APIMONDIA

BEE GENETICS, SELECTION AND REPRODUCTION

International Symposium on bee biology,
Moscow, USSR, August 1976

APIMONDIA PUBLISHING HOUSE
BUCHAREST 1977

THE HEREDITY OF COLOR PATTERNS IN THE HONEY BEE

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The color of the honey bees is the most distinct character of a bee race. It is the first which is described by a characterization of a honey bee race. Surprising the heredity of color in the honey bee is not explained.

NEWELL (1915), GOETZE (1940) and EL BANBY (1965) called the yellow color to be dominant, while ARMBRUSTER (1923) and WATSON (1927) assumed that the black color is dominant. SLADEN (1909), NOLAN (1929) and ROBERTS and MACKENSEN (1951) concluded on the other hand that the resulting F-l workers from black x yellow cross are intermediate. Segregation of the F-2 drones produced by hybrid F-l queens is also not clear. ZANDER (1923), NEWELL (1915), EL BANBY and LAIDLAW (1962) and EL BANBY (1965) reported segregation of yellow and black in proportion 1 : 1, ROBERTS and MACKENSEN (1951) obtained a continuous segregation that ranged from yellow to completely black, while ARMBRUSTER (1923) called for a matroclinous heredity.

Many misleading results were reported in the earlier papers because at that time the multiple mating of queens was not known. Only after instrumental insemination was applied, and when the queen was inseminated with one drone, detailed studies of the heredity of the color patterns were possible. ROBERTS and MACKENSEN (195 1) concluded that there are at least seven different loci for genes that affect the color of the abdomen. Drones produced by F-l hybrid queens showed gametic segregation for color. These ranged from yellow to complete black. F-l hybrid queen mated to a black drone produced progeny that ranged in color from intermediate to complete black, and F-I hybrid queen mated to a yellow drone produced progeny, that ranged in color from intermediate to parental yellow. The variation in color was continous. LAIDLAW and EL BANBY (1962) described a recessive black modifier *bl* with an epistatic effect on the yellow polygenes ; it inhibited the yellow phenotype. But there was noticed a limit to the number of yellow genes which the black modifier could completely inhibit. Further on TUCKER and LAIDLAW (1967) concluded that the combined action of most to all of the genes for black of the polygene series and the black gene, *bl* resulted in jet black drones. They believed that in the absence of *bl* the same genotypic series would vary in phenotype from black to golden. The progeny in the above investigations was only roughly classified and no numbers belonging to specific color classes were presented.

KULINCEVIČ (1966) made a detailed classification of drones originating from hybrid queens. He found males with all intermediary colors, but the distribution was bimodal with the two peaks near the parental types. The bimodality was not explained, but it was concluded that inheritance of body color is definitely polygenic.

KERR (in ROTHENBUHLER, KULINCEVIC and KERR 1968) found in *A. m. adansonii* one brown gene, *ac* (abdomen color) which changed yellow pigment to brown in males but did not act in females even when homozygous. KERR (1969) stated further that the gene *Ac* (regular wild gene in *A. m. adansonii)* causes 6-7 quantitative genes for yellow abdomen to become limited to females, since they will not show their action in the males.

Material and methods

Honey bees of the following races were investigated : *A. m. ligustica* and *A. m. lamarkii* (fasciata) of the yellow colored races, *A. m. mellifera*, *A. m. carnica* and *A. m. caucasica* of the black colored races and *A. m. adansonii* in which the females were yellow and the drones black.

Color patterns on the abdomen of the offspring was classified according to a 10 class scale. Class No. 1 is the lightest one and No. 10 the darkest. Drones of classes No. l-5 are considered as yellow colored, those of class No. 6 as intermediate and those of classes 7-10 as black colored. The color patterns in drones are different from those of the worker bees. Till now it was not shown which color class of the workers corresponds to the color of the drones. Therefore in this paper, only results concerning color classes in drones are presented. To obtain informations concerning homozygotes as well as zygotes, haploid as well as diploid drones were reared and classified.

At first haploid drones of pure races were classified. Next reciprocal crosses of yellow and black parents were made. Haploid drones of the parental queen as well as the father itself were classified. Next hybrid F-l queens were reared, and they were backcrossed to drones originating from the parental queen. This was a sister x brother mating. Color class of the drone used for insemination was noticed. Haploid as well as diploid drones resulting from these crosses were reared and classified.

Due to insufficient time, only small part of the results obtained is presented on this symposium.

Results

Pure races

Italian bees A. *m. Zigustica* produced haploid drones of only one class being the lightest one No. 1 as well as a variety of few classes within the yellow range. The Egyptian queen produced a variety of drones ranging from yellow to black, with two peaks, one in the yellow range and the other in the black range. It is not clear whether this queen was pure Egyptian, but similar results were presented by KULINCEVIČ (1966). Those queens of A. *m. mellifera* as well as *A. m. carnica* which were investigated produced only one class of the darkest drones. It should be noticed that the drones in hive did not look very dark due to brown or gray hairs. The color patterns of the Caucasian haploid drones were a little lighter varying from class No. 7 to No. 10 with an extreme peak in class No. 9. But it should be noticed that the drones were looking in the hive as jet black, due to black hairs, covering them. The African drones **A.** *m. adansonii* covered four dark classes No. 7 — 10. This was a surprising result, because according to the literature there was expected that due to the action of the *ac* gene, all the drones would be in one darkest class.

Crosses

A Polish ecotype queen of the **A.** *m. mellifera* race producing haploid drones of the darkest class No. 10 was instrumentally mated to an Italian drone class No. 2. The resulting F-l hybrid queens were yellow. Due to only one color class of garnets produced by their mother, the exact genotype of the F-l hybrid queens is known and it is designed as $\frac{\text{PO-}10}{\text{It}-2}$. The letters indicate the race, and the numbers the class of the parental garnets. Those hybrid queens produced two groups of haploid (drones : the yellow and bhe black ones in a proportion approximate to 1 : 1. But the yellow drones covered all the yellow classes from No. l-5, with the middle classes No. 2-4 being the most numerous. The black drones were all in one or two darkest classes. Insemination of those hybrid queens with a drone of the darkest class No. 10 resulted in diploids which were easily devided also into two groups : yellow and black. But contrary to the haploids all the yellow diploids fell in the darkest yellow class No. 5. The black drones covered the two darkest classes.

A reciprocal cross was made with an Italian queen producing all haploids of the lightest class No. 1 with a Polish drone of the darkest class No. 10. The F-l hybrid queens were yellow, and they produced also two groups of haploid drones : yellow and black. The yellow drones also covered the 5 yellow classes, but now the most numerous was the first class like in the parental mother. The black haploids covered the two darkest classes, but now the before last class No. 9 was numerous. After a hybrid F-l queen No. 2216 was mated to one black uncle, she produced two groups of diploid drones similar to the previous crosses, but after the hybrid queens No. 2273 and 2274 were mated to their yellow brothers, they produced only one group of yellow diploid (drones, ranging from class No. 1 to class No. 5.

Next Italian and African races were crossed. Parental yellow African queen No. 618 produced only black haploid drones ranging from class *No.* 7 to class No. 9. It was mated with light yellow Italian drone class No. 2. The resulting F-l hybrid queens were yellow. They produced two groups of yellow and black haploid drones. The frequency of drones in the classes of the yellow group was similar to that described in the previous crosses. But drones of the black group were also present in all classes of that group ranging from No. 6-7 to class No. *10.* Hybrid E-l queen No. 666 produced haploids among which the lightest class No. 65 was the most numerous in the black group. Thus a distinct difference in the distribution of haploids in the black group of *A. m. mellifera* and *A. m. adansonii* was noticed. In *A. m. mellifera* the black classes were concentrated in two to three darkest classes and in *A. m. adansonii* they are spread through all the range of the black group. After the F-l hybrid queens were backcrossed to black African brothers they produced two groups of diploid drores. The yellow diploid drones were gathered in the darkest classes No. 4 and 5 as previously, but the black diploids occupied three classes, with the peak in class N. 8 when an African drone class No. 7 was used, queens Nos. 626 and 665 and with peak in a darker class No. 9 when a darker father class No. 8 was used.

In a reciprocal cross, the parental Italian queen produced darker yellow drones (classes No. 3 to 5). The F-l hybrid queens produced both groups of yellow and black drones. But in the yellow group the darker classes No. 4 and 5 were the most numerous similar to that in the parental queen. Quite numerous was the intermediate class and the black group classes No. 7 to No. 9 were present.

It/af hybrid queens mated to dark yellow Italian drones produced diploids of one dark yellow class No. 5 and of the intermediate class No. 6. With darker father class No. 4, the intermediate class was more numerous (queen No. 722) than when a lighter father, class No. 3 was used.

Crosses were made also between all three types of races, the yellow, the black, and the African with yellow females but black males. F-l hybrid queens originating from Italian queen and black *(Bl)* drone (race not determined) produced haploids in similar class frequencies to those described already for this type of cross. The darkest class No. 10 was the most numerous in the black group. After those hybrid queens were mated to black African drones they produced two groups of diploids; the yellow one and the black one. Diploid drones of the black group covered all the classes of that group like it is characteristic for the African bee. When a light "black" father class No. 6 was used the intermediate class No. 6 was the most numerous in the black group. When a dark African father No. 9 was used, then the darkest class No. 10 was the most numerous within the dark group of diploid drones (queen No. 131).

Discussion and conclusions

There can not be concluded the existence of 6-7 poligenes which determine the yellow color and one black gene *bl* and one *ac* gene which inhibit the action of those poligenes. In a case like this, without the *bl* and *ac* genes the yellow poligenes should segregate freely giving in the F-2 gametes a normal distribution of a Gauss curve reaching from class No. 1 to No. 10. But actually two groups of 5 classes each were found and cumulation in a lightest as well as in the darkest yellow class was noticed several times as well as in other parental classes. The action of the *bl* and *ac* (or *Ac*) genes is also little different from that what was believed. They were supposed to inhibit the effect of the quantitative poligenes for color, but virtually they are modified by all those poligenes. In order not to eliminate or to change the symbols already introduced for color in the honeybee, they will be used further on, although their action will be modified.

Production of two distinct groups of haploid drones by the hybrid queens can be explained by the existence of two major allelic genes : one resulting in the yellow group and one in the black group. The major genes are modified by several modifiers. The results presented above showed clearly, that the yellow color is dominant over the black one. Thus the yellow major gene is designed as Y and the black one as y^{bl}.

Production of two groups of haploids by F-l hybrid queens of the Italian and African cross, shows that here similar mechanism operate. Thus the major African gene is an allele to the major yellow gene. The diploid drones showed that it is recessive to the yellow color. Thus it is designed as y^{ac}. Since both major genes resulting in black groups of drones are alleles to the same major yellow gene Y, they are alleles to each other, and so there are really altogether three major alleles for the color : Y, y^{bl} and y^{ac}. The y^{bl} allele and the y^{ac} allele are not identical. The y^{bl} allele act only in the drones. This was shown in a comparative test cross. After an *A. m. mellifera* queen y^{bl}/y^{bl} was inseminated by a black y^{bl} drone it produced only black workers like it is commonly known. But when several black *A. m. mellifera* queens y^{bl}/y^{bl} were inseminated by black African drones y^{ac}, they produced only workers with yellow bands.

The broad range of classes occupied by the black diploid (drones of the probable genotype y^{bl}/y^{ac} is similar to that of the *A. m. adansonii* drones. This would suggest that African y^{ac} allele is at least partly dominant over the y^{bl} allele. Thus the sequence of dominance would be $Y \rightarrow y^{ac} \rightarrow y^{bl}$.

Expression of the major genes is modified by several modifiers with alternative alleles for dark and light A/a, B/b, C/c ...; their action is cumulative. Increasing number of the dark alleles A, B, C, shift's the expression of the major genes into darker classes, and an increase of the light modifiers a, b, c. ... shifts the expression of the major genes into lighter classes. The expression of the yellow major gene Y can be modified mainly within the yellow group, class range No. 1 to No. 5, and that of the black major genes within the black group, mainly clas range No. 6-7 to No. 10.

The experimental results obtained showed that haploid drones originating from F-l hybrid queens and having the yellow major gene Y or the African major gene y^{ac} were spread through many color classes and those drones with the major black gene y^{bl} were concentrated in one or very few classes. This shows that the major genes Y and y^{a} are labile ones, and their expression can be easily modified by the modifiers. One or two more modifiers suffice to shift the expression of the major gene to a next class. But the major black gene y^{bl} is stable. More light modifiers are needed to shift the expression of that gene to the next class.

Concerning the number of the modifiers, segregation resulting in 5 classes in each group is obtained with 4 loci. But with this mechanism no cumulation in the lightest and in the darkest class of each group is accounted. There is assumed with accordance of the experimental results obtained, that the action of two modifiers is necessary to shift the yellow phenotype from class No. 1 to class No. 2. Action of each additional modifier shifts the resulting phenotype by one class. Again the results of two modifiers may be cumulated in the darkest class No. 5 of the yellow group. The same mechanism is valid for the y^{ac} major gene in the black group.

Theoretical segregation in accordance with this mechanism and very similar to the experimental results obtained, was reached when the action of 6 modifiers with alternative alleles for light and dark was assumed.

Mostly cumulation of dark alleles did not transpass the darkest yellow class No. 5 when the major Y gene was present, or cumulation of light alleles did not transpass the lightest class No. 6 in the black group when the y^{ac} or y^{bl} allele was present. But evidences were encountered that this can happen sometimes with the labile major genes Y or y^{ac}. Thus influence of environmental conditions may be considered or the existence of 7 modifiers should be assumed. The number of 6 or 7 polygenes modifying the effect of one major gene within each group of 5 classes is equal to the number of polygenes assumed by ROBERTS (1951), although he did not divide the offspring into two groups, and did not call for cumulation in the two extreme classes of each group. With this assumption several modifiers must be envolved to shift by one class the effect of the stable black major gene y^{bl}.

Regarding the diploid drones, (darker classes were more frequent among them than in the haploids. Diploid drones darker than the haploids resulted even then when they had very light fathers of class No. 2. This result seems to be true for homozygous Y/Y, and y^{ac}/y^{ac} as well as for heterozygous Y/y^{bl} and Y/y^{ac} diploids.

Thus dominance of the dark modifiers over the light ones must be concluded.

In the case of cumulative action of the heterozygote for two labile major genes Y/y^{ac} and many dark modifiers Af-9 $\times$ It-4 or Af-9 $\times$ It-3 (sum 9 + 4 = 13 or 9 + 3 = 12) the diploids transpassed even from the dark yellow class No. 5 to the intermediate class No. 6. This did not happen when in the heterozygote of the two major genes fewer dark modifiers were present It-22 $\times$ Af-7 or $\times$ Af-8 (sum $2 + 7 = 9$ or 2 + 8 = 10).

But diploid drones homozygous for the major black gene y^{bl}/y^{bl} were darker than the haploids in one case and lighter in another case. This differring result may be explained by intermediate action of the dark and light allelic modifiers in the homozygote for the major black gene y^{bl}/y^{bl}.

Resuming the studies, there is concluded that the heredity of color patterns in the honey bee is governed by three allelic major genes Y, y^{bl}, and y^{ac}. The expression of those major genes is modified by 6-7 polygenic modifiers with alternative alleles for light and dark.