Hybrid breeding is suited mainly for larger bee yards and professional beekeepers. The queens must be regularly replaced by systematically produced hybrids, which means intensive, progressive management methods. Crossing bees of varied geographic origin can doubtlessly raise yield in a very short time — more quickly than any other method. But it requires a lot of experience to find out the hybrid best suited for a given area, as the interactions between inheritance and environment can never be predicted. According to hitherto existing experience, it seems that crossing two strains of different origin (different ecotypes or geographical races) results in higher performance than crossing two lines from the same population.

In regions with a relatively uniform bee, the *over-all yield* of all colonies will likely decrease from the introduction of hybrids of a foreign race, even though only some of the beekeepers join the program; the others than get uncontrolled hybrids instead of their own adapted bees as a result of the circumstances (which is what has happened in Germany). Therefore, careful consideration is to be given to the breeding method that should be recommended for the general benefit of all according to the structure of local beekeeping. In many cases, selection from the local bee race or the production of hybrids from different ecotypes of the same race will be preferable to interracial hybrids.

Selection within the geographical race and hybrid breeding with naturally selected strains can be continued only as long as it is possible to maintain the local bee unmixed within the natural habitat. It should be a national concern of all beekeepers' organizations in countries with a native bee of economic importance to secure the preservation of this bee by creation of bee reservations, as they already exist in some countries. APIMONDIA is endeavoring to help such plans by doing its utmost to keep ways open for future breeding work.

DEVELOPMENT OF HYBRID BEE BREEDING IN THE UNITED STATES

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INTRODUCTION

In his address Prof. Ruttner has reviewed the biological properties of the honey bee colony, and the results of some bee breeding work in Europe. His work and those of others have shown that genetic variability exists within and between the various races of bees in the Old World. These differences are the result of biological changes in the bee itself plus the effects of natural selection over a long period of time. Strains of bees have evolved in many areas and selection has favored those with qualities best suited for survival in each specific habitat.

Such strains of bees are now not necessarily the most economically productive strain in their native habitats. This has been amply demonstrated in France, Germany, Russia and Israel. Two factors are involved here. (1) Agricultural crops and practices have changed the environment and (2) the strain best adapted to survival is not always the most productive strain for use under modern methods of beekeeping.

Importations

Indians in the U.S. called honey bees "the white man's fly". Honey bees are not native to the new world and their appearance in Indian territory heralded the colonization of the area by the white settlers. Most of these early imports into the new world were bees from northern Europe. They readily became adapted to our climate and beekeeping methods. As beekeeping grew in the new world bee'-eeping problems arose. European foulbrood appeared and began to decimate the populations. Italian bees were found to be less susceptible to EFB and these imports began to replace the black bees in the U.S. about 1860. The Caucasian, Carniolan and other races of bees were imported a short time later.

Examination of the records of these imports reveals some interesting observations. With each new import the new races were hailed as superior to existing stocks. Since controlied natural matings of honey bees was not possible the new stocks frequently mated with the existing stocks. These superior stocks were not pure breds of the new stocks but hybrids between the old and the new imported stocks. Within a few years some inbreeding occurred and these superior strains appeared to degenerate. New races or strains of bees were imported and their superiority was proclaimed. The beekeepers were unwittingly hybridizing several races of bees without realizing that their superior colonies were hybrids rather than pure races.

Early Bee Breeding

In 1937 a breeding program for the development of AFB disease-resistant bees was initiated in the U.S. This program was begun in cooperation with the states of Iowa, Texas, Wisconsin, and Wyoming. Work in Iowa had already shown that some colonies were more resistant than others. Each year colonies headed by daughters of highly resistant parents of the previous year were tested. Queens were mated at isolated mating stations. In the three principal lines carried until 1945, one showed definite increase in resistance, another less increase in resistance, and a third line apparently little or no increase. The lines became stabilized at characteristic levels considerably below complete resistance. Selection of negative colonies (showing no disease after inoculation) was more effective than selection of recovery colonies (recovered from disease produced in inoculation).

In this program artificial insemination was first used in 1944 on a small scale and was so successful that natural matings were entirely discontinued in 1946. Resistance increased immediately indicating that the slow progress with use of natural matings might have been due to mismating. By crossing the resistant lines with each other we found that the hybrids were not only resistant but also more productive than the parental lines.

These encouraging results with disease-resistant hybrids stimulated expansion of bee breeding to include other economically important characteristics. Lines of bees were started from queens that produced outstanding colonies of bees. These queens were selected because their colonies produced large crops of honey or possessed other desired qualities such as gentleness, vigor, high egg production, or nonswarming tendencies, and so forth.

It soon became evident that we could not follow the systems of matings with honey bees that were successfully used by other animal breeders. To produce uniform superior breeds a certain amount of inbreeding is usually necessary. When inbreedings were made with honey bees low quality brood patterns often resulted. Many queens that were mated to relatives appeared to be laying eggs which failed to hatch. It was discovered that there existed in honey bees a series of lethal allelic genes which in homozygous condition resulted in this low viability brood. Such queens never produced colonies with sufficient populations to be economically productive.

It was subsequently determined that there were many alleles of this gene in honey bees and that most unrelated matings resulted in high viable brood. Such matings produced very populous colonies and economic productivity was restored. These acts further impressed upon us the value of hybridization as a breeding method for bees.

Hybrid Breeding

Over 200 years ago a German Botanist, Joseph Kölreuter, artificially crossed plants and observed what is known today as "hybrid vigor." Certain plant hybrids were more vigorous and grew faster than their parents. Hybrid breeding has since been used effectively in many plant and animal species in which fertility (the number of offspring produced) is high. It is recognized that honey bees are particularly adapted to this method of breeding since thousands of queens can be produced from two parents — a queen and a drone.

The basic tools in hybrid breeding are selection, inbreeding and crossing. Applying this to honey bees we selected breeding queens from the many different stocks at our disposal. These included bees of several races and their crosses. Their offspring were inbred to produce genetically uniform lines and then lines were crossed. The resulting hybrids were superior to their parents and certain hybrid combinations were superior to the original selections. As had been observed in other species we found that the hybrid vigor obtained in the first cross was a transitory effect impossible of fixation. Hybrids when mated *inter se* regressed towards variable within groups. To continue to have superior hybrids it was necessary to their parental means. The subsequent generations were less productive and more maintain the inbred lines and cross these each time we desired to produce the superior hybrid.

Among the hybrids from the various inbred lines we observed many different character combinations. Since some of our inbred lines had been developed from hybrids between races we were offered opportunities to inbreed and then fix together in one line characteristics which had been derived from two or more sources. This convergent improvement resulted in new and more desirable inbred lines. Of course, not all new lines were valuable because the desirable and undesirable qualities were fixed in near equal ratio.

History

You may be interested in some of the history of the development of hybrid bee breeding. The development of a usable technique of artificial insemination of necessity preceeded any controlled bee breeding. The work of Watson, Nolan, Laidlaw, Mackensen and Roberts are well known.

In 1943 we first tested artificially inseminated queens in colonies of bees. Six queens were tested and four of these produced worker offspring throughout the four month test period. In the fall we extracted the first supers of honey that were produced by offspring of artificially mated queens — queens that had never been allowed to fly during their lifetime.

In 1944 we tested 30 and in 1945 62 artificially mated queens. These queens performed in colonies as good as their naturally mated sisters. In 1946 we had 200 test colonies. Of these 160 were headed by artificially mated queens. A bee breeding program based on artificial matings to insure known parentage of offspring thus became a reality.

Of 490 artificially inseminated queens in 1947 we obtained 395 laying queens — a percentage over 80% which is larger than would be expected from a like number of virgin queens allowed to mate naturally in our area. Out test colonies that year produced an average of 96 lbs. per colony. The highest producing line which averaged 144 lbs. surplus was a 3-way hybrid stock headed by artificially mated queens.

As you know each bee colony consists of a mated queen and her offspring. Two generations living together in mutual intradependence contribute to the performance of each colony. Weakness or undesirability in either generation affects the total desirability of the colony.

To obtain maximum desirability and fully utilize hybrid vigor we need both hybrid bees and a hybrid queen in the same colony. Our program thus required superior 3-way hybrids. Later a 4-way hybrid system of breeding was developed. This was described by us in beekeeping journals in 1951.

From these encouraging results in 1948 we intiated a cooperative program for the production of 4-way hybrid bees for distribution to commercial honey producers in the U.S. and Canada. Hybrid queens were produced at Kelley's Island, Ohio and Pelle Island in Canada. These queens were produced in quantity and mated naturally under isolated conditions to insure known parentage.

The beekeepers who received these queens reported to us on the performance of these hybrids. We were at first surprised to learn that not all beekeepers considered our hybrids superior to other stocks. We then discovered that the various hybrids differed in productivity in different environments of habitats. Some produced large populations early in the spring and these were best suited to a habitat which furnished an early honey flow. Similarly those that developed slower were more productive in areas having a later honey flow. It was apparent that many different hybrids would be needed for the many variable habitats in the U. S. and Canada.

In 1953 we set up an experiment to measure differences between seven inbred lines of bees and six of the 2-way hybrids between these lines. These were tested in one location. Among other things we observed differences in honey production, brood production, swarming tendencies, temper, and colony organization. On the average the hybrids were better than the inbreds but some inbreds were as good as the poorest hybrids. The most productive hybrids were crosses of the better inbreds. General combinability was thus more important than specific combinability.

Following our early succes in hybrid bee breeding the firm of Dadant and Sons entered the field. Their progress is attested to by the fact that their Starline and Midnight hybrids are known to beekeepers around the world.

Future Progress

Later work has shown that hybrid vigor is not only observed in certain crosses but hybridization is the touchstone to success in the production of superior bees. Hybrid bee breeding will also be important to the development of bees for specific purposes such as the development of the alfalfa pollen collecting line of bees.

Rapid progress in beekeeping economy is expected within a few years. A major portion of this will be the direct result of controlled bee breeding and hybridization based upon the techniques and knowledge developed in our lifetime.

There are, of course, many problems yet to be solved. Since most inbred lines are weak and incapable of survival in temperate climates without special care and attention we need to develop better methods of maintaining valuable stocks. With new and improved methods of queen and drone production, and further advances in artifical mating and handling of queens to insure safe introduction into colonies we may soon entirely dispense with natural matings.