribuer à établir une relation hôte–parasite équilibrée.

En Uruguay la tolérance à *V. jacobsoni* a été décrite il y a 15 ans par Ruttner. Nous avons pu confirmer la survie à long terme de colonies d’abeilles non traitées qui ont été classées comme non africanisées par les méthodes morphométriques. Il n’y avait pourtant aucun facteur de tolérance frappant et les taux d’infestation étaient plus élevés qu’au Brésil. Il est surprenant que, dans les régions non tropicales d’Argentine et même tout près de la frontière avec l’Uruguay, les colonies d’abeilles ne puissent survivre sans traitements. À l’évidence il existe au Brésil et en Uruguay divers modes et taux de tolérance à *V. jacobsoni*. Les données actuelles ne peuvent dire si la tolérance observée est due à un caractère de l’hôte ou à une moindre virulence du parasite. Des données complémentaires sur diverses races

d'abeilles au Brésil indiquent que les facteurs de l'hôte contribuent, au moins en partie, à la situation stable observée en Amérique du Sud. Il est urgent d'effectuer de plus amples études sur la virulence des populations de *V. jacobsoni* génétiquement différentes. Les conditions écologiques au Brésil et en Uruguay ont pu favoriser la sélection naturelle. Au Brésil la tolérance a pu apparaître au sein de l'immense population d'abeilles mellifères sauvages, continuellement soumise à une pression de sélection de la part de *V. jacobsoni*. Les pratiques apicoles au Brésil garantissent l'échange continu entre colonies sauvages et colonies conduites par les apiculteurs. En Uruguay, contrairement à l'Argentine, il faut noter l'absence de conduite extensive des colonies (l'apiculture y est principalement commerciale ou semi-commerciale) et l'absence de traitements acaricides. Les colonies d'abeilles conduites par les apiculteurs subissent vraisemblablement la même pression de sélection que la population d'abeilles mellifères sauvages.

Les exemples de tolérance à *V. jacobsoni* en Amérique du Sud soulignent l'importance de la pression de sélection naturelle dans l'établissement à long terme d'une relation hôte-parasite stable. © Inra/DIB/AGIB/Elsevier, Paris

***Varroa jacobsoni* / relation hôte-parasite / tolérance / Brésil / Uruguay**

Zusammenfassung – Varroatoleranz bei Honigbienen (*Apis mellifera*) in Südamerika. Die einzigen klaren Berichte über Toleranz gegen *Varroa jacobsoni*, definiert als die Fähigkeit von Bienenvölkern mit der Milbe zu koexistieren ohne daß eine Behandlung erforderlich ist, sind auf den Ursprungswirt *Apis cerana* sowie Populationen von *Apis mellifera* in Nordafrika und in Südamerika begrenzt. Das Studium von varroatoleranten Völkern von *A. mellifera* in Südamerika kann helfen, die grundsätzlichen Erfordernisse einer solcher Toleranz

zu verstehen. Hier werden die Situationen in Brasilien, Uruguay und Argentinien beschrieben.

Die Afrikanisierte Honigbiene im tropischen Brasilien weist extrem niedrige Befallsraten auf. Der Befall der Arbeiterinnen bleibt generell unter 5 % und die Bienenhalter führen keine Bekämpfung von *V. jacobsoni* durch. Der auffälligste Toleranzfaktor ist die verminderte Fertilität von *V. jacobsoni* in der Arbeiterinnenbrut (im Mittel sind nur 50 % der Milben fertil, im Gegensatz zu 80 % bei europäischen Bienen). Möglicherweise tragen einige weitere Faktoren wie das hygienische Verhalten oder die Attraktivität der Brut zu der balanzierten Wirt-Parasitbeziehung bei. Toleranz gegen *V. jacobsoni* wurde bereits vor 15 Jahren von Ruttner beschrieben. Wir konnten bestätigen, daß unbehandelte Honigbienenvölker über viele Jahre überlebten. Diese wurden mit morphometrischen Methoden als nicht afrikanisiert klassifiziert. Es gab allerdings keine auffälligen Toleranzfaktoren, und die Befallsgrade waren höher als in Brasilien. Überraschenderweise können in den nichttropischen Gebieten von Argentinien und sogar nahe an der Grenze von Uruguay die Honigbienen völker nicht ohne Behandlung der Varroose überleben.

Offensichtlich handelt es sich in Brasilien und Uruguay um unterschiedliche Arten und Level von Varroatoleranz. Aus den aktuellen Daten kann die Frage nicht beantwortet werden, ob die beobachtete Toleranz gegen *V. jacobsoni* auf einer Eigenschaft des Wirtes beruht oder auf eine geringere Virulenz des Parasiten zurückzuführen ist. Vergleichende Untersuchungen mit unterschiedlichen Rassen der Honigbienen deuten an, daß Wirtsfaktoren zumindest zu Teilen zu der stabilen Situation von *V. jacobsoni* beitragen. Weitere Studien über die Virulenz unterschiedlicher Populationen von *V. jacobsoni* sind dringend erforderlich.

Die ökologischen Bedingungen in Brasilien könnten die Auswirkung natürlicher Selektion begünstigt haben. In Brasilien könnte eine Varroatoleranz in der riesigen Wild-

population von Honigbienen entstanden sein, die unablässig einem Selektionsdruck durch *V. jacobsoni* ausgesetzt ist. Die Bienenhaltungspraktiken in Brasilien bedingen einen kontinuierlichen Austausch zwischen wildlebenden und bewirtschafteten Honigbienenvölkern. In Uruguay ist, im Gegensatz zu Argentinien, das Fehlen einer beständigen Völkerführung und Behandlung durch die Bienenhalter auffällig. Die bewirtschafteten Honigbienenvölker in Uruguay sind daher höchstwahrscheinlich einem ähnlichen Selektionsdruck wie wildlebende Bienenvölker ausgesetzt.

Die Beispiele von gegen *V. jacobsoni* tolerante Honigbienen in Südamerika unterstreichen die Bedeutung eines natürlichen Selektionsdrucks bei der Entstehung einer langfristig stabilen Beziehung zwischen Wirt und Parasit. © Inra/DIB/AGIB/Elsevier, Paris

***Varroa jacobsoni* / Wirt-Parasit Beziehung / Toleranz / Brasilien / Uruguay**

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