

RESISTANCE OF HONEY BEES TO TRACHEAL MITES

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It was suggested long ago that some genetic lines of honey bees resist infestation by tracheal mites. This possibility received little attention through many decades of this century, but the rise of mite associated problems in North America in the 1980s and 1990s prompted renewed interest in mite control techniques. Recent scientific inquiry has revealed much about genetic resistance to tracheal mites and beekeepers can use this knowledge to incorporate resistance into mite management strategies.

There are several important benefits of using resistant bees rather than chemicals to manage mites. A genetic resistance approach is less labor intensive and less expensive. After a queen of a resistant bee stock is installed in a colony, mite control is complete for at least as long as the queen lives, and a daughter queen may also provide useful level of resistance. When resistant bees are used, less acaricides are needed, and this reduces the exposure of bees and beekeepers to pesticides.

History. Anderson², writing about the outbreak of Isle of Wight disease in England that began at the turn of this century, noted that as early as 1911 some colonies of bees apparently were less susceptible than others to the problems that later were determined to be caused by tracheal mites. Anderson submitted a proposal in 1918 to test for resistance to the disease, but his application was denied; the beekeeping world perhaps lost an early chance to learn how bee stocks could be bred to resist hazards. Still, Anderson believed that genetic resistance would be the ultimate solution to the disease. He noted that the virulence of the disease subsided in an area through time, suggesting that surviving bees were resistant to the causative agent. He debated this issue with a Mr. Illingworth in the pages of *Bee World* in 1930 and 1931, and put forth ideas that we now know are correct.

Brother Adam at Buckfast Abbey in southwest England began breeding in 1916 from colonies that had survived the early tracheal mite problems. Colonies susceptible to mites probably were eliminated quickly from the breeding pool, given that an estimated 90% of colonies in England were killed. Adam¹ related that he first saw clear evidence of genetic control of mite susceptibility in 1922 and 1923 when two sister breeder queens of Italian origin produced daughter colonies that differed greatly in susceptibility to tracheal mites. His breeding of the Buckfast stock continued throughout the next seven decades with an emphasis on traits such as brood production, low swarming, etc., while the local intense pressure from mites was thought to have promoted mite resistance in the bees.

One beekeeping trial supported the contention of tracheal mite resistance in Buckfast bees. Calvert⁵, in Ireland, reported that he was able to overcome severe mite infestations within 12 months by requeening his infested colonies with either pure-mated Buckfast queens or with Buckfast queens mated to his own susceptible stock.

Subsequent to the devastation wrought by the mites early in this century, tracheal mite problems declined in Europe and the mites are now considered to be only an infrequent problem²⁵. This suggests that natural selection rendered European bees comparatively resistant to the parasite. However, it has not been established clearly that this is the case. Studies regarding possible differences in susceptibilities of mite-exposed European bees and non-exposed North American bees led Bailey^{3,4} to conclude that British and American bees were equally susceptible. Yet it also has been argued that Bailey's data do in fact support

the view that non-selected American bees were more susceptible than British bees¹⁸. There were no other investigations of possible resistance to tracheal mites in European bees, and seeking out and using resistant stock does not appear to have been a priority for European beekeepers. An apparent lack of need for active tracheal mite control is further circumstantial evidence that the susceptibility of European bees generally declined through years of exposure to tracheal mites.

Definitions. The term resistant is used to mean that it is unlikely that many bees in the described colony or population will become infested when exposed to tracheal mites. Colonies or populations in which few bees become infested are less likely to suffer damage or be killed by mites than are others which become highly infested26. Resistant bees are not immune to mite infestation. Rather, in the presence of mites, resistant colonies tend to have infestations that remain relatively low while susceptible colonies will tend to become infested to the point of being severely damaged or killed. It must be stressed that these infestation patterns are probabilities, not certainties, and resistant bees on occasion may be damaged by mite infestation. The term tolerance is less applicable than the term resistance because there are no data showing that colonies can perform well when infested with tracheal mites at levels known to cause problems (that is, when more than 15-25% of worker bees are infested in the autumn). Honey bees apparently are simply not able to tolerate high mite infestations.

Terminology suggested by the American Society of Parasitologists allows clear communication about the relationship of bees with their mite parasites. The percentage of mite-infested worker bees in a sample (or of infested colonies in a group) is called the *prevalence*. The number of mites per individual infested bee is the mite *intensity*, while the average number of mites per bee overall in a sample is the mite *abundance*. Fecundity refers to the number of offspring produced per female.

Scientific evidence of resistance. Soon after tracheal mites were found to cause severe beekeeping problems in North America, research in the United States and Canada turned to finding solutions to the mite problem. Several intensive searches for genetic resistance were among the research efforts. It did not take long for scientific inquiry to document that different lines of bees do indeed differ in susceptibility to the mites.

Gary & Page¹⁴ showed that different lines of bees having lesser and greater susceptibility to the mites can be selected from a common population. A key to their research was to develop a comparative testing protocol whereby different bee lines are simultaneously exposed to a uniform source of mite-infested bees. Page & Gary²⁷ furthermore showed that the differences in response to mites had a genetic basis. These findings together demonstrated that bee selection and breeding might provide a solution to beekeeping problems caused by tracheal mites.

Studies using comparative tests in Canada found significant variation in resistance to tracheal mites among bees from commercial sources⁶, and also within a closed population of bees originating from

queens produced in California²⁹.

The longstanding reputation of Buckfast bees being resistant to tracheal mites garnered research attention, and this stock has been the richest source of material for study. Buckfast bees maintained commercially in the United States were tested first. Colonies maintained low mite prevalences when compared with another commercial U.S. stock during a 7-month test²¹. Variance in the responses of Buckfast colonies suggested that the stock was not uniformly resistant.

Queens of Old World Buckfast stock were imported in 1990 from Great Britain to the United States and Canada for testing. In the United States, Buckfast bees went through a standard Department of Agriculture (USDA) quarantine procedure and then were put immediately into a field test conducted in four commercial beekeeping operations. In comparisons with three other stocks, Buckfast bees had low mite prevalences during the 1-year test and had other desirable traits

such as good honey production and survivability12.

In Canada, work at the University of Guelph found that Buckfast both from England and the United States had lower mite prevalences and abundances than a standard Canadian stock¹⁹. Colonies within all stocks varied in response to the mite, suggesting that selection could further enhance resistance. Hybrids of British Buckfast and Canadian stocks generally had the superior resistance of the Buckfast parent. These tests were conducted using both a short-term assay of test bees placed into infested colonies (similar to Page & Gary²⁷), and a field test in standard colonies for seven months. An important finding was that the two test methods gave comparable results, meaning that the short-term test is valid for evaluating the resistance of a stock. Further

research also showed a congruence of results from field tests and short assays. In sum, a variety of independent scientific tests verified earlier reports from beekeepers that Buckfast bees are resistant to tracheal mites.

Carniolan bees were imported from Yugoslavia by the USDA in 1989 and were found to resist tracheal mite infestation under commercial beekeeping conditions^{12,17}. When hybridized with British Buckfast bees, the F₁ colonies resisted mite infestation as well as, but not better than, the parent stocks, which were about equal in resistance¹⁶. The Yugoslavian bees were released by the Agricultural Research Service of the USDA as ARS-Y-C-1 Honey Bee Stock and have been available to the U.S. beekeeping industry since 1993.

Another importation of potentially mite resistant stock was made by Morse and comprised queens donated by beekeepers in Great Britain²². Worker bees from these British queens were found not to be strongly resistant to tracheal mites when compared to bees of other lines^{13,15}. The imported British stock was distributed to some North American beekeepers for cooperative testing, but was largely abandoned for beekeeping use.

The attempts of several individual beekeepers in the United States to develop resistant stock have been publicized. Taber30,31 outlined a method whereby a queen producer could select among potential breeder queens for mite resistance. He later offered mite resistant queens for sale. Hines, a southern Arizona beekeeper, teamed with USDA scientists in a resistance improvement program. No acaricides were used in Hines' entire operation of 600-700 colonies. New queens were raised from colonies that had low mite prevalences and mated to drones from other surviving colonies; these queens were then used in colonies made up to replace those that had died. Within four years, colony mortality apparently due to tracheal mites decreased from 33% to about 3% in the operation²⁰. Webster selected for mite resistance for several years by propagating from colonies that were thriving among others damaged or killed by parasitism in his Vermont apiaries32. In a field test, two of Webster's lines and Buckfast bees had relatively low mite prevalence13. Bees of a cross between Morse's British stock and some of Webster's selected lines generally had intermediate mite prevalences.

A common experience is that the impact of tracheal mites, as gauged by colony mortality, first increases but then decreases during the first few years that mites are present in an area. Around Baton Rouge,

Louisiana, for example, mites were first detected in 1989 and colony mortality of 30-50% was common in the winters of 1989-90 and 1990-91. Losses decreased dramatically thereafter, and colony deaths attributed to tracheal mite parasitism are now rare. Wilson & others³³ reported that a similar trend occurred in Mexico. After tracheal mites spread throughout the country in the 1980s, sampling in 1992-1995 revealed that mites continued to be found in about half of the colonies, but mite prevalences in worker bees were markedly lower than they were in the mid 1980s. The authors concluded that "surviving colonies now appear less susceptible to" tracheal mites. They also noted that the trend of lower infestations during the period was coincident with increased Africanization of bees in Mexico; Africanized bees are known to be somewhat resistant to tracheal mites⁸.

Details of resistance. After resistance was documented scientifically, questions arose regarding what mechanisms regulate resistance and how the characteristic of resistance is inherited when bees are hybridized. Answers to both of these questions are potentially important in enabling bee breeders to select resistant bees more effectively and efficiently. Work to address these issues has been carried out mostly using bees derived from Buckfast stock in comparative tests against stocks known to be susceptible.

Mechanism. Resistant bees significantly reduce the number of tracheal mites that are able to enter and become established in the tracheae^{9,19}. A direct mechanism by which infestation is suppressed is by autogrooming; young resistant stock bees apparently are more effective at cleaning migrating mites off themselves¹⁰. Autogrooming can occur as part of a "grooming dance" which occurs more frequently when mite infestation is high²⁸. Susceptible bees are able to autogroom to some extent, and the frequency of this trait probably can be increased in a random population by selection. It does not appear that differences in cuticle chemistry, the presence of the hairs surrounding the prothoracic spiracles, or grooming among nestmates are major determinants of resistance¹¹. Resistant bees cause little or no reduction in fecundity of the mites which infest them^{9,19}.

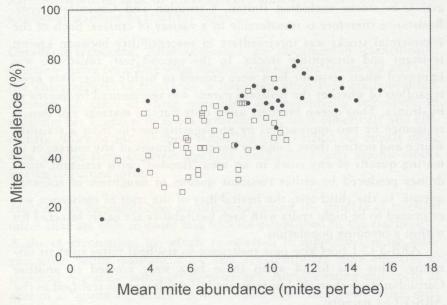
Inheritance. The beekeeper Calvert⁵ successfully reduced tracheal mite problems by requeening with Buckfast bees, and wrote that "the resist-

ance characteristic is inherited and holds good in a first cross" (of Buckfast queens mated to susceptible drones). Recent studies have confirmed this assertion about the inheritance of resistance. In crosses of British Buckfast or commercially available U.S. Buckfast bees with a susceptible Canadian stock, hybrids had intermediate mite prevalences both in short bioassays and in a field test19. Cobey & Smith7 reported that Buckfast-Carniolan reciprocal crosses were intermediate in prevalences, although the data are difficult to interpret because of the very low infestations in all test colonies. Three recent tests11 confirmed and expanded our understanding of inheritance. In the first test, resistance was improved when resistant stock drones were mated to five commercial U.S. stocks including Italian, Carniolan and Caucasian types. Resistance therefore is transferable in a variety of crosses. Each of the commercial stocks was intermediate in susceptibility between known resistant and susceptible stocks. In the second test, resistance was improved when resistant bees were crossed to highly susceptible bees, regardless of whether the resistant parent was represented by queens or by drones. Thus queen breeders using only natural matings can impart resistance by two approaches: by propagating queens from a resistant source and mating those daughter queens to drones of any source; or by mating queens of any stock in an area "flooded" with resistant stock drones produced by either resistant queens or daughters of resistant queens. In the third test, the heritability of the trait of resistance was estimated to be high; traits with high heritability are easily selected for within a breeding population.

ARS-Y-C-1 bees also pass resistance to tracheal mites to their offspring. This was found when these bees were crossed to another Carniolan stock that was less resistant¹⁷. Hybrids were as resistant as the ARS-Y-C-1 parents.

Resistant stocks in North American beekeeping. The most successful system for improving tracheal mite resistance in commercial bee stocks has been a joint program of the Ontario Bee Breeders' Association and the provincial government. Progeny of potential breeder queens are screened for relative resistance using a short bioassay and participating queen producers use the test results to select their breeder queens²⁴. From 1992 to 1997, the number of participating beekeepers rose from five to 28, and the number of breeder colonies evaluated annually increased concurrently. After initially screening 28 colonies in 1992,

about 350 colonies were tested during the peak of selection in 1994 and 1995 and about 165 colonies now are evaluated annually to maintain selection pressure in the breeding stock. Mite resistance was improved quickly by selection. Overall mite abundance in stock tested by the program decreased from 13 to 1.5 mites per bee from 1992 to 1997. A comparison of progeny of selected and non-selected stock showed 72% of selected stock colonies versus 19% of non-selected colonies had mite abundances below the mean for the entire group after just two generations of selection²³ (Fig. 9.1). This testing and selection system stands as a model by which other local, regional or national groups could design stock improvement programs.



▲ Figure 9.1 Progress in selection for tracheal mite resistance as exemplified by data from Ontario, Canada²³. Compared are progeny of the second generation of stock selected for tracheal mite resistance (□, representing 46 colonies) and progeny of non-selected stock (•, representing 31 colonies). Colonies were tested using a colony level bioassay similar to that described in the text and shown in Fig. 9.2. Tracheal mites were significantly less abundant and prevalent in the progeny of selected resistant stock. Approximately 72% of resistant stock colonies (versus 19% of non-selected colonies) had less than the average abundance of all colonies in the test (8.3 mites per bee).

Although there seems to have been a slackening of efforts to breed tracheal mite resistant bees in the United States in recent years, beekeepers interested in keeping resistant bees have several stocks available from which to choose. Various stocks of domestic and foreign origin have been advertised in industry publications within the past five years as being mite resistant.

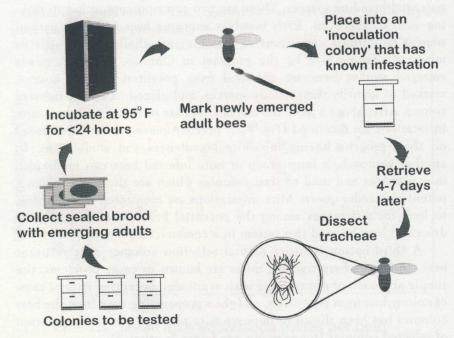
Recommendations for stock selection. A queen breeder can make the best improvement in mite resistance by making careful comparisons of potential breeding sources. There are two common approaches to making such comparisons. Each involves exposing bees from the various sources to uniform conditions so that they are challenged equally by mites. As exemplified by the program in Ontario, Canada²⁴, newly emerged worker bees are obtained from potential breeder queens, marked to identify their colony sources, and placed in a mite-infested colony. After about a week the marked bees are retrieved and their mite infestations are measured (Fig. 9.2). Breeder queens are selected based on their progeny having low mite prevalences and abundances. In another approach, a large group of mite infested bees can be divided into packages and used to start colonies which are then each given a potential breeder queen. Mite infestations are monitored through time to look for differences among the potential breeder colonies. Taber³⁰ described how he used this system in a commercial program.

A third option is to let natural selection enhance mite resistant bees. In areas where tracheal mites are known to cause problems, the simple approach of not treating with acaricides, accepting natural rates of colony loss from parasitism, and then propagating only from the best colonies has been shown to improve mite resistance in the population of selected colonies (for example, see Loper & others²⁰).

In all these approaches, the best results are obtained when queens are raised from the best breeding colonies and mated to drones also of resistant colonies, either by instrumental insemination, by conducting matings in isolated areas, or by maintaining large populations of select-stock drones in mating areas. However, the high heritability of the trait of resistance suggests that acceptable progress could be achieved using queens outcrossed to non-selected drone sources.

Summary. These are times of both extraordinary challenges and opportunities in North American beekeeping. Beekeepers who are willing to

broaden their management repertoire will be best able to cope with the challenges. It is clear that tracheal mite resistant stocks of bees exist and can be useful to mitigate problems. Several different resistant stocks are available, and bee breeders can use these to incorporate resistance into breeding lines as new stocks are being developed. Alternatively, breeders can select within existing stocks for improved resistance. A willingness for bee breeders to create new and improved bee stocks and for beekeepers to experiment with and adopt new stocks is essential for the continued vitality of the craft of beekeeping.



▲ Figure 9.2 Schematic diagram of a procedure that can be used to determine the relative susceptibility of colonies to infestation by tracheal mites. Brood combs with emerging bees are brushed free of adult bees and then placed in cages or screen bags to isolate bees of each test colony. The caged combs are held in an incubator or in a colony, and 30-60 worker bees that emerge within 12-24 hours are marked with plastic tags or enamel paint to differentiate colony sources. The young marked bees are placed into an inoculation colony in which the mite prevalence of worker bees ideally is 30-70%. After retrieval, marked bees are dissected to determine mite prevalences or mite abundances for the bees from each test colony source.

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