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Heritabilities and correlations for several characters in the honey bee

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ABSTRACT: An array of inbred honey bee queens (*Apis mellifera* L.) were mated to single drones from either European (Baton Rouge, Louisiana) or Africanized (Maturin, Monagas, Venezuela) honey bee colonies. Worker bee offspring from these matings were evaluated for a variety of characteristics, and heritabilities (h^2) and phenotypic and genetic correlations were estimated using the European data, the Africanized data, and the combined data. In four laboratory measures of honey production (hoarding day 2, 3, 4, and average hoarding), h^2 ranged from 0.20 to 0.92. In a laboratory test measuring responsiveness to an alarm pheromone, h^2 for initial activity of the bees was low (0.04 to 0.12) and h^2 for speed of the reaction was variable (0.31, 0.83, and 1.28). The h^2 values of nine colony defense measures made in the field also were variable (0.1 to 0.93). Comb cell size had h^2 estimates of 1.15 and 0.49. Phenotypic correlations were generally less than the corresponding genetic correlations. For some traits, the three estimates of the parameters were very different. Heritability estimates were sufficiently high to expect success in a selection program for gentler, more productive bees.

ACCURATE ESTIMATES of genetic parameters are very useful for an efficient selection program. Although selection programs for improving the honey bee, *Apis mellifera* L., have existed for a long time, they have not utilized the complete arsenal of genetic information applied to other domestic animals. Only a few estimates of heritability (h^2) have been published for honey bees[1,5,14] and all can be criticized for their methods. The fact that the honey bee has some major biological differences from the usual diploid domestic animal may partially explain the lack of genetic sophistication in its breeding.

Honey bees are a highly social insect living in groups, or colonies, composed of a single reproductive female called a queen, thousands of her worker-daughters and several hundred of her drone-sons. Drones are haploid, developing from unfertilized eggs, while the nonreproductive workers are the product of the queen's eggs fertilized by semen from as many as fifteen drones, stored in the queen's spermatheca. Queen-daughters also can develop from fertilized eggs if they are reared in the necessary specialized environment. Polhemus et al.[11] pointed out that drones represent the gametes from the queen as all the semen produced by a drone is identical. If one views the situation in terms of a dam-queen mated to a sire-queen through the intermediary of drones as gametes, a diploid-diploid genetic structure can be imposed on the haploid-diploid biology.

Other complications arise because many of the characters of economic value in the honey bee, such as honey production, are the result of the combined activity of many workers. Thus, many characters must be measured on nonreproductives that are sisters or daughters of the reproductive individuals.

In addition, the entire colony must become the unit of selection. Under normal conditions, we are working with a collection of super-sib families having the same dam-queen but different sire-queens. Sibs from the same family have a coefficient of relationship of 0.75 because of identical sperm from a single drone, sibs from different families have a coefficient of relationship of 0.25.

Rothenbuhler[13] proposed the inbred queen-single drone mating technique to obtain colonies with genetically uniform workers. By using one haploid drone (all sperm identical) to artificially inseminate a queen that is highly homozygous, a colony of workers with coefficients of relationship greater than 0.75 (as a result of the inbreeding) is produced. If we mate several sire-queens to an array of inbred dam-queens, the between sire-queen variance

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component can be used to estimate h^2. This approach and the reasons for it have been discussed in greater detail by Rinderer[12].

Materials and Methods

This experiment was one part of a larger project to study the Africanized bee in South America and compare it to the European honey bee used in the United States. Numerous differences are said to exist between these two populations in defensive behavior, swarming frequency, size, and related traits[10]. One-hundred-fifty colonies in the area of Baton Rouge, Louisiana and 147 colonies in the areas of Maturin, Monagas, Venezuela were evaluated for level of colony defense using a standardized test sequence[2,3]. The two most defensive, the two least defensive, and the two intermediate colonies from each population (Venezuela and Louisiana) were chosen as sire-queen sources. Drones (which can mate only once) from these 12 sources were used to singly inseminate (one drone per queen) nine dam-queens, three each from three inbred lines maintained by USDA bee labs in Wisconsin and Louisiana. Each dam-queen headed a small colony consisting of about 1 kg (9000) of her worker-daughters on 3–4 standard (20 × 43 cm) combs. The worker-daughters from these colonies were evaluated for the characters under study. Table I lists the numbers of colonies on which each character was measured for each sire-queen.

The characters evaluated in the laboratory included a measure of response to an alarm pheromone, isopentyl acetate[4], and a measure of honey production referred to as hoarding[9]. For these tests, mature brood was emerged in a 35°C incubator for 24 hours. The newly emerged adult bees were caged in disposable posterboard test cages similar to the wooden cages designed by Kulincevic and Rothenbuhler[9] with a small strip of empty comb, and water and 50 percent (w/w) sugar/water solution in gravity feeder vials, and kept in the incubator. Three cages of 25 bees each were prepared from the bees of each colony.

Once a day, the amount of sugar syrup removed from the vial was measured, and any nearly empty vials replaced with full ones. Estimates of h^2 were made for days 2, 3, and 4 following caging and their average.

Three times each day, on days 2, 3, and 4 every cage was tested in place on the incubator shelves for response to an alarm pheromone, isopentyl acetate (IPA). Measurement of the behavior included the initial activity level of the bees prior to testing (number of bees moving around the cage) and the time elapsed following presentation of the IPA (0.03 ml of IPA 1:10 v/v in paraffin oil on a cork under the wire cage floor) until a group response was seen in seconds).

When the daughter-workers of each mated queen were at least three weeks old, an age appropriate for expression of colony defense, the colony was tested twice using a standardized field test sequence[2]. A photograph was taken of the entrance and flightboard area of the colony to get a pretest measure of the number of bees. At time zero, an alarm pheromone was sprayed at the entrance and the interval until alerted bees began to emerge was measured. At 30 seconds, a second entrance picture was taken and the colony jolted by shooting it with a large marble from a slingshot. Following a 60 second photograph, a mechanical apparatus jiggling two blue suede patches (5 cm × 5 cm each) was moved into position in front of the colony and left in place for 30 seconds. Time until the first bee landed on a target was recorded. A final picture was taken after the jiggler was removed, at 90 seconds. The number of stings left in the suede targets (near = at the entrance, far = ½ meter away) was counted.

Each colony was stimulated to build a piece of comb without the usual foundation base. Foundation, a thin sheet of beeswax impressed with a pattern of comb cell bottoms, guides the bees to build a standard size cell rather than the different sizes found in the two bee populations[10]. Cell size was determined by meas-

Table I. Number of colonies measured for each character set within each sire-queen

Set (no. characters)	Sire-queen: European 1	2	3	4	5	6	Africanized 7	8	9	10	11	12
Laboratory test (6)	9	9	9	9	10*	10*	9	8	8	9	8	8
Field test (9)	8	8	7	8	8	9	6	3	3	3	4	5
Comb (1)	8	8	4	6	6	7	7	7	5	6	8	4

* For these two sire-queens, a backup colony was tested along with the nine basic colonies

Table II. Least-squares means ± SD for each character, by population

Character†	Sire-queen: European (Louisiana)	Africanized (Venezuela)	No. obs. per colony
Hoarding (ml/day)			
day 2	5.38 ± 0.44	4.98 ± 0.46	3
day 3	5.20 ± 0.39	4.50 ± 0.41	3
day 4	4.89 ± 0.32	4.80 ± 0.33	3
average	5.16 ± 0.34	4.76 ± 0.36	3
Response to IPA			
initial activity (no. bees)	3.80 ± 0.24	3.65 ± 0.24	27
time (s) to react	3.16 ± 0.21*	3.92 ± 0.22*	27‡
Colony defense			
time (s) to react to:			
pheromone	13.28 ± 1.19	15.77 ± 1.70	2
targets	5.46 ± 0.58	4.78 ± 0.83	2
No. stings in target			
near	7.40 ± 0.93	9.30 ± 1.33	2
far	1.21 ± 0.21	1.47 ± 0.31	2
total	8.61 ± 0.98	10.77 ± 1.41	2
No. bees in picture			
pre	4.84 ± 0.66	4.43 ± 0.94	2
30s	11.17 ± 1.31	8.43 ± 1.87	2
60s	13.22 ± 1.56	11.05 ± 2.23	2
90s	10.22 ± 1.13	11.28 ± 1.61	2
Comb cell size (mm/cell)	5.28 ± 0.02	5.26 ± 0.02	3

† $df = 1,10$ from sire mean square term
* Means are significantly different at $F = 6.55$, $P < 0.05$
‡ This is a maximum number because the bees did not always respond during a test

uring the length of three series of 10 cells each.

Replicate observations on each colony were used to calculate a colony mean, the best estimate of the colony value for each characteristic. These colony means were then used in the estimation of h^2 and the correlations. Analysis was by the mixed model least-squares method (Henderson's method three[8]). The statistical model included population, sire-queen within population, dam-queen, sire-queen by dam-queen within population, and colony within sire-queen, dam-queen and population. Population and dam-queen were considered fixed effects, all others were random. The analysis was done for the Venezuela and Louisiana populations separately and for the two combined.

Heritability was estimated by:

$$h^2 = \frac{4\,\hat{\sigma}^2_S}{\hat{\sigma}^2_S + \hat{\sigma}^2_{S\bullet D} + \hat{\sigma}^2_{Col.}}$$

Where: $\hat{\sigma}^2_S$ = sire-queen variance component

$\hat{\sigma}^2_{S\bullet D}$ = sire-queen * dam-queen variance component

$\hat{\sigma}^2_{Col.}$ = colony variance component

The standard error of h^2 was by the method of Hazel and Terrill[7]. Genetic correlations and their standard errors were estimated by the method of Falconer[6].

Results and Discussion

Least-squares means and standard errors for each of the 16 traits in the two populations are presented in Table II. The only means that are different for the two sire-queen populations are those for seconds to react to alarm pheromone during the laboratory test.

The estimates of heritability and genetic and phenotypic correlations are presented in Tables III, IV, V, and VI. For most of the characteristics, this is the first time such estimates have been published. Collins[1] reported a h^2 of 0.68 for time to react to IPA in the same lab test using regression of offspring on midparent. The three values presented here are quite variable (1.28, 0.31, and 0.83), but the combined h^2 is similar to the 1979 estimate.

El-Banby[5] and Soller and Bar-Cohen[14] published heritability values for honey production (change in colony weight) and brood rearing (area of brood). The only similar trait in this study is hoarding, a laboratory measure of honey production. The h^2 values for hoarding (0.20–0.92) were similar or slightly higher than the previous estimates (0.75, 0.57, 0.58, 0.60). The laboratory measure is probably less influenced by environmental fluctuations. Initial activity level (lab test) was the only trait with very low h^2 (0.04–0.12).

There were no h^2 estimates for time to respond to pheromone (field test), number of stings in the far target, and number of bees in the 30-second picture due to negative variance components. For number of stings in the near target, total stings, number of bees in the prepicture and 60-second picture and comb cell size, there were one or two of the heritabilities nonestimable due to negative variance components. For the field defense test particularly, there were minimal numbers of colonies (Table I) tested due to time limitations in Venezuela and the overly young ages of the bees in many of the colonies.

The genetic correlations were generally higher than the corresponding phenotypic correlations. The four hoarding measures correlate highly with each other and negatively with field defense measures (especially number of bees) in the Venezuela population, but not the Louisiana population. Laboratory test

Table III. Estimates of heritability and genetic and phenotypic correlations of laboratory tests (including comb cell size)*

Trait	Population†	Hoarding				Response to IPA		Comb cell size
		day 2	day 3	day 4	average	initial activity level	time to react	
Hoarding (ml/day):								
day 2	E	0.86 ± 0.46	>1.0	0.90 ± 0.06	>1.0	<−1.0	<−1.0	...‡
	A	0.51 ± 0.61	>1.0	>1.0	>1.0	<−1.0	<−1.0	0.11 ± 0.20
	E + A	0.74 ± 0.42	>1.0	>1.0	>1.0	<−1.0	−0.88 ± 0.01	0.26 ± 0.10
day 3	E	0.73	0.72 ± 0.47	>1.0	>1.0	<−1.0	<−1.0	...‡
	A	0.91	0.57 ± 0.63	0.37 ± ...‡	>1.0	<−1.0	0.10 ± 0.12	0.30 ± 0.19
	E + A	0.78	0.72 ±0.42	>1.0	>1.0	<−1.0	−0.74 ± 0.02	0.51 ± 0.09
day 4	E	0.44	0.41	0.58 ± 0.42	1.00 ± 0.001	−0.24 ± 0.25	<−1.0	...‡
	A	0.94	0.82	0.20 ± 0.45	0.58 ± ...‡	<−1.0	>1.0	−0.35 ± ...‡
	E + A	0.66	0.54	0.44 ± 0.34	>1.0	<−1.0	−0.65 ± 3.26	0.18 ± 0.17
average	E	0.87	0.91	0.69	0.92 ± 0.44	<−1.0	<−1.0	...‡
	A	0.99	0.95	0.95	0.66 ± 0.69	<−1.0	−0.28 ± 0.10	0.08 ± 0.19
	E + A	0.93	0.91	0.79	0.88 ± 0.43	<−1.0	−0.74 ± 0.02	0.32 ± 0.09
Response to IPA:								
initial activity level (no. bees)	E	−0.04	0.07	0.07	0.05	0.05 ± 0.01	>1.0	...‡
	A	0.50	0.64	0.39	0.54	0.12 ± 0.01	>1.0	>1.0
	E + A	0.12	0.19	0.15	0.18	0.04 ± 0.01	>1.0	0.95 ± 0.01
time (s) to react	E	0.16	0.18	−0.12	0.11	−0.57	1.28 ± 0.04	...‡
	A	−0.64	−0.72	−0.65	−0.70	−0.26	0.31 ± 0.01	0.45 ± 0.03
	E + A	−0.19	−0.10	−0.30	−0.20	−0.49	0.83 ± 0.01	−0.84 ± 0.01
Comb cell size	E	0.25	−0.004	0.14	0.13	−0.10	0.10	...‡
	A	−0.24	−0.06	−0.40	−0.22	−0.30	0.12	1.15 ± 0.11
	E + A	0.02	−0.02	−0.05	−0.02	−0.15	0.11	0.49 ± 0.03

* Genetic correlations are above the diagonal, heritabilities are on the diagonal, and phenotypic correlations are below the diagonal

† E-European, A-Africanized; E + A are combined populations

‡ Value not estimable due to negative variance components

Table IV. Estimates of heritability and genetic phenotypic correlations—field test of colony defense*

Trait	Population†	Time to react to: pheromone	Time to react to: targets	No. of stings: near target	No. of stings: far target	No. of stings: total	pre	30s	60s	90s
Time (s) to react to:										
pheromone	E	...‡	...	...	<−1.0	...	>1.0	...	...	...
	A	...	...	>1.0	>1.0	>1.0	...	>1.0	>1.0	...
	E + A	...	...	...	>1.0	>1.0	...	...	...	...
targets	E	0.47	0.31 ± 0.20	...	...	<−1.0	...	0.63 ± 0.02	0.11 ± 0.09	−0.25 ± 0.10
	A	0.69	0.59 ± 0.31	...	...	...	−0.95 ± 0.03	...	...	>1.0
	E + A	0.51	0.38 ± 0.19	<−1.0	...	...	−0.42 ± 0.33	>1.0	>1.0	0.28 ± 0.09
No. stings:										
near target	E	−0.42	−0.54	0.66 ± 0.25	...	>1.0	...	0.32 ± 0.08	0.33 ± 0.06	−0.34 ± 0.07
	A	−0.26	−0.15	...	−0.46 ± ...	−0.93 ± ...	...	−0.57 ± ...	−0.61 ± ...	...
	E + A	−0.39	−0.48	0.01 ± 0.12	...	...	<−1.0	>1.0	>1.0	<−1.0
far target	E	−0.27	−0.30	0.12	...	...	0.18 ± ...	...	...	...
	A	−0.27	−0.13	0.51	...	−0.55 ± ...	...	−0.40 ± ...	−0.69 ± ...	...
	E + A	−0.27	−0.27	0.19	...	<−1.0	...	...	...	...
Total	E	−0.45	−0.58	0.98	0.30	0.57 ± 0.24	...	0.40 ± 0.00	0.39 ± 0.06	−0.26 ± 0.08
	A	−0.28	−0.16	0.99	0.65	...	...	−0.58 ± ...	−0.66 ± ...	...
	E + A	−0.42	−0.51	0.98	0.36	...	...	...	...	...
No. bees in picture:										
pre	E	−0.47	−0.14	0.04	0.00	0.04	...	<−1.0	...	...
	A	−0.58	−0.48	0.33	0.71	0.44	0.56 ± 0.25	...	...	>1.0
	E + A	−0.49	−0.21	0.10	0.16	0.13	0.26 ± 0.17	...	...	−0.48 ± 0.36
30s	E	−0.85	−0.62	0.49	0.35	0.53	0.52	0.47 ± 0.02	0.42 ± 0.05	0.75 ± 0.01
	A	−0.90	−0.53	0.35	0.38	0.39	0.68	0.71 ± 0.01	−0.95 ± ...	...
	E + A	−0.86	−0.60	0.46	0.36	0.50	0.55	0.12 ± 0.00	>1.0	0.63 ± 0.00
60s	E	−0.79	−0.61	0.32	0.33	0.37	0.42	0.91	0.73 ± 0.02	0.22 ± 0.02
	A	−0.72	−0.56	0.51	0.28	0.51	0.64	0.87	...	...
	E + A	−0.74	−0.57	0.35	0.30	0.39	0.49	0.87	0.14 ± 0.00	−0.39 ± 0.00
90s	E	−0.62	−0.40	0.29	0.31	0.34	0.58	0.76	0.75	0.93 ± 0.03
	A	−0.27	−0.30	0.66	0.38	0.66	0.69	0.38	0.60	0.17 ± 0.01
	E + A	−0.49	−0.35	0.37	0.32	0.41	0.60	0.61	0.68	0.55 ± 0.02

* Genetic correlations are above the diagonal, heritabilities are on the diagonal, and phenotypic correlations are below the diagonal
† E-European, A-Africanized; E + A are combined populations
‡ Value not estimable due to negative variance components

Table V. Genetic correlations between laboratory test and field test traits

Field test traits	Population*	Laboratory test traits: Hoarding day 2	Hoarding day 3	Hoarding day 4	Hoarding average	Response to IPA: initial activity level	Response to IPA: time (s) to react	Comb cell size
Time (s) to react to:								
pheromone	E	...†	...	...	...	...	...	<−1.0
	A	...	...	...	...	...	...	...
	E + A	...	...	...	...	...	...	...
targets	E	0.74 ± 0.13	1.01 ± 0.02	0.66 ± 0.27	0.80 ± 0.12	>1.0	−0.82 ± 0.03	...
	A	<−1.0	<−1.0	−1.00 ± ...	<−1.0	>1.0	0.36 ± 0.08	0.84 ± 0.05
	E + A	0.06 ± 0.31	0.56 ± 0.23	0.05 ± 0.51	0.22 ± 0.28	>1.0	−0.55 ± 0.04	0.75 ± 0.05

* E-European, A-Africanized; E + A are combined populations. † Value not estimable due to negative variance components

Table VI. Phenotypic correlations between laboratory test and field test traits

Field test traits	Population*	Laboratory test traits: Hoarding day 2	Hoarding day 3	Hoarding day 4	Hoarding average	Response to IPA: initial activity level	Response to IPA: time (s) to react	Comb cell size
Time (s) to react to:								
pheromone	E	0.47	0.22	0.33	0.39	−0.21	0.15	0.23
	A	−0.40	−0.31	−0.39	−0.38	−0.07	0.04	−0.24
	E + A	0.16	0.10	0.15	0.15	−0.19	0.12	0.11
targets	E	0.06	−0.01	0.42	0.15	−0.19	−0.01	0.11
	A	−0.39	−0.26	−0.24	−0.32	0.12	−0.17	−0.46
	E + A	−0.08	−0.06	0.25	0.01	−0.14	−0.05	−0.03
No. stings:								
near target	E	−0.13	0.05	−0.05	−0.03	0.09	0.13	−0.04
	A	0.54	0.48	0.71	0.58	−0.04	−0.41	−0.05
	E + A	0.08	0.14	0.13	0.13	0.07	0.01	−0.04
far target	E	−0.12	−0.09	−0.09	−0.12	0.10	−0.21	−0.35
	A	0.41	0.59	0.35	0.47	0.39	−0.36	0.43
	E + A	0.07	0.08	0.03	0.07	0.15	−0.25	−0.14
total	E	−0.15	0.04	−0.07	−0.05	0.10	0.09	−0.10
	A	0.56	0.54	0.70	0.61	0.04	−0.43	0.04
	E + A	0.09	0.15	0.12	0.14	0.09	−0.04	−0.07
No. bees in picture:								
pre	E	−0.43	−0.66	−0.38	−0.62	−0.20	0.02	0.14
	A	0.81	0.84	0.66	0.81	0.66	−0.43	0.16
	E + A	0.06	−0.24	−0.06	−0.10	−0.02	−0.11	0.15
30s	E	−0.33	−0.32	−0.30	−0.38	0.22	−0.05	−0.15
	A	0.51	0.50	0.49	0.52	0.26	−0.31	0.23
	E + A	−0.01	−0.11	−0.08	−0.08	0.22	−0.12	−0.04
60s	E	−0.20	−0.26	−0.26	−0.29	0.37	−0.25	−0.22
	A	0.70	0.66	0.68	0.71	0.15	−0.55	0.16
	E + A	0.25	0.08	0.11	0.16	0.30	−0.36	−0.07
90s	E	−0.08	−0.25	−0.17	−0.21	−0.03	−0.09	0.08
	A	0.95	0.88	0.95	0.96	0.50	−0.55	−0.33
	E + A	0.44	0.17	0.28	0.33	0.11	−0.27	−0.09

* E-European, A-Africanized; E + A are combined populations

Table V. Cont'd.

Field test traits	Popula-tion*	Laboratory test traits: Hoarding day 2	Hoarding day 3	Hoarding day 4	Hoarding average	Response to IPA: initial activity level	Response to IPA: time (s) to react	Comb cell size
No. stings:								
near target	E	−0.95 ± 0.02	−0.90 ± 0.06	−0.92 ± 0.06	−0.89 ± 0.05	>1.0	>1.0	...
	A	...	...	...	...	...	...	...
	E + A	<−1.0	<−1.0	<−1.0	<−1.0	>1.0	>1.0	<−1.0
far target	E	...	...	...	...	...	...	>1.0
	A	...	...	...	...	...	...	...
	E + A	...	...	...	...	...	...	...
total	E	<−1.0	<−1.0	<−1.0	<−1.0	>1.0	>1.0	...
	A	...	...	...	...	...	...	...
	E + A	...	...	...	...	...	...	...
No. bees in picture:								
pre	E	...	...	...	...	...	...	0.94 ± ...
	A	<−1.0	−0.79 ± 0.17	<−1.0	<−1.0	<−1.0	−0.70 ± 0.04	−0.65 ± 0.08
	E + A	0.02 ± 0.35	0.44 ± 0.31	0.32 ± 0.53	0.23 ± 0.32	<−1.0	<−1.0	−0.06 ± 0.14
30s	E	0.14 ± 0.08	−0.18 ± 0.11	−0.50 ± 0.09	−0.15 ± 0.08	<−1.0	0.74 ± 0.01	...
	A	...	...	...	...	...	...	...
	E + A	>1.0	0.68 ± 0.00	0.62 ± 0.00	0.81 ± 0.00	<−1.0	>1.0	>1.0
60s	E	0.26 ± 0.06	−0.03 ± 0.09	−0.12 ± 0.10	0.06 ± 0.07	<−1.0	0.03 ± 0.02	...
	A	...	...	...	...	...	...	...
	E + A	0.31 ± 0.00	0.12 ± 0.00	−0.02 ± 0.00	0.15 ± 0.00	−0.70 ± 0.00	>1.0	...
90s	E	−0.36 ± 0.06	−0.20 ± 0.09	−0.65 ± 0.06	−0.36 ± 0.07	<−1.0	0.51 ± 0.02	...
	A	>1.0	>1.0	>1.0	>1.0	>1.0	−0.90 ± 0.01	0.82 ± 0.02
	E + A	0.19 ± 0.08	−0.10 ± 0.09	−0.43 ± 0.11	−0.05 ± 0.08	−0.86 ± 0.02	0.52 ± 0.01	0.46 ± 0.03

measures of reaction to pheromone had low correlations (0.1-0.21) with the field measures. The field defense measures also correlate highly with each other as reported by Collins and Kubasek[2]. Speed of the reaction is negatively correlated with number of stings and number of bees, as is expected. Comb cell size is not well correlated with any of the other characters.

This experiment has documented that all the characters measured except initial activity level should respond to appropriate selection procedures. The high genetic correlations predict that there will be correlated changes in the traits listed, with the possible exception of comb cell size.

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