

## HETEROSIS IN THE HONEY BEE (*APIS MELLIFERA* L.)

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**T**HERE are three castes in the honey bee colony: the drone, queen, and worker. The latter two are both females. The drone bee is a male, representing a haploid gamete of the queen bee heading his hive. The honey bee colony is composed of two generations of bees. The queen bee is, in effect, a potent egg-laying machine, while the workers are morphologically and functionally fitted for honey and pollen gathering and for most other work of hive and field, except that under normal circumstances they do not lay eggs. The queen bee is the parent mother of the colony, and the worker bees are her progeny.

Breeding methods to insure heterosis have led to increased vigor and productivity in corn, sorghum, *Drosophila*, poultry and other species. These species are diploid in both sexes. It is of interest to examine another species, having a different system of reproduction, for heterotic effects and to analyze for the responsible mechanisms. In this study hybrid vigor is regarded as the superiority of the hybrid over the better parent. The characters chosen for study are egg production of the queen, a character largely dependent on the queen's own genotype, and honey yield, a character dependent on the vigor and well being of the queen's worker progeny. Honey yield consequently differs from egg production in being influenced by the genome of the drones to which the queen is mated. The single queen will contribute a genome to each of the 50 or 60 thousand workers making up the colony.

In the past the honey bees must have been intensely selected for the capacity to produce large numbers of progeny and workers active in gathering food supplies. The individual worker bee lives about 6 weeks during the active summer season. Rapid replacement of this worker force depends on the egg laying of the single queen mother. For existence the colony must harvest sufficient nectar in six to ten weeks to last the balance of the year. Till recently, numbers for egg laying and colony replacements have been rather vague, 200 to 5000 eggs per day were estimated. NOLAN (1923) has presented data indicating that rates of less than 2000 eggs per day over a 12 day period were to be expected. Larval deaths will reduce the effective worker groups. The effective oviposition rate will be less than the observed eggs laid, the actual oviposition, by any genetic or other factors favoring the death of the larva. In the inbreeding necessary to the formation of the inbred lines utilized in this study hypothesized sex alleles could be factors in this loss of larvae. MACKENSEN (1951), using brood viability counts, has postulated for the honey bees a series of haplo-viable alleles which are lethal in homozygous diploid females. However, earlier work of CALE (1952) indicated that the oviposition rate of inbred queens was independent

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of percentage inbreeding in the range 31 to 77 percent. The queens utilized in this study were observed to have high egg viability prior to collection of the data.

#### MATERIALS AND METHODS

The genetic material for this study was composed of four inbred lines of honey bees. Following an original selection, no further selections were practiced during the inbreeding of any of these lines. No precise method of inbreeding was used in establishing and continuing any of the lines. Selection of male and female parents from one generation to the next within each strain was more often determined by the availability of males than by attempting to retain a strict parent-offspring or brother-sister system of inbreeding. The coefficients of inbreeding for the four lines at the initiation of these experiments were as follows: D, 56.7%; F, 54.6%; H, 65.8%; J, 64.8%. All matings in the formation of these inbred lines were instrumental inseminations, the sperm being gathered from several suitable males.

Eleven groups of queens and the honey producing capabilities of their worker progeny were studied. These groups included the following: inbreds D, F, H, and J;  $F_1$  females representing all possible non-reciprocal single crosses of the four inbred lines; and a random group representing the available so-called line-bred stock obtained from the queen breeders of this country. The four inbred lines and their six single cross  $F_1$ 's were all daughters of instrumentally mated queens.

It was considered impractical to inseminate instrumentally the inbred and  $F_1$  females chosen for study. Each queen would have needed at least two inseminations. This would have meant more than 500 artificial inseminations—a task beyond the limits of the equipment and personnel available. These queens were allowed to fly from small nuclei colonies and mate with whatever drones they encountered. TABER (1954), using a genetic marker called cordovan, has indicated that queen honey bees allowed free flight mate on an average six and one-half times. This fact is considered important in view of the assumption of random contribution of the males to the yield potential of the worker progeny.

Queens were reared and mated in the summer of 1953. They were then randomly assigned to the test apiaries and introduced to the bee colonies in the fall of 1953. In the spring of 1954 each apiary, or replication, was handled as a unit. Within the apiary, any necessary adjustment of pollen supply, honey, or bees was confined to adjustments within—rather than between—groups being studied.

Only one determination of effective oviposition rate was made, since earlier work indicated that one count of oviposition rate based on large numbers would show real differences (CALE 1952). The oviposition rate determined was a 12-day average preceding the honey flow by 10–22 days. The technique for this determination was fully described in the above citation.

The data on yield were collected at the end of the honey flow period. Each of the 247 colonies was weighed and a record made of the total weight of the colony as well as the number of hive units represented for each colony. The total yield of honey was obtained by subtracting the weight of the hive units from the total weight of the colony.

For the purposes of this study, general combining ability was defined as the aver-

TABLE 1

*Average productivity expressed as eggs per day and pounds of honey by breeding group and replication*

Replicate	F <sub>1</sub> females											
	H × F		J × F		D × H		J × H		J × D		D × F	
	Eggs	Honey	Eggs	Honey	Eggs	Honey	Eggs	Honey	Eggs	Honey	Eggs	Honey
1	1539	308	1596	252	1145	228	1353	282	1664	243	1384	243
2	1365	186	1341	156	1078	191	1378	225	1520	204	1149	203
3	1672	254	1268	172	1264	167	1695	259	1609	245	1591	221
4	1345	193	1474	199	1148	154	1569	208	1468	162	1101	138
5	1208	181	1324	195	1401	195	1524	284	1523	202	1276	191
6	1638	288	1554	301	1215	259	1507	281	1422	243	1444	207
Averages	1461	235	1426	213	1208	199	1504	256	1534	216	1324	201

  

	Inbred females								Randomly mated females	
	J		D		F		H			
	Eggs	Honey	Eggs	Honey	Eggs	Honey	Eggs	Honey	Eggs	Honey
1	836	234	830	239	1140	243	1216	281	1423	239
2	851	144	986	151	1160	200	1201	235	1310	200
3	678	114	891	114	1110	146	1343	162	1368	217
4	773	173	766	121	793	133	1163	180	1167	177
5	1107	137	959	148	666	165	1103	147	1305	190
6	1015	248	1107	152	877	206	817	189	1313	223
Averages	876	175	922	154	957	182	1140	199	1314	207

age performance of a line in contrast to the average of the group, specific combining ability as the performance of the specific cross in relation to the average performance of the lines which were the parents of the cross.

## EXPERIMENTAL RESULTS

The mean oviposition rates and honey yields by group and replicate have been assembled in table 1. Inbred H had the greatest degree of inbreeding, and also had the highest 12-day oviposition rate of the four inbreds studied—1140 eggs per day. The next highest oviposition rate, 957 eggs per day, was associated with inbred F, the inbred having the least percentage inbreeding. It was indicated previously that oviposition rate was practically independent of the percent of inbreeding which had taken place in the formation of lines. These figures confirmed this fact. For all four inbreds, the range of oviposition rate was from 876 eggs per day for line J, to 1,140 eggs per day for line H. The average of the inbreds for the period under consideration was 974 eggs per day.

The F<sub>1</sub> females yielded mean oviposition rates ranging from 1,208 to 1,534 eggs per day, with an average for all six F<sub>1</sub>'s of 1,409 eggs per day. Measurements of the productivity of the F<sub>1</sub>'s were from 68 to 658 eggs per day greater than similar measurements of the parental inbreds.

TABLE 2

*Sources of variation and their contributions to variations in oviposition rate and honey yield*

Source	Oviposition rate		
	d.f.	M.S.	F
Locations	5	35220.1	1.7
Groups	10	345641.9	16.5**
Random & parents versus hybrids	1	2208936.3	105.6**
Random versus parents	1	554987.7	26.5**
Parents	3	80270.7	3.8*
Hybrids	5	90336.7	4.3**
General	3	85197.7	4.1*
Specific	2	98045.3	4.7*
Error	50	20925.1	
<b>Total</b>	<b>65</b>		
	Honey yield		
	d.f.	M.S.	F
Locations	5	12504.9	33.2**
Groups	10	4706.5	12.5**
Hybrids versus random	1	16377.8	43.5**
Inbreds versus random	1	12828.7	34.0**
Parents	3	2068.9	5.5**
Hybrids	5	2929.9	7.8**
General	3	3660.9	9.7**
Specific	2	1833.4	4.9*
Error	50	376.8	
<b>Total</b>	<b>65</b>		

\* Indicates significance at 0.05.

\*\* Indicates significance at 0.01.

The random group, averaging 1,314 eggs per day, laid more eggs than the  $D \times H F_1$ , was about equal to the  $D \times F F_1$ , and was inferior to the other four  $F_1$ 's. The productivity of the random group exceeded all four of the parental inbreds.

An analysis of the contributions to the observed variation in oviposition rate and honey yield is presented in table 2.

There was a significant difference between the productivities of the 11 groups. The analysis further breaks down the 10 degrees of freedom associated with groups, into some of the contributing causes to the group differences. For oviposition rate, the random and parents, taken as a group, are significantly less productive than the hybrids; the random group was significantly more productive than the parental inbreds; and, the parents differ from each other in relative productivity. The hybrids differed from each other in productivity, with both general and specific combining abilities making significant contributions to the total measured variance.

The oviposition rates given above were measures of the queen mothers' genotypes. The honey yields were measures of productivity associated with the worker progeny of the colonies. The mean honey yield for group and replicate are presented in table 1.

The yields associated with progeny of random mated inbred females range from a low of 154 pounds for line D, to a high of 199 pounds for line H. The average for the four inbred female lines was 177 pounds.

Progeny of the random  $F_1$  queens gave yield figures ranging from 199 to 256 pounds. The averages given were all as high as, or higher than, the yields observed for the progeny of random mating inbred females. The average for all of the random mating  $F_1$  queens was 219 pounds, an increase of 42 pounds of honey over the average of the hives led by an inbred queen.

The random group, averaging 207 pounds of honey per colony, was about midway between the inbred and  $F_1$  groups. The random group exceeded all four parental groups, but was itself exceeded by four of the six  $F_1$  groups.

A variance analysis based on the honey yield table of means is presented in table 2. There was a significant difference between the honey gathering capacity of the 11 groups. In the breakdown of the 10 degrees of freedom associated with groups, the hybrids were shown to be significantly greater in yield than the randoms. The randoms, on the other hand, were significantly better yielders than the average of the inbred parental progeny. The inbred parents were shown to be different from each other in their ability to transmit genes associated with honey yield.

The hybrids differed from each other in yield. The sum of squares associated with the hybrids was broken down into that portion due to general and specific combining ability.

#### DISCUSSION AND INTERPRETATION

##### *Replication differences*

The data from the six replicated apiaries indicated comparatively little difference between apiaries for oviposition rate, and a significant difference between replications for honey yield. This could have been predicted for the organism concerned. Honey bee colonies of equal worker strength would be expected to vary in yield if the apiaries were widely separated.

Those factors affecting oviposition rate—such as length of daylight hours, high and low temperatures, early nectar and pollen availability, climatic effects—would be expected to be fairly equal in their effects over the 25 mile range of these apiaries. On the other hand, factors affecting yield—such as concentration of nectar-bearing plants, variation in soil types, and variation in soil fertility—would be expected to vary to a considerable extent over the same 25 mile range.

##### *Parent-progeny comparisons*

Table 3 summarizes the performance of the inbreds and their  $F_1$  crosses for both yield and oviposition rate data. It is apparent from a study of these data that the inbred performance was a poor criterion by which to judge the potential performance of  $F_1$  crosses. In the oviposition data, the poorest performing inbred, J, with an 876 egg per day average, was a parent in  $F_1$  combinations yielding the highest average performance, 1,486 eggs per day. The highest producing inbred, H, with a 1,140 eggs per day average, was a parent of the  $F_1$ 's giving the next to the lowest average performance, 1,391 eggs per day. Inbreds J and D, the two lowest performing inbreds

TABLE 3  
*Inbred and crossbred productivities*

Oviposition rate					Honey yield				
	D	F	H	J		D	F	H	J
D	922	1324	1208	1534	D	154	200	199	216
F		957	1461	1426	F		181	234	212
H			1140	1504	H			198	256
J				876	J				174

  

Average for inbreds based on crossbred performance							
D	F	H	J	D	F	H	J
1355	1404	1391	1486	205	215	229	228

for egg production, produced the F<sub>1</sub> with the highest productivity for the same characteristic.

Inbred H, the highest performing inbred for yield, was a parent of the F<sub>1</sub> having the highest performance. Inbred J, on the other hand, the next to the lowest in inbred performance, was in hybrid combinations that almost equalled the performance of the F<sub>1</sub>'s involving the H line.

The comparisons of these means merely state in a different form what may be shown with regard to general and specific combining ability. These components of variance may be derived in a variety of ways, SPRAGUE and TATUM (1942), etc. A recent summary of ROJAS (1951) presents an easy approach to the computation of these values.

$$\begin{aligned}
 g_i &= \text{additive effect for the } i\text{th line} \\
 &= \frac{1}{r(a-2)} Y_{i..} - \frac{2G}{ra(a-2)}
 \end{aligned}$$

Where,  $Y_i$  equals the total of all crosses involving line  $i$ ,  
 $G$  equals the total for all six crosses over all replications,  
 $r$  equals the number of replications,  
and  $a$  equals the number of lines involved.

The effects of specific combining ability for particular crosses were computed using the following formula:

$$\begin{aligned}
 s_{ij} &= y_{ij.} - y \dots - g_i - g_j \\
 &= \text{mean value of the } ij \text{ cross, minus the overall mean of experiment, minus} \\
 &\quad \text{the additive effects of } i, \text{ minus the additive effects of } j.
 \end{aligned}$$

The calculated values for general and specific combining abilities for both honey yield and oviposition rate are presented in table 4.

For oviposition data, table 4 ranks the inbreds with regard to high egg laying general combining ability in the following descending order: J, F, H, and D. Of the four lines, only inbred J exhibits high general combining ability for high egg laying. These

TABLE 4

*Line contributions for honey yield and oviposition rate general and specific combining abilities*

General combining ability	Yield	Oviposition	Specific combining ability	Yield	Oviposition
D	-22.0	- 81.2	JH	+ 8.5	+ 4.5
J	+12.8	+117.8	JD	+ 5.7	+88.0
H	+15.2	-27.7	JF	-14.2	-92.3
F	- 6.0	-8.9	HF	+ 5.7	+88.0
			HD	-14.2	-92.6
			DF	+ 8.5	+ 4.5

results are a parallel of the observations presented in table 3. It must be remembered, however, that the general combining ability given here was computed on a small amount of data. Only four inbred lines were used in this study and comparisons for general combining ability were based entirely upon the performance of these four lines in cross combinations.

In spite of these limitations, these comparisons are of interest because of the information they give on particular types of gene action. General combining ability, taken as a measure of additive gene action, is shown to vary widely between the four inbred lines studied. Specific combining ability, measuring specific gene combinations leading to the expression of dominance, over-dominance, or epistacy in the phenotypes, is shown to be of importance in the determination of four of the six  $F_1$ 's studied for oviposition rate. In table 2 general combining ability for the 4 inbreds is shown to be slightly less important to egg yield than specific interactions of the parental genotypes. For honey yield, however, general combining ability is twice as important, 3660.9 to 1833.4, as specific combining ability. In both cases the mean squares indicate that genes having both additive and dominance effects are significant to yield.

Table 4 ranks the inbreds with regard to high yield general combining ability in the following descending order: H, J, F, and D. These results parallel the means given in table 3. Two inbreds, H and J, were about equal in their contributions of additive gene effects for yield. Specific effects for yield were more uniformly distributed over the six  $F_1$  genotypes than for the oviposition data. For the particular data, the high yield performance of the random mated  $J \times H$   $F_1$  was accounted for by high additive gene effects contributed by the two inbred parents.

#### *F<sub>1</sub> versus higher parent*

Using the original data, each hybrid was tested against its higher parent in a series of 12 analyses of variance. The productivity of one of the hybrids, (D  $\times$  H), was no better than its higher parent, H, in the oviposition rate comparisons. All of the other  $F_1$ 's exceeded their better parents in oviposition rate. Expressed as a percentage of the higher parent, these productivities ranged from 128 percent to 166 percent, with an average productivity increase over all  $F_1$ 's of 35.5 percent.

Honey yield comparisons showed that two of the random mating  $F_1$ 's could not be considered statistically different from their random mating higher parents. The remaining four random mating  $F_1$ 's outproduced their higher parents. Expressed as a

percentage of the higher parent, these yields ranged from 117 percent to 129 percent. The average yield of all six  $F_1$ 's was 115 percent of the highest yielding parent in each cross.

#### *Hybrids versus random*

The comparison of the hybrids with the random stock available in the country is interesting from the standpoint of the advisability of the use of inbreeding and hybridization as an economic breeding tool in the honey bee.

Table 1 indicated that the mean oviposition rate of the hybrid queens was 1,409 eggs per day, while that of the random check stock was 1,314 eggs per day. Expressed in terms of the random stock performance, the average of the hybrids was 107.2 percent of the random stock. One hybrid was less than the random stock, one was equal, and the other four exceeded the random stock mean. The two better oviposition rate hybrids, (J  $\times$  H) and (J  $\times$  D), exhibited productivities of 114.4 and 116.7 percent of the random stock.

Table 1 showed a mean honey yield of 207 pounds for the random stock colonies, while the progeny of the random mated  $F_1$ 's yielded an average of 220 pounds per colony. Expressed in terms of the random stock, the average of the hybrids was 106.2 percent. The better yielding hybrid, (J  $\times$  H), produced at the rate of 123.7 percent of the random stock.

#### *Significance of environmental and inheritance effects on hybrid phenotypes*

Recognition of factor combinations which will be low, medium or high in performance under given environments is desirable in any attempt to utilize hybrid vigor. The yield data of table 1 on hybrids and their parental strains as observed in six locations were compared for this purpose. The variance, correlation and regression analyses are found in tables 5 and 6.

The first analysis showed that the hybrid honey yields were affected strongly by the type of cross and particularly by the location of the hive. Adjusting the honey yield of the hive for the estimate of the egg laying capacity of the queen heading the hive reduced the significance of the type of cross somewhat while the effect of location on yield, although reduced in value, still remains highly significant. High egg producing characteristics in the queen were desirable although they did not supply all that was necessary to high honey yield. Good honey gathering ability in each worker was important. The effects of location indicated that adequate quantities of honey plants were necessary to any type of bees.

The second analysis in table 5 considered the data of the inbred parental strains. The conclusions were like those for the hybrids but good honey environment came in for greater emphasis. This was due presumably to the lesser activity of the inbreds.

Tables 5 and 6 present the analyses for honey and egg laying characteristics in the parental inbreds and hybrids. There were important hybrid differences in egg production even after adjustment for mid-parent egg production. This supports the conclusions from table 2 that the contributions of the parents for inherited egg production in the hybrids were only in part additive in type. Dominance and interactions of gene pairs contributed to the egg laying capacity of these bees.



TABLE 5

*Variances of hybrid and mid-parent egg productions and honey yields in different crosses, locations and within crosses and locations*

Sources of variation	Variance analysis			
	d.f.	Mean square	d.f.	Mean square
Hybrid honey yield	Hybrid honey yield adjusted for hybrid egg production			
Among hybrids	5	2936**	5	1509*
Among locations	5	7424**	5	5052**
Within	25	717	24	532
Mid-parent honey yield	Mid-parent honey yield adjusted for mid-parent eggs produced			
Among hybrids	5	621*	5	366
Among locations	5	10774**	5	10238**
Within	25	203	24	194
Hybrid honey yield	Hybrid honey yield adjusted for mid-parent honey yield			
Among hybrids	5	2936**	5	2372*
Among locations	5	7424**	5	4217**
Within	25	717	24	747
Hybrid eggs produced	Hybrid eggs produced adjusted for mid-parent eggs produced			
Among hybrids	5	90247**	5	92663**
Among locations	5	37428	5	37382
Within	25	17122	24	17307

TABLE 6

*Correlations and regressions of hybrid honey yield and egg production as related within themselves, in different locations and to mid-parent yields*

Sources of variation	Regression equations	Correlation
A. Crosses	Hybrid honey yield = $41 + 0.13 F_1$ egg yield	0.705
A. Locations	Hybrid honey yield = $-207 + 0.30 F_1$ egg yield	0.681
Within	Hybrid honey yield = $78 + 0.10 F_1$ egg yield	0.504
A. Crosses	Hybrid honey yield = $-2462 + 1.51$ mid-parent honey yield	0.694
A. Locations	Hybrid honey yield = $-790 + 0.57$ mid-parent honey yield	0.685
Within	Hybrid honey yield = $178 + 0.02$ mid-parent honey yield	0.013
A. Crosses	Hybrid egg yield = $1948 - 0.59$ mid-parent egg yield	0.304
A. Locations	Hybrid egg yield = $1305 + 0.11$ mid-parent egg yield	0.083
Within	Hybrid egg yield = $1190 + 0.23$ mid-parent egg yield	0.172

Variances in hybrid honey yields were noticeably reduced for both among hybrids and among locations when adjustment was made for hybrid egg yield on mid-parent performance. The among hybrid reduction in variance may be attributed to genes which were largely additive in their actions on the phenotypes. Analysis of the data in table 2 bears out this conclusion. The reduction in the location variance may be interpreted as due to the hybrid honey yields being affected by many of the same factors as those important to the parental inbreds. Adjustment for mid-parent honey yield consequently reduces the among locations variance. The hybrid honey yield variance was but partially controlled by the mid-parental performance or by the performance in a given location.

The correlations and regressions of hybrid yields with the different attributes are presented in table 6.

The first set of regressions and correlations relate worker collected honey yields to the estimates of egg yields by the queens. The correlations show that among strains of hybrids there is a high correlation between honey stored and the egg laying capacity of the queen. This relation is somewhat less among locations. It is even less within strains and locations. In terms of the method by which the egg production of the hybrid queen was estimated among crosses, an increase of 10 eggs would indicate an increase of 1.3 pounds of honey over the season. For among the hybrid queens in different locations an increase of 10 eggs would increase the honey yield 3.0 pounds. The significance of a good environment for honey gathering was again evident.

The second set of regressions and correlations measures the effects contributed by the mid-parent to the productivity of the hybrid. The correlation between hybrid honey yields and the mid parent honey yields among crosses is rather high. This indicates that in selecting inbred strains to cross the ones chosen should have high honey yields if the hybrids are to be superior. The relation of the hybrid and mid-parent honey yields among locations indicates that the effect of the availability of food supplies was as great as that of inheritance in influencing honey yields. The mean squares and correlations of hybrids and mid-parents within crosses and location were low indicating that most of the information on hybrid performance had been gained when account was taken of inbred mid parents and location differences.

The third set of regressions and correlations measures the effects of the mid-parent egg yields on the egg yields of the hybrids. These correlations are rather low. The highest correlation is negative. This would indicate that lower inbred parent egg productions result in higher egg yields of the  $F_1$  queens. Such a relation would be expected if increasing homozygosity tends to lower performance. The genotypes of the homozygous strains would tend to differ. If the degree of homozygosity is related to the lowering of the yields then the crosses of the most homozygous but genotypically different strains should tend to have the highest yields.

These results on bees have significant parallels in other species. In untested inbred corn material, SPRAGUE and TATUM (1942) showed that general combining ability was of greater importance to yield than was specific combining ability. This was taken as an indication that with untested material additive effects were more important than epistatic and dominance effects. In tested lines, however, it was shown that specific combining ability was about ten percent greater than general combining

ability. ROJAS (1951), in an analysis of combining ability in corn, showed that the average general and specific combining abilities were of about the same importance, but that interactions of specific combining ability with districts and years were of considerably greater magnitude than the same interactions for general combining ability.

The genetic mechanism of heterosis has been investigated experimentally in *Drosophila melanogaster*. STRAUS (1942) showed that the factors responsible for heterosis were located on all chromosomes and that the relationship between vigor and chromosomal heterozygosis was linear. GOWEN and JOHNSON (1946) were able to show racial differences in egg production with higher egg productions for the hybrid *Drosophila* studied. Heterotic increase in egg production was shown to be associated with greater daily egg-laying rates. A later study by GOWEN, *et al.* (1946) indicated agreement with the hypothesis that hybrid vigor was caused by differences in gene constitution and genic interaction between alleles rather than by some unknown physiological stimulation.

LOH (1949) found no trend in the correlation coefficients between successive generation tests on the same top crosses in *Drosophila*. The top cross tests contributed little information of value for predicting subsequent performance in later generations. Correlation coefficients between general combining ability values of three different generations were found to be negative and small. In a synthesis and analysis of *Drosophila* data relating to heterosis, GOWEN (1952) showed that unselected parental inbreds gave  $F_1$  progeny in which general combining ability was more important to productivity than was specific combining ability.

#### SUMMARY

Two honey bee characteristics, oviposition rate and honey yield, were studied in four inbred lines, their six non-reciprocal  $F_1$ 's, and a random check stock in 6 different locations.

Heterotic effects were demonstrated for both oviposition rate and honey yield. These effects were such that five of the six hybrid queen groups exceeded their higher parent in oviposition rate, and four of the groups headed by hybrid queens exceeded their higher parent for honey yield.

Expressed as a percentage of the higher parent, the egg productivities of the hybrid queens ranged from 128 percent to 166 percent, with an average productivity increase of 35.5 percent.

Hybrid queen honey yields ranged from 100 percent to 129 percent of the higher parent, with an average yield over the higher inbred parent of 15 percent.

The oviposition rate of the average hybrid queen was 107.2 percent that of queens selected at random from the stock distributed throughout the United States. The two better hybrids exhibited productivities of 114.4 and 116.7 percent of the random stock.

Under the conditions of this experiment, inbreds were shown to exhibit both general and specific combining ability for oviposition rate and honey yield. Gene action leading to general combining ability was of greater importance for honey yield than for egg laying ability. Gene combinations having additive effects and those having

dominance and epistatic effects were of importance in determining egg laying and honey gathering ability. Location differences in nectar plants etc. were shown to be important to the yield performance of the different genotypes.

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