Growth of *Varroa destructor* (Acari: Varroidae) Populations in Russian Honey Bee (Hymenoptera: Apidae) Colonies

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ABSTRACT The growth rate (r) of *Varroa destructor* Anderson & Trueman (Acari: Varroidae) populations in Russian and Italian honey bee, *Apis mellifera* L., colonies was monitored from 2001 to 2003 in Baton Rouge, LA. Over this period, our results consistently showed lower mite growth in the Russian than in the Italian colonies. In 2001, instantaneous growth rates per week (r_7) were $r_7 = 0.191 \pm 0.011$ for mites in Italian colonies and $r_7 = 0.137 \pm 0.012$ in Russian honey bees for 24.3 wk. These growth rates were equivalent to 159.1- and 61.6-fold increase, respectively. Divergence in r_7 values also was observed in 2002 when Russian colonies supported a lower growth rate of $r_7 = 0.061 \pm 0.016$ (9.3-fold increase) than the Italian colonies ($r_7 = 0.122 \pm 0.01$ or a 31.7-fold increase) did after 26 wk. The lowest rate of $r_7 = 0.021 \pm 0.011$ (a 1.4-fold increase) was recorded for Russian honey bees in 2003, whereas the Italian bees in that year supported $r_7 = 0.145 \pm 0.009$ (an 18.9-fold increase) after 19 wk. This low growth rate of mite populations in Russian colonies may be attributed to several factors. Notably, as this study showed, Russian bees were less attractive to varroa mites. Furthermore, the Russian stock supported low proportions of brood infested and fewer multiply infested cells in both worker and drone brood, reduced mite reproduction, and extended phoretic period.

KEY WORDS Russian honey bees, resistance, *Varroa destructor*, *Apis mellifera*, instantaneous growth rate

Varroa destructor Anderson & Trueman (Acari: Varroidae) (Anderson and Trueman 2000) is a major parasite of honey bees, *Apis mellifera* L., worldwide. Without acaricidal treatment, high infestations of varroa mites invariably induce a complex of disease symptoms called parasitic mite syndrome (PMS) that usually results in colony mortality within 1 to 2 yr (Shimanuki et al. 1994) or even as soon as 8 mo to 1 yr despite chemical treatments particularly in areas where brood rearing is year-round (Branco et al. 1999).

The growth rates of varroa mite populations vary between geographic locations. In southeastern France, varroa populations can increase ≈100-fold within one summer (Fries et al. 1991), whereas an increase of 300-fold per year was recorded in California (Kraus and Page 1995). Mite population growth rates also can vary through time within one location; Harris et al. (2003) reported a low mite growth during a prolonged drought in Louisiana.

Also, variation in mite fecundity may be a consequence of its genetic makeup. Anderson and Fuchs (1998) reported differences between the reproductive ability of mites from Germany and mites from Papua New Guinea. Although several varroa haplotypes have been identified (Zhou et al. 2004), the Russian or Korean haplotype is the most abundant worldwide. The Japanese haplotype is scarce and is commonly found only in areas where mite infestations are less intense (de Guzman and Rinderer 1999, de Guzman et al. 1999).

Several studies have shown that some honey bee stocks are able to resist mite attack by physiological or behavioral means. Rinderer et al. (2001a,b) reported resistance in honey bees from far-eastern Russia. Harbo and Harris (1999, 2001) showed that honey bee colonies possessing the suppressed mite reproduction (SMR) trait display a kind of hygiene (Harbo and Harris 2005) that can suppress varroa mite populations. Ritter et al. (1990) reported resistance to varroa in honey bees from Tunisia; however, these bee colonies were considered too defensive to be generally used in different countries.

Overall, Russian honey bees regulate the growth of varroa populations. Fernandez (1997) claimed that parasitic proliferation is usually affected by the phenology of flowering plants, which directly affects the growth of bee populations. Russian honey bees are resource-responsive. Russian colonies build large populations in spring when pollen becomes available. Consequently, their honey production is comparable with that of Italian colonies (Rinderer et al. 2001c).

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However, unlike Italian colonies they either slow down or completely stop brood production in response to a lack of nectar flow (Tubbs et al. 2003). This resource sensitivity may contribute to Russian honey bees' varroa resistance. Also, Russian honey bees have many more injured and dead mites on the bottom boards of their hives, suggesting that they have a greater tendency to groom mites from their nests and nest mates (Rinderer et al. 2001a). However, a full examination of the possible mechanisms of resistance to varroa mites that may occur in Russian honey bees has not been reported. This study examined the role of various infestation parameters and honey bee colony populations in regulating mite population growth in Russian honey bee colonies.

Materials and Methods

Colony Setup. For the three experiments, all Russian queens were open-mated on an island, whereas all Italian queens were open-mated and were purchased from a queen breeder in California. All experiments were conducted in Baton Rouge, LA.

2001 Experiment. Twenty-one 1.4-kg packages of honey bees (10 Russian and 11 Italian) were made on 4 April 2001. To minimize numbers of phoretic mites, all packages were treated with Apistan (Wellmark International, Schaumburg, IL) strips following manufacturer's recommendations. Thereafter, packages were installed in medium-sized hive bodies containing 10 frames of wax foundation. Each package received corresponding queen stock, i.e., Russian honey bees received a Russian queen and Italian honey bees received an Italian queen. All colonies were fed with sugar syrup to enhance comb-building. Initial infestations of colonies were determined by sampling adult bees from each colony during the early stage of first brood production. Sampling was done by collecting ≈300–500 adult bees per colony (Rinderer et al. 2001a,b).

Because chemical residues present in combs from treated colonies are known to affect mite population growth (Kraus and Page 1995), only frames with wax foundation were used in this experiment. Likewise, only new wooden ware such as supers, hive covers, frames, and bottom boards were used.

2002 Experiment. Thirty (15 Italian and 15 Russian) 1.4-kg packages were made on 1 May 2002 by using the large package technique (Harbo and Hoopingarner 1997) to obtain packages with uniform numbers of bees and mites. The use of drawn combs for the 2002 study was restricted to the honey bee stock that produced them such that Italian colonies only used combs drawn by the Italian bees and Russian colonies exclusively used combs that were produced by Russian bees. When drawn or used combs were unavailable, frames with wax foundation were used. All combs used never received any form of chemical treatment. The initial mite infestation of packages was estimated from five samples taken from the large package, each had ≈781–1,677 bees (1,087 ± 453 [mean ± SD]). All colonies received one new drone comb from 2001 colonies.

2003 Experiment. Thirty-five (25 Russian and 10 Italian) 1.4-kg packages of honey bees were made on 2 May 2003 by using the large package technique as described above. To determine the initial infestation of the colonies, nine samples of ≈322 to 1,253 bees (602 ± 302 [mean ± SD]) were taken from the large packages.

Data Collection. For all experiments, we evaluated colonies for mite reproduction and bee population.

Mite Population. Varroa mite population for each colony was estimated by counting adult female mites in cells containing tan-bodied pupae. For the 2001 and 2003 experiments, mite counts were done from at least two frames of brood during each sampling time; five samples in 2001 and two in 2003. However, in 2002, only one frame was repeatedly used for four continuous cycles; each cycle represents ≈17 d (egg oviposition to tan-bodied pupae). Brood cells were examined until 30–40 infested cells were obtained per colony per sampling time. For samples with infestation of 8% or less, ≈500 cells were examined. Estimates of infestation rates were based on observed rates in these samples.

Nonreproduction was determined as described by Harbo and Harris (2001). Mites are considered nonreproductive (NR) when they enter the cells but 1) produce no progeny, 2) produce males only, 3) produce progeny too late to mature, or 4) when a foundress dies before she can reproduce. (Nonreproduction is the observation of the expression of the SMR trait that is the result of hygienic behavior (Harbo and Harris 2005). Our observation of nonreproduction also may be a result of hygienic behavior). Proportion of nonreproductive females was estimated in colonies with brood cells infested with only single foundress mites. Colonies with <10 singly infested cells were excluded from the analysis. Brood cells infested with two or more foundress mites were considered multiply infested (MI). Nonreproduction and multiple infestation were not estimated in 2003 due to the low mite infestation levels particularly in the Russian colonies. The growth of mites in each colony was derived from numbers of adult female mites in infested cells, and mites on adult bees. The instantaneous growth for a mite population was calculated based on the formula $P_2 = P_1 e^{rn}$, where P_2 is final mite population, P_1 is initial mite population, r is growth rate, n is number of weeks, and e is base of the natural logarithm (Branco et al. 1999, Harris et al. 2003).

Bee Population. The numbers of sealed brood cells potentially infested by mites was determined by visual estimation of comb area covered by capped brood (Rogers et al. 1983). Adult bee population was estimated by visual estimation of the percentage of a comb occupied by adult bees (Burgett and Burikam 1985).

Data Analyses. Data on the number of mites, percentage of worker and drone brood infested, proportion of nonreproductive mites in worker brood, proportion of multiply infested worker and drone brood cells, number of brood cells, and number of adult bees

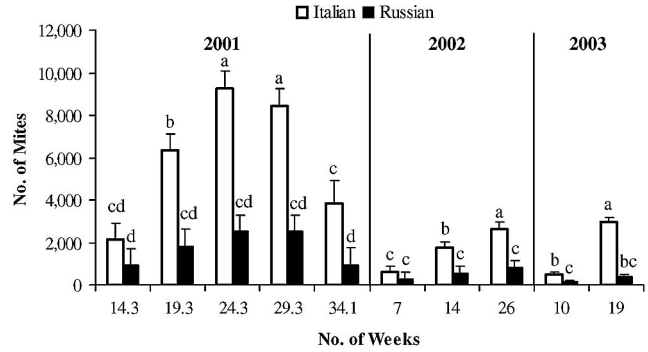

Fig. 1. Number (mean ± SE) of *V. destructor* in colonies of Italian and Russian honey bees in 2001, 2002, and 2003. For each year, bars with the same letters are not significantly different ($P > 0.05$).

per colony were subjected to analysis of variance (ANOVA) for repeated measures by using PROC MIXED (SAS version 8.2, SAS Institute 2001). A two-way factorial ANOVA was used to analyze instantaneous growth rates per week (r_7) with honey bee type and year modeled as fixed effects and colony within type as random effects. Distribution of mites and proportion of nonreproductive mites in drone brood in 2002 were compared for each sampling time by using the Wilcoxon two-sample test. Pearson's correlation coefficient was used to determine relationships among mite numbers and infestation parameters and bee populations. Before analyses, data on the proportion of brood infested, nonreproductive mites and multiply infested cells were subjected to arcsine transformation. Square-root transformation was used to transform data on the intrinsic growth rates of varroa mites (SAS version 8.2, SAS Institute 2001).

Results

Mite Population Growth. In 2001, ANOVA revealed a significant interaction between stock and sampling time ($F = 5.13$; df = 4, 69.5; $P = 0.001$) for the number of mites in the colonies (Fig. 1). In June 2001, the Russian and Italian colonies had similar (Wilcoxon two-sample test; $P = 0.445$) initial numbers of mites of 40 ± 11 and 58 ± 15 (mean ± SE) mites, respectively. After 14.3 wk, mite populations increased 36-fold (from 58 to 2,143 mites) in the Italian colonies compared with a 22-fold increase in the Russian colonies (from 40 to 924 mites) within the same interval. The highest mite counts were recorded in the Italian colonies after 24.3 wk, an average of 159-fold increase comparable with the 145-fold increase obtained after 29.3 wk from the same colonies. The Russian colonies consistently had lower numbers of varroa mites throughout the experimental period than Italian bees. By the end of the experiment (34.1 wk), mite populations in the Italian colonies averaged significantly fewer mites than in the Italian colonies earlier in the experiment particularly because the most highly infested colonies had already died. Five Italian and nine Russian colonies survived until termination of the study.

A significant ($F = 4.24$; df = 2, 45.3; $P = 0.021$) interaction between stock and sampling time also was detected in 2002. After 7 wk, mite populations in both stocks increased at similar rates, ≈6.2-fold increase (from 81 to 585 mites) in the Italian colonies and 2.6-fold (from 81 to 290 mites) in the Russian colonies (Fig. 1). After 14 wk, mite population in the Italian colonies increased significantly higher than in Russian colonies. The highest number was observed in Italian colonies after 26 wk. The numbers of mites in the Russian colonies remained very low throughout the experiment.

In 2003, mite populations in both stocks were very low (Fig. 1). As in previous years, statistical analyses showed significant interaction between stock and sampling time ($F = 74.69$; df = 1, 34.4; $P < 0.0001$). After 10 wk, the Italian colonies had significantly higher mite populations (from 150 to 479 ± 145 mites) than did the Russian colonies which actually had numerically reduced mite populations (from 150 to139 ± 87 mites). At 19 wk, the Italian colonies had a significant increase in mite populations (from 150 to 2,985 ± 196 mites or an 18.9-fold increase), whereas mite populations in the Russian colonies only grew by 1.4-fold (from 150 to 366 ± 103 mites) during this period.

For each year, the r_7 values of varroa mites were estimated at the highest infestation periods: 24.3 wk in 2001, 26 wk in 2002, and 19 wk in 2003. ANOVA revealed a significant interaction between honey bee type and year of observation ($F = 3.76$; df = 2, 61; $P = 0.029$). For the Italian colonies, r_7 varied among years ($r_7 = 0.191 \pm 0.011$ in 2001, $r_7 = 0.122 \pm 0.012$ in 2002, and $r_7 = 0.145 \pm 0.019$ in 2003), but no consistent trend was apparent. For the Russian honey bee colonies, mite growth rate was $r_7 = 0.137 \pm 0.012$ in 2001, $r_7 = 0.061 \pm 0.013$ in 2002, and $r_7 = 0.021 \pm 0.01$ in 2003, showing a significant downward trend. In the Italian bees, r_7 was significantly correlated with the amount of brood ($r = 0.532$, $n = 27$, $P = 0.004$), percentage of worker brood infested ($r = 0.607$, $n = 16$, $P = 0.013$) and the proportion of multiply infested cells ($r = 0.522$, $n = 16$, $P = 0.038$). No correlation was found between r_7 and number of adult bees ($r = 0.368$, $n = 27$, $P = 0.06$) and proportion of nonreproductive mites ($r = -0.134$, $n = 16$, $P = 0.622$) in the Italian colonies.

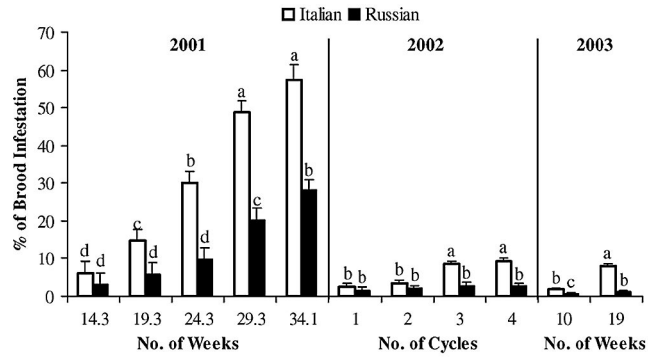

Fig. 2. Percentage (mean ± SE) of worker brood infested in colonies of Italian and Russian honey bees in 2001, 2002, and 2003. For each year, bars with the same letters are not significantly different ($P > 0.05$). In total, 15,642 Russian and 9,675 and Italian worker brood cells were examined.

Instantaneous growth rate in the Russian colonies was correlated with the percentage of brood infested ($r = 0.712$, $n = 29$, $P < 0.0001$) and negatively correlated with the proportion of nonreproductive mites ($r = -0.684$, $n = 16$, $P = 0.0003$).

Percentage of Worker Brood Infested (PI). Analysis of the PI in 2001 showed a significant interaction between stock and sampling time ($F = 7.16$; df = 4, 69.9; $P < 0.0001$) (Fig. 2). In the Italian colonies, the PI increased significantly each period through week 29.3 and then plateaued until the end of the study. The Russian colonies had initial PI similar to that of the Italian colonies. However, it did not increase significantly during the next two periods. Significant increases in PI occurred in Russian colonies during the last two periods.

Russian and Italian colonies had PIs below 10% in 2002 and 2003 (Fig. 2). In 2002, they differed with observation periods ($F = 7.57$; df = 3, 65.3; $P < 0.0002$). The Italian colonies had significantly higher infestations during the third and fourth cycles, whereas the Russian honey bees maintained a low PI throughout the experimental period. In 2003, a significant interaction between stocks and sampling time ($F = 21.01$; df = 1, 30.6; $P < 0.0001$) also was detected. The Italian bees had significantly higher PIs than the Russian colonies after 10 wk. Infestations significantly increased after 19 wk in both stocks with the Italian having higher infestations than the Russian honey bee colonies.

Proportion of NR Mites in Worker Brood. In 2001, the proportion of NR foundress mites also showed a significant interaction between stock and week of observation ($F = 3.96$; df = 4, 66.3; $P = 0.006$) (Fig. 3). Proportions of nonreproductive females decreased at 24.3 wk in the Italian colonies and increased again when colonies were afflicted with PMS. The highest proportion of nonreproductive females was observed at the end of the experiment (34.1 wk) in the Italian colonies. In the Russian bees, nonreproductive females also numerically peaked at 34.1, although levels did not differ statistically from those previously observed at 19.3 and 29.3 wk.

In 2002, a significant ($F = 3.02$; df = 3, 43.8; $P = 0.04$) interaction between stock and sampling time also was observed (Fig. 3). The highest NR was observed during the fourth cycle in the Russian colonies, but this was comparable with the proportion observed during the first and second cycles in the Russian colonies, and second cycle in the Italian colonies. The lowest NR was recorded in the Italian colonies during the third cycle but was also similar to those observed during the

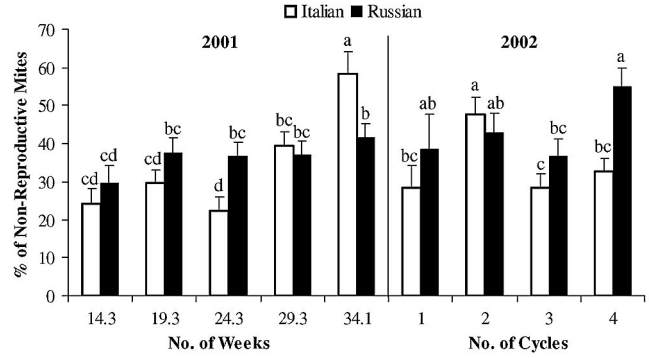

Fig. 3. Proportion of nonreproductive mites (mean ± SE) in worker brood of Italian and Russian honey bees in 2001 and 2002. For each year, bars with the same letters are not significantly different ($P > 0.05$).

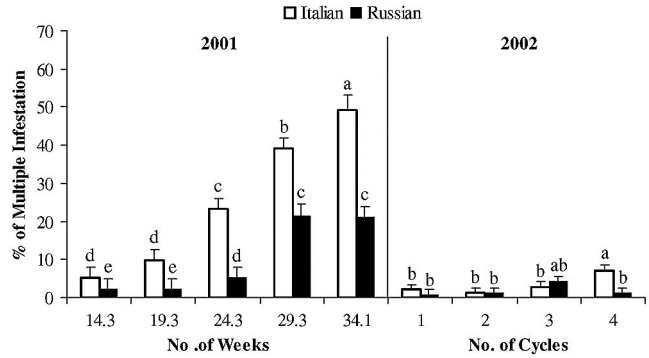

Fig. 4. Proportion of multiply infested cells (mean ± SE) in worker brood of Italian and Russian honey bees in 2001 and 2002. For each year, bars with the same letters are not significantly different ($P > 0.05$).

first and fourth cycles in the Italian colonies, and during the third cycle in the Russian bees.

Proportion of Multiply Infested Worker Brood Cells. A significant interaction between stock and sampling time ($F = 6.16$; df = 4, 71; $P = 0.0003$) was detected for the proportion of MI cells in 2001 (Fig. 4). MI increased steadily and significantly in the Italian colonies after 19.3 wk. The growth of MI in Russian colonies, although slower than in Italian colonies, had significant increases at 24.3 and 29.3 wk. Similarly, MI varied significantly ($F = 3.27$; df = 3, 66; $P = 0.027$) with stock and sampling time in 2002 (Fig. 4). Although the overall MI was low for both stocks throughout the experiment, a significantly high MI was observed in the Italian colonies during the fourth cycle.

Drone Brood Infestation. Because all colonies used wax foundations in 2001, production of drones was very minimal throughout the study. Between 14.3 and 29.3 wk, only four Russian (seven observations) and five Italian (eight observations) colonies produced drones. Drone brood observed in the Italian colonies had a mean infestation of 43.56 ± 9.6% similar to that of the Russian colonies at 34.14 ± 7.7% (Wilcoxon two-sample test; $P = 0.650$).

In 2002, drone infestation was determined between July and September by examining 1,975 and 2,282 drone cells for Italian and Russian colonies, respectively. ANOVA revealed a significant interaction between stock and sampling time ($F = 4.61$; df = 2, 31.5; $P = 0.018$) in the percentage of drone brood infested (Fig. 5). In the Italian colonies, drone brood infestation increased significantly at each observation until the last sampling time. A significant increase in infestation occurred during the last sampling time in Russian drone brood.

For the proportion of multiply infested drone cells, no significant interaction between stock and sampling time ($F = 0.80$; df = 2, 15.8; $P = 0.465$), and no time effects ($F = 2.61$; df = 2, 15.8; $P = 0.105$) were detected (Fig. 5). Overall, MI in the Italian drone brood was significantly ($F = 4.55$; df = 1, 17; $P = 0.048$) higher than in the Russian drone brood. Analyses of NR in drone brood showed no difference between stocks during each sampling time. On average, Italian and Russian drone brood provided similar NR (Wilcoxon two-sample test; $P = 0.341$) (Fig. 5).

Distribution of Mites in Colonies. In 2001, the relative distribution of mites in the brood and on adult

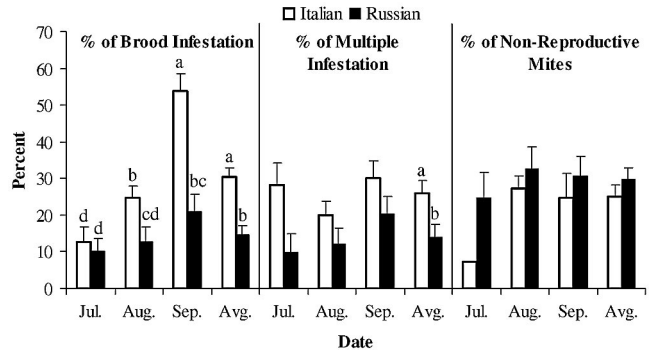

Fig. 5. Proportions (mean ± SE) of brood infested, nonreproductive females and multiply infested cells in drone brood of Russian and Italian colonies in 2002. Bars (monthly means and overall averages) with different letters are significantly different ($P < 0.05$). Bars without letters indicate no significant differences between the stocks ($P > 0.05$). July observation for nonreproductive mites had only one Italian colony. In total, 2,282 Russian and 1,975 Italian drone brood cells were examined.

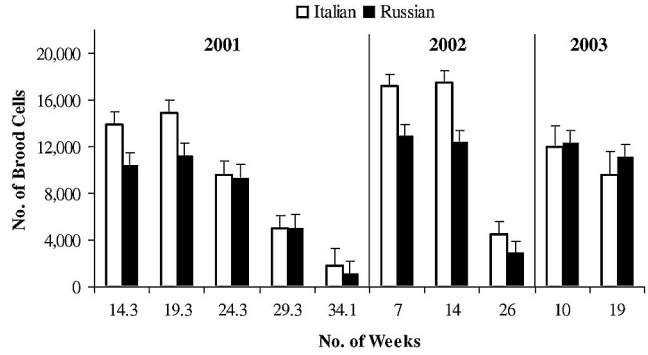

Fig. 6. Average number (mean ± SE) of brood cells in colonies of Russian and Italian honey bees in 2001, 2002, and 2003. For each year, bars with the same letters are not significantly different ($P > 0.05$).

bees did not vary between the two stocks at 14.3 wk (Wilcoxon two-sample test; $P = 0.808$). During this time, ≈76.38 ± 7.9% of the mites were found on worker brood and 21.27 ± 8.0% on adult bees in the Italian colonies. In the Russian colonies, 72.8 ± 7.0 and 24.22 ± 6.2% were on the brood and on adult bees, respectively. (In both groups a few mites were infesting drone brood). At the end of the experiment (34.1 wk), a significantly (Wilcoxon two-sample test; $P = 0.04$) higher proportion of the mites were still in the worker brood of the Italian bees (90.91 ± 3.0%) compared with 76.87 ± 4.1% in the worker brood of Russian bees.

A similar trend was observed in 2002. Seven weeks after the colonies were established, similar (Wilcoxon two-sample test; $P = 0.808$) distributions of mites in both stocks were observed with 79.68 ± 4.4% of mites on Italian and 78.87 ± 3.8% on Russian worker brood. However, a significantly (Wilcoxon two-sample test; $P = 0.018$) higher mite infestation was observed in the Italian worker brood (79.2 ± 3.5%) compared with those in Russian worker brood (51.01 ± 7.5%) at the end of the experiment (26 wk).

In 2003, the distribution of mites in the colonies after 10 wk was very similar ($P = 0.56$), with the Italian brood having ≈79.27 ± 4.9% of the mites as compared with 65.06 ± 7.5% infesting Russian worker brood; ≈20 and 35% of the mites were phoretic, respectively. After 19 wk, a significantly higher (92.15 ± 2.06%) proportion of mites were found in the brood of the Italian bees, whereas the Russian brood had ≈69.61 ± 6.82% of the mites. Thus, only 8% were phoretic on Italian adult bees, whereas 30% were phoretic on Russian adult bees after 19 wk of observations.

Number of Brood Cells. In 2001, there was no significant interaction ($F = 2.08$; df = 4, 87; $P = 0.090$) between stock and sampling time detected for the number of brood cells in the colonies (Fig. 6). However, significant ($F = 50.43$; df = 4, 87; $P < 0.0001$) differences among the sampling times were observed. The highest brood production was recorded at 14.3 and 19.3 wk with the lowest amount of brood observed at 34.1 wk. Both stocks had similar ($F = 2.05$; df = 1, 19.2; $P = 0.169$) brood size with a mean of 9,051 ± 814 and 7,399 ± 818 brood cells for Italian and Russian honey bees, respectively.

For 2002, there was no significant interaction between stock and sampling time ($F = 2.94$; df = 2, 67; $P = 0.06$) detected for the amount of brood in the colonies (Fig. 6). However, brood production was influenced by stock ($F = 9.89$; df = 1, 22.9; $P = 0.005$) and sampling time ($F = 155.01$; df = 2, 67; $P < 0.0001$). Italian colonies (13,067 ± 808 brood cells) had more sealed brood than the Russian colonies (9,400 ± 841 brood cells); the highest brood production was observed after 7 wk (15,044 ± 715 brood cells) and 14 wk (14,941 ± 715 brood cells).

Analysis showed no interaction between stock and sampling time ($F = 0.34$; df = 1, 59; $P = 0.564$) in 2003 (Fig. 6). No stock ($F = 2.93$; df = 1, 59; $P = 0.092$) or sampling ($F = 0.23$; df = 1, 33; $P = 0.634$) effects were observed.

Adult Bee Population. For the number of adult bees in 2001, a significant interaction between stock and sampling time was observed ($F = 12.68$; df = 4, 68.4; $P < 0.0001$) (Fig. 7). The highest number of adult bees was recorded at 14.3 wk in the Italian colonies. Thereafter, both stocks significantly exhibited reduced adult bee production with the lowest number of bees recorded at 34.1 wk in the Italian colonies when they were inflicted with PMS.

Analysis of the number of adult bees in 2002 revealed no stock by sampling time interaction ($F = 1.83$; df = 2, 67; $P = 0.169$) (Fig. 7). The Italian colonies (9,378 ± 612 bees) produced significantly ($F = 4.81$; df = 1, 22.4; $P = 0.039$) more adult bees than the Russian honey bees (7,441 ± 637 bees). Significantly ($F = 19.02$; df = 2, 67; $P < 0.0001$) more bees populated the colonies after 14 wk than at any other sampling time.

In 2003, ANOVA showed no interaction between stock and sampling time ($F = 0.05$; df = 1, 60; $P = 0.817$) (Fig. 7). No differences were detected between the two stocks ($F = 0.06$; df = 1, 33.3; $P = 0.805$) and sampling time ($F = 0.03$; df = 1, 60; $P = 0.874$).

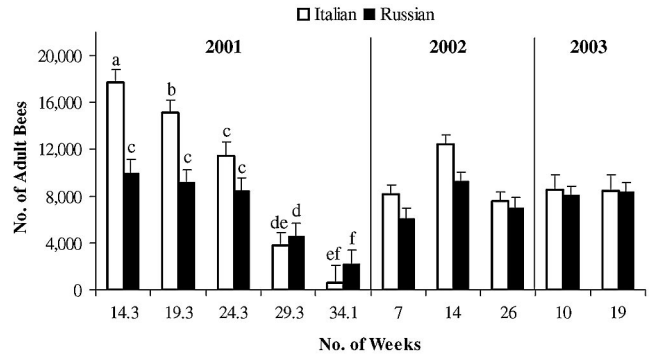

Fig. 7. Average number (mean ± SE) of adult bees in colonies of Russian and Italian honey bees in 2001, 2002, and 2003. For each year, bars with the same letters are not significantly different ($P > 0.05$).

Discussion

The growth rate of the varroa mite population determines its severity in honey bee colonies. However, varroa mite populations vary according to bee genotype, mite genotype, geographical location, and climatic conditions (Otten 1990; Thrybom and Fries 1991; Kraus and Page 1995; Harbo and Hoopingarner 1997; Anderson and Fuchs 1998; Branco et al. 1999; de Guzman and Rinderer 1999; de Guzman et al. 1999; Rinderer et al. 2001a,b; Harris et al. 2003; Harbo and Harris 2005). Despite the yearly variation in growth rates observed in this study, our results consistently confirmed previous studies showing relatively slow growth of varroa mite populations in Russian bee colonies (Rinderer et al. 2001a,b). Variation in r_7 also had been observed by Harris et al. (2003) showing growth rates of $r_7 = 0.008–0.214$ per week for apiaries of unselected miscellaneous colonies in a 10-yr (1993–2002) study in Louisiana. For 2001, the authors reported a growth rate of $r_7 = 0.047$ per week or a three-fold increase for 16 wk. We conducted our studies in the same general area as Harris et al. (2003). However, we observed higher growth rates of $r_7 = 0.191$ per week or a 159-fold increase (Italian) and $r_7 = 0.137$ or a 62-fold increase (Russian) for 24.3 wk in our 2001 study. In their 2002 results, Harris et al. (2003) recorded different r_7 values for each of their two apiaries by using different bee genotypes: $r_7 = 0.159 \pm 0.02$ (apiary 1, five bee genotypes) and $r_7 = 0.095 \pm 0.06$ (apiary 2, two bee genotypes). Using two stocks, we also observed divergent r_7 values in 2002. Mite populations in the Russian colonies had a lower growth rate ($r_7 = 0.061 \pm 0.016$) than those in the Italian colonies ($r_7 = 0.122 \pm 0.01$), despite being located in one apiary. In 2003, we observed a much lower rate of $r_7 = 0.021 \pm 0.011$ or a 1.4-fold increase for 19 wk in the Russian colonies compared with $r_7 = 0.145 \pm 0.009$ or an 18.9-fold increase in the Italian colonies. A differential increase (2.5-fold in the Russian versus 17.3-fold in the control colonies) also was reported by Rinderer et al. (2001b) after a 13-wk observation in Louisiana. Although Harris et al. (2003) used different queen sources (1–13 sources per year), the authors claimed that climatic factors influenced most of the variation in mite growth. However, the discrepancy in the authors' 2001–2002 results and our results during these same years suggest the importance of bee genotypes or microclimate in the regulation of mite growth. Variation among honey bees in brood and adult bee production, and their ability to resist pests and diseases have been widely known (Fries et al. 1991; Rinderer et al. 2001a,b; Harbo and Hoopingarner 1997; Harbo and Harris 2001, 2005).

The poor growth of varroa mites observed in the Russian colonies could be attributed to several factors, including nonpreference or unattractiveness for this honey bee stock to varroa. This study suggested that the Russian bees may have been less attractive to varroa infestation. Trouiller et al. (1992) claimed that attraction of mites to last larval instars of workers and drones is triggered by chemical cues. Whether Russian bees produce these allelochemicals has not been studied. Other less likely effects might be nonpreference, such as mite-infested adults avoiding the brood nest area. Nevertheless, previous studies (Rinderer et al. 2001a,b) and the present report consistently showed lower percentages of brood infested and lower numbers of multiply infested worker brood in Russian colonies. For 5 mo (24.3 wk), the percentage of brood infested and multiply infested cells in the Russian colonies were below 10% in 2001. In contrast, Italian bees suffered from high varroa mite infestations (≥20% PI and MI) after 24.3 wk, eventually losing >50% of the colonies at the end of the experiment. MI was found associated with the increase in mite numbers in the Italian colonies. In cells with more than one foundress mite, the proportion of males increased (Fuchs and Langenbach 1989). Thus, mite reproduction is invigorated with the likely out-crossing of mites. Although varroa mites generally prefer drone brood ≈3–8 times more than worker brood (Fuchs 1990), mite infestation (PI and MI) of drone brood was lower in the Russian than in the Italian colonies. High mite infestations in the Italian bees in 2001 resulted in early expression of PMS (Shimanuki et al. 1994) and eventual death of colonies; six of the 11 Italian colonies died with mite infestations in brood ranging from 27 to 80%. In the same apiary, Russian colonies had a higher

proportion of healthy bees. Only one (with 46% worker brood infestation) of the 10 Russian colonies died.

Previous studies showed that nonreproduction has little effect on mite growth when it occurs at <30% (Harbo and Hoopingarner 1997). During our 2001–2002 experiments, the average proportion of nonreproductive varroa in the Russian worker brood and drone brood in 2002 per sampling time was ≥30%. Hence, NR significantly reduced rate of mite development particularly in Russian colonies in 2002.

Harbo and Harris (2001) observed that resistance to varroa mites in the stock with the SMR trait is associated with poor brood production, which is probably a consequence of the removal of brood infested with reproductive mites (Harbo and Harris 2005). Our current study also showed a correlation between mite growth and the number of capped brood present in the colonies that was incongruent with the findings of Kraus and Page (1995), who found no correlation between levels of varroa infestations and colony strength expressed as amount of brood and number of bees. However, Kraus and Page claimed that constant presence of brood was the major cause of rapid growth of varroa populations in honey bee colonies in dry subtropical climates (Mediterranean climates) such as in California. In Louisiana, there is a brief break in brood production brought on by weather change (such as cold winter conditions), bee genotype and the bees' need for nectar and pollen flow. Russian bees are known for being resource responsive (Tubbs et al. 2003) such that when food becomes scarce, Russian queens either slow down or completely stop brood production even in spring or summer seasons. This characteristic behavior detrimentally affects brood parasites such as varroa because brood rearing is directly associated with the flowering periods of plants (Fernandez 1997). In contrast, susceptible Italian bees continue with their brood production under the same circumstances. Extended brood production offers a constant supply of hosts for mite reproduction. Ritter (1984) reported a 10-fold increase in mite population in southwestern Germany where the brood-rearing period is longer than in southeastern France (as cited by Fries et al. 1991).

Furthermore, a break in brood production may lessen the availability of brood for infestation, and thereby provide a longer phoretic period for the mites. For 3 yr, we consistently observed a higher proportion of phoretic mites on Russian adult bees than on Italian adult bees. Phoresy, which also may be a consequence of brood unattractiveness, may reduce reproductive cycles of varroa as well as reduce damage to the developing bees. As a result, bees that survive the winter are healthier and thus live longer. Phoretic mites also are more susceptible to grooming activities of adult bees (Büchler et al. 1992, Ruttner and Hanel 1992, Delfinado-Baker et al. 1992). Rinderer et al. (2001a) found higher proportion of phoretic mites and higher percentage of injured dead mites in the Russian colonies than in domestic colonies. High phoresy also may be derived from the hygienic removal of brood infested with varroa. Russian honey bees exhibit a high level of hygiene in standard tests (de Guzman et al. 2002, Kavinseksan et al. 2004).

In conclusion, there was no single resistance mechanism to varroa mites in the Russian honey bees. Several factors such as less attractiveness (low PI and MI) of both worker and drone brood, less reproduction of mites and extended phoretic period for the mites seemed to influence mite growth. These factors seem to act in concert and cause substantial inhibition of varroa mite population growth. Moreover, the reduction in growth rates observed in the Russian colonies as the experiment proceeded suggested that selection improved the resistance of the Russian bees over the years.

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