Does the Varroa resistance trait follow the queen when she is used to re-queen another colony without the trait? A review.

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With Varroa being the main adversary of the honey bee almost world-wide, there has been much interest in obtaining Varroa resistant bees by natural or artificial selection. A frequent aim of selection is to produce queens that can be sold to beekeepers who would then be able to reduce or eliminate Varroa treatment, or at least have stocks that are healthier and survive winter etc. This review aims to show to what extent Varroa resistance can be passed on solely by introducing a 'Varroa resistant queen'. I use that somewhat inaccurate term here for brevity.

Hoskins (2015) selected colonies for efficient removal and damage of mites and was able to maintain his stocks without treatment and with low losses. In one experiment he transferred a queen with the efficient grooming trait to a colony without that trait, and vice versa. The colony without the trait started efficient grooming and the colony formerly with the trait stopped efficient grooming. Because of the low number of samples, and because of where the experiment was published, this finding would be treated as anecdotal. Even so, it is worth including here because it refers to a well known population of Varroa resistant bees and has attracted the interest of scientists researching deformed wing virus variants.

A more robust crossing study than Hoskins' was that of Barbara Locke (2016) using bees from the Gotland (G) Varroa resistant population and from the non-resistant population at Uppsala (U). Using artificial insemination, she created single drone crosses (queen x drone) coded as GG, GU, UG & UU. All the bees that had G genetics showed statistically significantly reduced mite reproduction. Even so, she acknowledged a low sample number and the study lasted only 8 weeks, just long enough to get most of the bees in each colony expressing the introduced genetics.

But when Tom Seeley (2007) moved his Arnot Forest Varroa resistant queens to colonies in Cornell University research apiary, the resistance was not transferred with them.

Furthermore, Correa-Marques et al. (2002) brought Fernando de Noronha (Brazil) Varroa resistant queens to Germany to make pairwise comparisons with local mite-susceptible honeybees (A. m. carnica), but no differences in mite infestation rates were found. Moreover, grooming behaviour was significantly lower in the colonies headed by Fernando de Noronha queens (Correa-Marques et al. 2002). Whatever was enabling the bees of Fernando de Noronha to maintain a low mite infestation was not effective in Germany. This suggests that their ability to survive is due to something other than genetic host-resistant mechanisms (Correa-Marques et al. 2002).

Indeed, Meixner et al. (2015) reported that "when colonies descending from the Avignon survivor [Varroa resistant] population were tested outside their native environment in a Europe-wide experiment ..., neither their Varroa infestation rate after one year without treatment, nor their survival outperformed that of colonies descending from non-selected genotypes tested at the same locations".

Rinderer et al. (2010) review the outcome of Varroa resistant queens imported to the USA from the Primorski region of Russia: "Overall, daughters of 42 queens identified by individual tests of the 362 queens imported from Russia were evaluated in sib-tests and 18 queen lines (5%) were included in the closed breeding population." These 'Russian' queens retained a degree of Varroa resistance and were eventually released to members of the Russian Honey Bee Breeder's Association.

But in 2003, in a 149-colony study in Germany, Varroa resistant queens bred from Primorski bees in the USA did not show a statistically significant difference in Varroa population growth compared with local *Apis mellifera carnica* bees (Berg et al. 2004).

In 2001-2003, in a 117-colony study on an Adriatic island with strains selected and unselected for Varroa resistance only 15 colonies survived, 11 out of 63 selected and 4 out of 54 unselected, but the higher survivability rate of colonies from selected strains could not be correlated to differences in the relative natural mite mortality (mite mortality/1000 bees), the number of damaged mites in the natural mite fall, hygienic behaviour (pin-killed brood test), or the infertility rate of Varroa in worker brood (Büchler et al. (2010). This Adriatic experiment should therefore be classed as neutral in relation to our enquiry.

Rinderer et al. (2010) also reviews another Varroa-sensitive hygiene breeding programme in the USA, one that started by trait selection from single drone inseminated queens. This eventually resulted in useful Varroa resistant breeding material that was initially released to USA queen breeders via Glenn Apiaries and subsequently via VP Queen Bees.

Another USA programme, in this case selecting for freeze-killed pupae removal hygiene as a single trait, produced queens that were commercially useful and were released initially to three queen breeders in Minnesota (Spivak et al. 2009). These 'Minnesota Hygienic Queens' have a trait that requires at least 50% of 'hygienic drones' to maintain it in each generation. The trait is recessive and therefore cannot strictly be classed as 'following the queen'. Furthermore, one seller of 'Minnesota Hygienic Queens' writes on his website 'We still recommended you treat your bees' (Sennes 2019).

Answering the question posed here was the subject of a so-called 'ring test' proposed at a conference in Wageningen, Netherlands in 2015 (Neumann et al. 2015): "...we will conduct a ring test across Europe. We will import queens from the three populations [of naturally resistant colonies] and test whether the bees are able to survive without treatment in different environments." At the time of compiling this review the experiment has been completed and data are being analysed (Neumann, 2019). That such an experiment was done, no doubt involving considerable investment, one can only assume that there is uncertainly whether Varroa resistance 'follows the queen'.

So, to sum up, out of nine papers included in this review, four appear to answer our question in the affirmative, three in the negative and two count as neutral. We look forward with interest to the publication of the results of the 'ring test'.

Various suggestions have been made to account for the failure of Varroa resistance traits to follow the queen. The commonest seems to be gene-environment interactions. The trait is expressed in one location/colony but not in another. This takes us into the realm of epigenetic effects which could cover anything from molecular factors altering gene expression to the favourability or otherwise of the landscape, climate and colony management. Even social learning has been floated as possibly involved. Further complicating factors include the virulence of Varroa and what variants may be present of Varroa-vectored deformed wing virus, often the main cause of collapsing colonies.

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