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Factors Limiting the Growth of *Varroa destructor* Populations in Selected Honey Bee (*Apis mellifera* L.) Colonies

[1]Berna Emsen, [2, 3]Tatiana Petukhova and [3]Ernesto Guzman-Novoa
[1]Department of Animal Science, Ataturk University, 25240 Erzurum, Turkey
[2]Department of Mathematics and Statistics,
[3]School of Environmental Sciences, University of Guelph,
Guelph ON, N1G 2W1, Canada

Abstract: The objective of this study was to compare the hygienic behavior of worker bees (*Apis mellifera*) as well as infestation and reproduction parameters of the parasitic mite *Varroa destructor* between groups of honey bee colonies with high and low rates of Varroa population growth. More than 150 colonies were screened for mite fall in early spring and again 16 weeks later. The 10 colonies with the Lowest rates (L) and the 10 colonies with the Highest rates (H) of mite population growth were selected. These 20 colonies were evaluated for hygienic behavior, brood and adult bee infestation rates and mite reproduction in cells. The amount of brood and the adult bee population of the selected colonies were also estimated. No differences were found between the two groups of colonies for brood or adult bee population or for hygienic behavior. However, significant differences were detected for mite infestation levels and for mite reproduction. Brood and adult bee infestation rates in the colonies of the H group were 17 and 6 times higher, respectively than in the colonies of the L group. The proportion of reproductive mites was 0.92±0.05 in the H colonies vs. only 0.40±0.16 in the L colonies. Additionally, two times more immature mites were found in singly Varroa-infested cells of H colonies than in similarly infested cells of L colonies. Furthermore, the ratio of brood to adult bee infestation rate was 2.4 times greater for the H colonies in comparison with that of the L colonies. These results indicate that brood-associated effects may influence the growth of varroa mite populations in honey bee colonies. The implications of these results are discussed.

Key words: *Varroa destructor*, *Apis mellifera*, hygienic behavior, mite reproduction, resistance

INTRODUCTION

Varroa destructor is a parasitic mite that has become the most important health problem of the Western honey bee, *Apis mellifera*, worldwide. This mite has killed millions of colonies, causing the loss of billions of dollars in agricultural crops (Sanford, 2001). There is evidence that the varroa mite is one of the factors associated with the unprecedented loss of honey bee colonies recently experienced in parts of Europe and North America (Stankus, 2008; Guzman-Novoa *et al*., 2010; Le Conte *et al*., 2010).

Several synthetic acaricides have been used to control *V. destructor* in honey bee colonies but mite resistance to the active ingredients in these pesticides has quickly developed and is now widespread worldwide (Milani, 1999). Therefore, it is possible that mite populations have become more difficult to control and are causing more damage to colonies in recent years. Other ways of controlling these mites are thus necessary. One potential approach to controlling varroa mites would be the development of honey bee strains resistant to them and several efforts are being made in Europe (Buchler *et al*., 2010) and the United States (Hunt, 2010; Rinderer *et al*., 2010) towards this goal.

Some of the natural mechanisms of resistance against varroa mites seem to be associated to adaptations that reduce mite reproduction in bee brood as well as to low brood attractiveness to the mites (Rinderer *et al*., 2010; Fries *et al*., 1994; Martin *et al*., 1997; Harbo and Harris, 2005; Danka *et al*., 2011; Locke *et al*., 2012). Additionally, hygienic behavior (Spivak, 1996; Spivak and Reuter, 2001; Ibrahim *et al*., 2007) and grooming behavior of worker bees, Moretto *et al*. (1993), Moosbeckhofer, (1997), Guzman-Novoa *et al*. (1999, 2012), Arechavaleta-Velasco and Guzman-Novoa (2001), Rinderer *et al*. (2001), Mondragon *et al*. (2005, 2006), Hunt (2010) and Andino and Hunt (2011) have been mentioned as other factors of resistance to the varroa mite.

Corresponding Author: Berna Emsen, Department of Animal Science, Ataturk University, 25240 Erzurum, Turkey

The objective of this study was to compare the hygienic behavior of worker bees as well as infestation and reproduction parameters of *V. destructor* between groups of honey bee colonies with high and low rates of varroa mite population growth.

MATERIALS AND METHODS

Screening for high and low Varroa population growth in honey bee colonies: Experiments were conducted at the Honey Bee Research Centre of the University of Guelph in Guelph, Ontario, Canada (43°N, 80°W). A total of 152 honey bee colonies headed by queens of Buckfast descent, housed in Langstroth hives were initially evaluated for adult bee population size and for varroa mite infestation levels during the last week of April (spring) and 16 weeks later in August (summer). None of the colonies in the experiments had been treated against parasitic mites since at least the previous fall.

Colony populations were estimated by counting the number of frames covered by bees. A frame was counted as 1 unit, only if completely covered by bees and this included frames in the brood chamber as well as those in the supers. Deep super frames were counted the same as brood chamber frames whereas shallow super frames were counted as 0.5 relative to deep super or brood chamber frames.

The mite population level of the colonies was determined by using screened (4 mm mesh) hive bottom boards containing sticky papers (to trap falling mites) in the surveyed hives. The number of mites that fell onto the sticky papers in a period of three days was counted and divided by 3 to obtain an average mite fall per 24 h. This evaluation was repeated on three separate and consecutive occasions over the course of 9 days for each colony, both in spring and summer. To determine how much mite populations increased in each colony in 16 weeks, the average mite fall count in the spring was deducted from the average mite fall count in the summer and the resulting figure was used to select the colonies with the highest (n = 10) and the lowest (n = 10) mite population growth (H and L, respectively from now on). In the summer, only the colonies of the two selected groups were additionally tested for hygienic behavior, brood area, varroa mite infestation levels in workers and brood and rates of mite reproduction.

Hygienic behavior evaluations: The hygienic behavior of worker bees was evaluated in each colony after freeze killing capped brood contained in four sections (4 cm diameter each) of a comb using liquid nitrogen as per Spivak and Reuter (1998). The number of capped cells within each frozen section was counted and the frame was returned to its respective hive. The number of cells that were uncapped by the bees as well as the number of cells which after being uncapped had the brood removed was recorded 48 h after brood freezing. Percentages for cell uncapping and brood removal were calculated using these data. This evaluation was repeated on three separate days for each colony with 72 h between applications of liquid nitrogen.

Evaluations of brood area: The capped brood area in each colony was estimated with digital photography. A picture of each side of brood frames was taken with a digital camera. The capped brood area from the digital pictures of each colony was measured to the nearest cm^2 using Adobe Photoshop® CS2 9.0 with a computer as per Knoop *et al.* (2006).

Evaluations of Varroa infestation levels and mite reproduction: Mite infestation levels on adult bees and worker brood were determined as follows. For adult bees, a sample of approximately 200 workers was collected from the brood frames of each hive in a jar containing 70% ethanol. The bees and the ethanol were transferred to a modified 1 L Nalgene plastic container which was internally separated into two compartments by a 3 mm screen placed horizontally near its bottom and shaken for 30 min on a shaker machine (Eberbach, Ann Arbor, MI, USA). The bottom of the container was removed and the mites were washed out into a tea strainer (1 mm mesh). The number of bees was calculated by weighing the sample and by dividing the total weight by 0.186 g, the average weight per bee. This average was obtained by weighing 100 single ethanol-soaked bees in preliminary assessments. The number of mites per 100 bees was calculated for each sample. This test was performed three times per colony and an average adult bee infestation rate was calculated.

The brood evaluations consisted of selecting two combs of capped brood from each colony. On each brood comb, 250 cells containing pupae with tanned body were manually uncapped and the contents examined under a stereoscopic microscope to determine brood infestation by varroa mites and to detect reproduction where single foundress mites were found; mites without offspring were considered infertile. Rates of mite infestation and reproduction were calculated. Additionally, the numbers of immature mites found in singly infested cells were counted and mean numbers of immature parasites per cell were obtained for the two colony groups. Ratios between the number of mites found in 100 worker brood cells and the number of mites found on 100 adult bees were

obtained to determine proportion of mites in brood and adults as a possible indication of brood attractiveness.

Statistical analyses: A paired comparison of L and H colonies for the variables measured was done. The data on percentage of uncapped cells and removed brood were arcsine square root transformed and subjected to student t-tests. The data on reproductive parameters were analyzed with Mann Whitney U tests because they were not normally distributed and could not be normalized with transformations. All statistical analyses were performed with the R-Statistical Program (R Development Core Team, Auckland, New Zealand).

RESULTS AND DISCUSSION

Mite and bee population growth: No differences were found between L and H colonies for the number of mites dropped on sticky boards in the spring ($p>0.05$) but significant differences were detected for this variable in the summer ($p<0.001$). Mite fall counts were 11 times lower in the L colonies compared to the H colonies and mite populations increased by 30 fold in H colonies, compared to a 2 fold increase in L colonies (Table 1). Regarding bee populations, no differences were detected between L and H colonies neither in the spring nor in the summer ($p>0.05$). Furthermore, there were no differences in brood area between the two groups of colonies ($p>0.05$; Table 1).

Hygienic behavior evaluations: Bees of H and L colonies did not differ for cell uncapping ($t = -1.34$; $df = 8$; $p = 0.216$) or removal of frozen brood ($t = -1.44$; $df = 8$; $p = 0.188$) although L colonies had slightly higher scores for these variables (Fig. 1).

Adult bee and brood infestation rates: Adult bees and brood of H colonies were significantly more infested with varroa mites than workers and brood of L colonies ($p<0.001$). The difference in adult bee and brood infestation rates between the two groups of colonies was 6 and 17 times, respectively. Additionally, the ratio of brood to adult bee infestation was 2.4 times greater in H colonies in comparison with L colonies and the two groups differed significantly ($p<0.05$) for this parameter (Table 2).

Varroa mite reproduction: A significantly higher proportion of Varroa foundress mites reproduced in H colonies relative to female mites in L colonies ($p<0.01$). Additionally, two times more immature mites were found in singly Varroa-infested cells of H colonies than in similarly infested cells of L colonies (Table 2).

Mite and bee population growth: No significant differences were detected in varroa mite populations between colonies in the spring but significant differences were evident 16 weeks later between L and H colony groups. Mite fall increased >30 times in the H colonies but

Table 1: Mean *Varroa destructor* and *Apis mellifera* populations per colony (±SE) estimated in colonies showing low (L, n = 10) and high (H, n = 10) mite population growth in a period of 16 weeks

Population variable[1]	L	H	U[2]	P[2]
Mite fall spring	3.5±0.80	2.9±1.10	36.5	0.3022
Mite fall summer	7.8±1.40	88.8±7.40	5.5	0.0007
Mite population growth	4.3±1.10	85.9±1.40	2.0	0.0003
Bee population spring	15.3±2.00	13.9±2.10	42.5	0.5665
Bee population summer	17.9±2.50	17.4±2.50	42.5	0.5623
Brood area	3862.1±76.6	3924.1±91.7	10.0	0.6015

[1]Mite populations were measured as number of mites fallen per day on sticky boards whereas adult bee populations were calculated from number of frames covered by bees. The amount of brood was measured in cm^2 using digital photography; [2]Comparisons and p-values within the same row indicate significant differences between L and H colony groups based on Mann Whitney U-tests

Table 2: Mean number of adult *Varroa destructor* mites in 100 worker cells or 100 worker bees or proportion of reproducing female mites or number of immature mites per reproductive foundress mite (±SE). These variables were estimated in colonies showing low (L, n = 10) and high (H, n = 10) mite population growth in a period of 16 weeks

Variable	L	H	U[2]	P[2]
Mites/100 Cells (MC)	0.8±0.100	13.7±4.900	0	0.0002
Mites/100 Bees (MB)	1.1±0.200	7.0±1.400	0	0.0002
MC/MB ratio[1]	0.7±0.200	1.7±0.300	18	0.0275
Proportion of reproducing foundress mites	0.40±0.16	0.92±0.05	24	0.0240
Immature mites/cell	1.65±0.35	3.15±0.29	14	0.0051

[1]A ratio between the number of mites in 100 worker cells and the number of mites in 100 adult bees was obtained; [2]Comparisons and p-values within the same row indicate significant differences between L and H colony groups based on Mann Whitney U tests

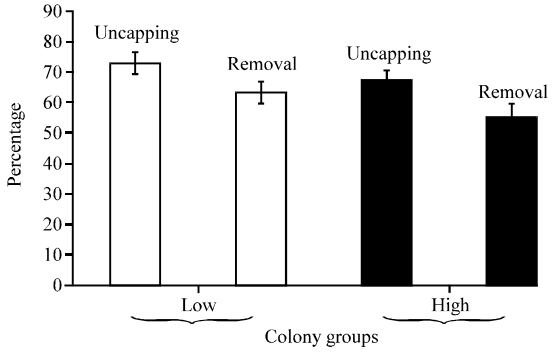

Fig. 1: Hygienic behavior of honey bee colonies with high and low Varroa population growth. Percentage of cells in comb sections containing freeze-killed brood that were uncapped and percentage of pupae that were removed (±SE) by worker bees 48 h after being introduced into honey bee colonies showing low (n = 10) and high (n = 10) mite population growth in a period of 16 weeks

only 2 times in the L colonies and the difference in Varroa population growth between H and L colonies was 20 fold. It is unlikely that these dramatic differences in mite increase had happened by chance. It is more plausible that they resulted from differences in genotypic resistance to the mite between the two groups of colonies.

It has been found in earlier studies that colonies with lower varroa infestation rates may also have less brood or adult bee populations than colonies with high varroa infestation rates (Locke and Fries, 2011), possibly as a consequence of host adaptations so that the mites have less brood cells to reproduce. However, in this study, worker bee population and amount of brood probably did not influence mite populations because there were no significant differences between both groups of colonies neither for worker bee population nor for amount of brood. Therefore, other factors were probably responsible for the differences observed in mite population growth.

Hygienic behavior evaluations: Colonies of the L group uncapped and removed a higher percentage of frozen brood than colonies of the H group but these differences were not significant. Therefore, the results do not indicate that hygienic behavior was an important factor in restraining Varroa population growth in the colonies evaluated. Other studies have suggested that hygienic behavior may provide some degree of resistance to varroa mites in honey bee colonies (Spivak and Reuter, 2001; Ibrahim *et al*., 2007; Danka *et al*., 2011) however that has not been evident in other reports (Locke and Fries, 2011), like in this case. The lack of consistency between different studies regarding the effect of hygienic behavior on the resistance of honey bees to Varroa may be due to differences in experimental settings, genotypes and assays used locality effects and *V. destructor* strains among other potential causes.

Brood (B) and Adult bee (A) infestation rates and B/A ratio: Significant differences were observed between L and H colonies for rates of varroa mite infestation in brood and adult bees in the summer which confirms the differences found in mite population growth for the same colonies. Interestingly, the two groups of colonies also varied for the ratio of Varroa infestation between brood and adult bees. A significantly higher proportion of parasitic mites were infesting adult bees rather than brood in L colonies in comparison with H colonies where most of the mites were infesting the brood. This result suggests that it was more likely that a higher proportion of mites reproduced in H colonies than in L colonies because in L colonies, most of the parasites were phoretic. Long phoretic periods would result in fewer opportunities for mite reproduction and in higher chances of being groomed off the bees' bodies. It is not possible to know why these differences in ratios of brood to adult bee infestation occurred because the experiments conducted do not permit a deeper analysis of this matter. However, like in the case of L colonies, other studies have also found lower proportions of varroa mites infesting brood than infesting adult bees which may be related to lower brood attractiveness to the mites (Harbo and Hoopingarner, 1997; De Guzman *et al*., 2007, 2008). It is also known that cuticular compounds on the brood can inhibit or favor the reproduction of varroa mites (Trouiller and Milani, 1999; Garrido and Rosenkranz, 2003; Rosenkranz and Garrido, 2004). Therefore, the identification of chemical differences in the brood of honey bee genotypes that vary in Varroa resistance, seems like a sensible step to follow in further studies aimed at finding new traits that could be useful in honey bee breeding programs.

Varroa mite reproduction: Mites in L colonies reproduced significantly less than mites in H colonies. Together with differences in the proportion of mites parasitizing brood relative to adult bees, this is the most significant result of the study. Numerous reports exist in the literature about the relationship between low rates of Varroa reproduction and lower rates of mite infestation in honey bee colonies (Ritter and De Jong, 1984; Rosenkranz and Engels, 1994; Harris and Harbo, 1999; Martin and Medina, 2004; Mondragon *et al*., 2005; Locke and Fries, 2011). However, a clear association between resistance to mite population growth and low mite reproduction rates has not been sufficiently documented in the literature.

The effect that brood seem to have on reduced varroa mite reproduction is at least in part, genetic in nature. Recently, Behrens *et al*. (2011) found three QTLs related to suppression of Varroa reproduction in a population of honey bees. Additionally, it has been suggested that brood of selected bee genotypes differentially favor or suppress Varroa reproduction and we are just beginning to understand the underlying basis of these effects. Harbo and Harris (1999) were able to breed bees for a trait they called Suppression of Mite Reproduction (SMR) by selecting and reproducing queens from colonies showing a high proportion of infested cells where female mites did not reproduce. Further studies showed that the SMR trait was in part a result of the actions of highly sensitive workers that uncapped cells containing brood with reproducing mites and removed a high proportion of them before bee

emergence (Harbo and Harris, 2005; Ibrahim and Spivak, 2006). Additionally, it has been found that when foundress mites escape from brood removed by sensitive bees they may have reduced reproductive success when they re-infest other cells (Kirrane *et al*., 2011). This trait, now called varroa sensitive hygiene or VSH could have been a factor in the results but researchers did not test for this particular trait; future evaluation of these bee populations for VSH is thus warranted. In addition to VSH, apparent low mite reproduction may be also influenced by brood associated factors that cause infertility in the mites (Harris *et al*., 2010; Danka *et al*., 2011; Kirrane *et al*., 2011).

Other factors accounting for honey bee resistance to Varroa: It has been demonstrated that grooming behavior may also contribute to the resistance of some colonies of honey bees to Varroa (Ruttner and Hanel, 1992; Fries *et al*., 1996; Rosenkranz *et al*., 1997; Moosbeckhofer, 1997; Arechavaleta-Velasco and Guzman-Novoa, 2001; Rinderer *et al*., 2001; Mondragon *et al*., 2005, 2006; Hunt, 2010; Andino and Hunt, 2011). In fact, some of the same colonies used in this study were also tested along with colonies of other genotypes in a study aimed at evaluating grooming behavior (Guzman-Novoa *et al*., 2012). It was found that bees of colonies selected for low mite population growth performed significantly more instances of intense grooming and removed a significantly higher number of mites from their bodies compared with the susceptible genotypes.

CONCLUSION

Based on the overall results of this study as well as on the results of other studies earlier, it may be hypothesized that several mechanisms could be interacting, effecting in parallel the growth of mite populations in honey bee colonies which may result in the successful limitation of varroa mite populations. This could be the case of brood-associated effects causing reduced mite reproduction, (e.g., lower brood attractiveness and induced mite infertility) coupled with a higher expression of grooming behavior and possibly hygienic behavior.

This study shows that the for practical purposes, beekeepers could select for low Varroa population growth to take advantage of several mechanisms working in synergy to provide resistance to honey bees against the mite. However, the relative importance of different mechanisms limiting Varroa population growth remains to be investigated.

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REFERENCES

Andino, G.K. and G.J. Hunt, 2011. A scientific note on a new assay to measure honeybee mite-grooming behavior. Apidologie, 42: 481-484.

Arechavaleta-Velasco, M.E. and E. Guzman-Novoa, 2001. Relative effect of four characteristics that restrain the population growth of the mite *Varroa destructor* in honey bee (*Apis mellifera*) colonies. Apidologie, 32: 157-174.

Behrens, D., Q. Huang, C. Geaner, P. Rosenkranz and E. Frey *et al*., 2011. Three QTL in the honey bee *Apis mellifera* L. suppress reproduction of the parasitic mite *Varroa destructor*. Ecol. Evol., 1: 451-458.

Buchler, R., S. Berg and Y. Le Conte, 2010. Breeding for resistance to *Varroa destructor* in Europe. Apidologie, 41: 393-408.

Danka, R.G., J.W. Harris and J.D. Villa, 2011. Expression of *Varroa* Sensitive Hygiene (VSH) in commercial VSH honey bees (Hymenoptera: Apidae). J. Econ. Entomol., 104: 745-749.

De Guzman, L.I., T.E. Rinderer and A.M. Frake, 2007. Growth of *Varroa destructor* (Acari: Varroidae) populations in Russian honey bee (Hymenoptera: Apidae) colonies. Ann. Entomol. Soc. Am., 100: 187-195.

De Guzman, L.I., T.E. Rinderer and A.M. Frake, 2008. Comparative reproduction of *Varroa destructor* in different types of Russian and Italian honey bee combs. Exp. Applied Acarol., 44: 227-238.

Fries, I., S. Camazine and J. Sneys, 1994. Population dynamics of *Varroa jacobsoni*: A model and a review. Bee World, 75: 5-28.

Fries, I., W. Huazhen, S. Wei and C.S. Jin, 1996. Grooming behavior and damaged mites (*Varroa jacobsoni*) in *Apis cerana cerana* and *Apis mellifera ligustica*. Apidologie, 27: 3-11.

Garrido, C. and P. Rosenkranz, 2003. The reproductive program of female *Varroa destructor* mites is triggered by its host *Apis mellifera*. Exp. Applied Acarol., 31: 269-273.

Guzman-Novoa, E., B. Emsen, P. Unger, L.G. Espinosa-Montano and T. Petukhova, 2012. Genotypic variability and relationships between mite infestation levels, mite damage, grooming intensity and removal of *Varroa destructor* mites in selected strains of worker honey bees (*Apis mellifera* L.). J. Invertebrate Pathol., 110: 314-320.

Guzman-Novoa, E., L. Eccles, Y. Calvete, J. McGowan, P.G. Kelly and A. Correa-Benitez, 2010. *Varroa destructor* is the main culprit for the death and reduced populations of overwintered honey bee (*Apis mellifera*) colonies in Ontario, Canada. Apidologie, 41: 443-450.

Guzman-Novoa, E., R. Vandame and M.E. Arechavaleta-Velasco, 1999. Susceptibility of European and Africanized honey bees (*Apis mellifera* L.) to *Varroa jacobsoni* Oud. in Mexico. Apidologie, 30: 173-182.

Harbo, J.R. and J.W. Harris, 1999. Heritability in honey bees (Hymenoptera: Apidae) of characteristics associated with resistance to *Varroa jacobsoni* (Mesostigmata: Varroidae). J. Econ. Entomol., 92: 261-265.

Harbo, J.R. and J.W. Harris, 2005. Suppressed mite reproduction explained by the behaviour of adult bees. J. Apicult. Res., 44: 21-23.

Harbo, J.R. and R.A. Hoopingarner, 1997. Honey bees (Hyntenoptera: Apidae) in the United States that express resistance to *Varroa jacobsoni* (Mesostigmata: Varroidae). J. Econ. Entomol., 90: 893-898.

Harris, J.W. and J.R. Harbo, 1999. Low sperm counts and reduced fecundity of mites in colonies of honey bee (Hymenoptera: Apidae) resistant to *Varroa jacobsoni* (Mesostigmata: Varroidae). J. Apicult. Res., 92: 83-90.

Harris, J.W., R.G. Danka and J.D. Villa, 2010. Honey bees (Hymenoptera: Apidae) with the trait of *Varroa* sensitive hygiene remove brood with all reproductive stages of *Varroa* mites (Mesostigmata: Varroidae). Ann. Entomol. Soc. Am., 103: 146-152.

Hunt, G.J., 2010. Breeding bees for resistance to parasites and diseases. Am. Bee J., 150: 667-669.

Ibrahim, A. and M. Spivak, 2006. The relationship between hygienic behavior and suppression of mite reproduction as honey bee (*Apis mellifera*) mechanisms of resistance to *Varroa destructor*. Apidologie, 37: 31-40.

Ibrahim, A., G.S. Reuter and M. Spivak, 2007. Field trial of honey bee colonies bred for mechanisms of resistance against *Varroa destructor*. Apidologie, 38: 67-76.

Kirrane, M.J., L.I. de Guzman, T.E. Rinderer, A.M. Frake, J. Wagnitz and P.M. Whelan, 2011. Asynchronous development of honey bee host and *Varroa destructor* (Mesostigmata: Varroidae) influences reproductive potential of mites. J. Econ. Entomol., 104: 1146-1152.

Knoop, J.A., A.M. Saffari, P.G. Kevan and J. Boone, 2006. Measuring brood digitally: An easy way to measure and record brood production in your colony. Bee Culture, 134: 19-22.

Le Conte, Y., M. Ellis and W. Ritter, 2010. *Varroa* mites and honey bee health: Can *Varroa* explain part of the colony losses?. Apidologie, 41: 353-363.

Locke, B. and I. Fries, 2011. Characteristics of honey bee colonies (*Apis mellifera*) in Sweden surviving *Varroa destructor* infestation. Apidologie, 42: 533-542.

Locke, B., Y. Le Conte, D. Crauser and I. Fries, 2012. Host adaptations reduce the reproductive success of *Varroa destructor* in two distinct European honey bee populations. Ecol. Evol., 2: 1144-1150.

Martin, S., K. Holland and M. Murray, 1997. Non-reproduction in the honeybee mite *Varroa jacobsoni*. Exp. Applied Acarol., 21: 539-549.

Martin, S.J. and L.M. Medina, 2004. Africanized honeybees have unique tolerance to *Varroa* mites. Trends Parasitol., 20: 112-114.

Milani, N., 1999. The resistance of *Varroa jacobsoni* Oud. to acaricides. Apidologie, 30: 229-234.

Mondragon, L., M. Spivak and R. Vandame, 2005. A multifactorial study of the resistance of honeybees *Apis mellifera* to the mite *Varroa destructor* over one year in Mexico. Apidologie, 36: 345-358.

Mondragon, L., S. Martin and R. Vandame, 2006. Mortality of mite offspring: A major component of *Varroa destructor* resistance in a population of Africanized bees. Apidologie, 37: 67-74.

Moosbeckhofer, R., 1997. Observations on reproduction rate of *Varroa jacobsoni* and the occurence of mutilated mites in *Apis mellifera carnica* colonies. Apidologie, 28: 193-195.

Moretto, G., L.S. Goncalves and D. de Jong, 1993. Heritability of Africanized and European honey bee defensive behavior against the mite *Varroa jacobsoni*. Rev. Brasil. Genet., 16: 71-77.

Rinderer, T.E., J.W. Harris, G.J. Hunt and L.I. de Guzman, 2010. Breeding for resistance to *Varroa destructor* in North America. Apidologie, 41: 409-424.

Rinderer, T.E., L.I. de Guzman, G.T. Delatte, J.A. Stelzer and V.A. Lancaster *et al*., 2001. Resistance to the parasitic mite *Varroa destructor* in honey bees from far-Eastern Russia. Apidologie, 32: 381-394.

Ritter, W. and D. De Jong, 1984. Reproduction of *Varroa jacobsoni* O. in Europe, the Middle East and tropical South America. Z. Angewandte Entomol. J. Applied Entomol., 98: 55-57.

Rosenkranz, P. and C. Garrido, 2004. Volatiles of the honey bee larva initiate oogenesis in the parasitic mite *Varroa destructor*. Chemoecology, 14: 193-197.

Rosenkranz, P. and W. Engels, 1994. Infertility of *Varroa jacobsoni* females after invasion into *Apis mellifera* worker brood as a tolerance factor against varroatosis. Apidology, 25: 402-411.

Rosenkranz, P., I. Fries, O. Boecking and M. Stuermer, 1997. Damaged varroa mites in the debris of honey bee (*Apis mellifera* L.) colonies with and without hatching brood. Apidologie, 28: 427-437.

Ruttner, F. and H. Hanel, 1992. Active defence against Varroa mites in a Carniolan strain of honeybee (*Apis mellifera carnica* Pollmann). Apidologie, 23: 173-187.

Sanford, M.T., 2001. Introduction, Spread and Economic Impact of *Varroa* Mites in North America. In: Mites of the Honey Bee, Webster, T.C. and K.S. Delaplane (Eds.). Dadant and Sons, Mansfield, OH., USA., pp: 149-162.

Spivak, M. and G.S. Reuter, 1998. Performance of hygienic honey bee colonies in a commercial apiary. Apidologie, 29: 291-302.

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

Spivak, M., 1996. Honey bee hygienic behavior and defense against *Varroa jacobsoni*. Apidologie, 27: 245-260.

Stankus, T., 2008. A review and bibliography of the literature of honey bee Colony Collapse Disorder: A poorly understood epidemic that clearly threatens the successful pollination of billions of dollars of crops in America. J. Agric. Food Inform., 9: 115-143.

Trouiller, J. and N. Milani, 1999. Stimulation of *Varroa jacobsoni* Oud. oviposition with semiochemicals from honeybee brood. Apidologie, 30: 3-12.