

GENIC BALANCE, HETEROZYGOSITY AND INHERITANCE OF SIZE OF TESTES IN DIPLOID DRONE HONEYBEES*

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Summary

In order to rear diploid drones with larger testes, the inheritance of testis size was investigated. The genic balance hypothesis was tested in relation to the different additive effects of various *X*-alleles. Different levels of heterozygosity of multiple loci were also considered.

Apis mellifera adansonii and *A.m. ligustica* were crossed to determine the *X*-allele composition of the offspring; this resulted also in different degrees of heterozygosity in the progeny. About 300 queens were instrumentally inseminated, and haploid and diploid drones originating from 23 queens were investigated; 1460 testes were measured.

The size of the testes of haploid drones of various groups differed very little. The average volume of the testes of various groups of haploid drones was 2.7–6.5 times as large as that of diploids of the same groups. Diploid drones of African bees had larger testes (mean volume 4.14 mm³) than those of Italian bees (mean 1.82 mm³), and backcrosses to Italian queens resulted in medium-sized testes (mean 2.76 mm³).

Homozygosity of *X*-alleles reduced the size of the testes of diploid drones, but this size did not follow the *X*-allele compositions of the individuals. Thus the different additive ability of various *X*-alleles was not detected here.

An increase of the heterozygosity of loci other than the *X*-locus did not decrease the size of diploid testes. The inheritance of this size was in accordance with additive action of special polygenes. Thus, breeding diploid drones with larger testes should be carried out on the basis of polygenes.

Introduction

The author (1965*a*, 1965*b*, 1969*b*, 1973) showed that the testes of diploid drones were much smaller than those of the haploids. This is one of the difficulties in instrumental insemination of queens with semen of diploid drones, and it would be useful to be able to rear diploid drones with large testes producing more semen.

Woyke (1973) also showed that diploid drones produced by different queens had testes which differed significantly in size. This suggests that breeding and selection for this character is possible, and some knowledge of the inheritance of the testes of diploid drones would facilitate this. It can be concluded from previous results that

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homozygosity of the sex alleles makes the testes small, but it is not known how the size of testes in drones produced by a given queen are determined. There are several hypotheses which need testing.

Cunha and Kerr (1957) presented a genic balance hypothesis, according to which the multiple X -alleles are interpreted as femaleness genes which lose their cumulative property unless they are heterozygous. Therefore, homozygous XX are males, but they have some female-like characters, such as the small testes of adult diploid drones (Woyke, 1965a, 1965b) and the weaker development of the slit in the ventral side of the 9th abdominal segment of larvae 1 hour old (Kerr & Nielsen, 1967). Differences have been found in various diploid male organs: in facet size (Rothenbuhler, 1957; Drescher & Rothenbuhler, 1964), and in rudiments of parts of the copulatory apparatus (Kerr & Nielson, 1967). Kerr (1967) suggested that the different X -alleles have lost the additive ability to a varying degree. Thus, for example, X_1X_1 individuals could be more female-like and the X_5X_5 more male-like. Our results on the size of testes (Woyke, 1973) supported this hypothesis, as a higher degree of femaleness of the diploid drones could be expressed by small testes, and a different additive ability of X -alleles by varying size of testes.

A second hypothesis suggested that heterozygosity of sex-limited loci reduced the size of testes (Woyke, 1966, p. 38); thus an increase of homozygosity of diploid drones should increase the size of their testes. Crozier (1971) also suggested that heterozygosity of several sex loci leads to feminization of the individual.

The third hypothesis, to be investigated here, is that the genes responsible for the size of testes in diploid drones have a possible polygenic action. Since the size of testes is the character showing the greatest difference between haploid and diploid drones, it seems to be the best character for testing this hypothesis.

To investigate these questions, crosses were made which enabled the X -allele composition in the offspring to be determined, and which resulted in different degrees of heterozygosity of the progeny. Then drones were reared, to establish which of the hypotheses best fitted the data on testis size.

Materials and Methods

The length and volume of both testes from 283 haploid and 447 diploid drones were measured. The drones were the progeny of 23 queens, 20 of which produced diploid drones. Not more than 25 diploid drones from any one queen were used for this work. Combs of drone brood were mostly placed in queenless nuclei where the emerged drones were kept until they were used for instrumental insemination; the hive entrances were kept closed with queen excluders all the time. Drones whose semen was used for insemination were preserved in alcohol.

Fig. 1 shows the crosses made*. The original Italian queen, *Apis mellifera ligustica* (no. 7), originated from USA and was mated naturally in the USA in an area of Italian drones. The original African queen, *Apis mellifera adansonii* (no. 63), originated from Brazil, where she was mated naturally in an area of African bees. Both queens produced normal brood. All other matings were made instrumentally, and after the queens were inseminated they were given an identification number. Sibling matings within the progeny of both queens were then made, using the semen of one drone. After the survival rate of brood had been checked, 6 African queens and 4 Italian queens producing scattered brood were used for rearing diploid drones (Fig. 1. SM).

* The original Italian and African queens and the F_1 generation were supplied by Dr. L. Gonçalves.

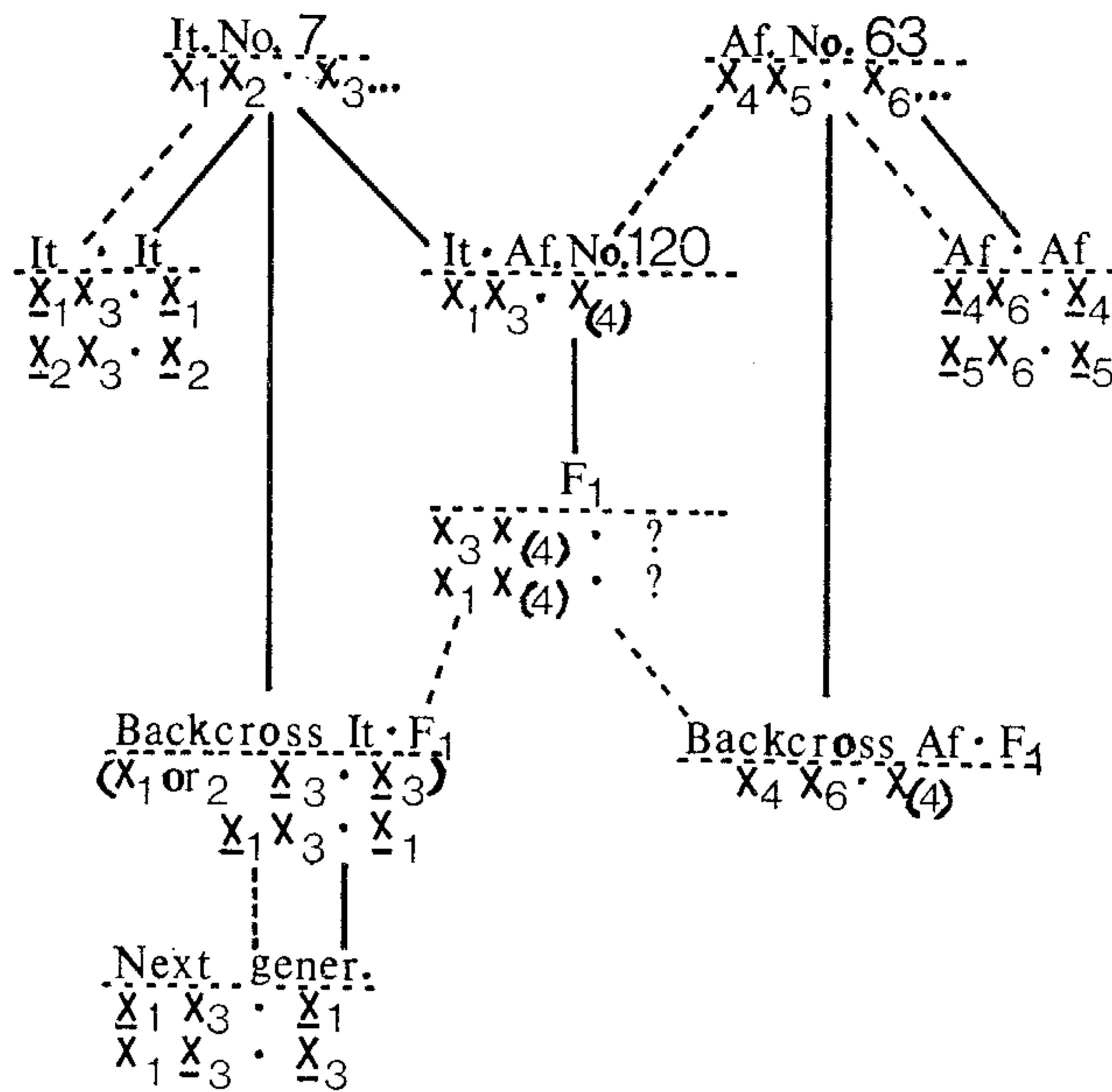


FIG. 2. Possible composition of X -alleles in the crosses made.
 Continuous lines: queens. Dotted lines: drones.

one drone can produce only one type of diploid drone, but all the Italian sibling-mated queens together could produce two different types: X_1X_1 and X_2X_2 .

The African queens could also produce two types of diploid drone: X_4X_4 and X_5X_5 . Crosses of the two races (queen no. 120 and some others not used for further investigation) did not result in brood of low survival rate, which indicated that the X -alleles of the present two races were not the same, so queen no. 120 was designated as $X_1X_3 \cdot X_4$. The F_1 queens reared from this mating could be of two types: X_1X_4 and X_3X_4 . Drones produced by seven F_1 queens were used for backcrosses. But the backcross to 103 African queens (daughters of queen no. 63) with drones from the F_1 queens did not give any queens producing brood of low survival rate. The drone mated to queen no. 120 was re-examined and confirmed as African; this drone could have originated from a laying worker. Due to this uncertainty, the African X_4 allele is shown in brackets in Fig. 2. This did not seriously affect the investigation. It was sufficient to have one type of backcross, namely the Italian queens mated with drones from F_1 queens having some African genomes. The backcross to the Italian queens with drones from four F_1 queens also failed to produce any low survival brood. The F_1 queens are considered to have had X_3X_4 alleles (Fig. 2). Allele X_3 is that which could have been present in the Italian daughters (of queen no. 7) mated with the drones from F_1 queens. But the original Italian queen no. 7 was mated naturally with many drones (the average number in natural matings is 8), and the F_1 queens X_3X_4 produced only 50% drones with the X_3 allele. So the chance of a backcross producing diploid drones after mating with drones from X_3X_4 queens was very low, although it was not excluded. Backcrosses to the Italian queens with drones from three other F_1 queens (2, 4, 48) repeatedly gave queens of which approximately a quarter produced diploid drones. These three F_1 queens are considered to have been

of X_1X_4 composition, and the diploid drones resulting from the backcross of X_1X_1 composition. Sibling mating within offspring of the backcross resulted theoretically in two types of diploid drones: X_1X_1 and X_3X_3 . Queens inseminated with several brothers could produce both types of diploid drones.

Thus, the combinations of X -alleles in the diploid drones produced by the crosses would be: two types produced by the Italian sibling matings X_1X_1 and X_2X_2 , two types produced by the African sibling matings X_4X_4 and X_5X_5 , and in practice only one type produced by the Italian backcross X_1X_1 (although two types of diploid drones X_1X_1 and X_3X_3 are not excluded here). The more common type of diploid drone resulting from the backcross X_1X_1 is the same as half of the pure Italian diploid drones. The next generation of sibling-mated queens originating from the backcross would produce two types of diploid drones: X_1X_1 and X_3X_3 . The first type is the same as in the pure Italian and the backcross. The second type X_3X_3 could rarely appear in the backcross to the Italian.

Length of testes

Table 1 gives the mean testis length in each group, and Tables 2 and 3 show the frequency distributions within each group.

The original queen, no. 63, produced haploid drones whose testis length mostly fell within a very small range (4.4–5.4 mm), showing that this queen had a high degree of homozygosity (Table 2). The daughter queens 128, 141 and 146 produced haploid drones whose testes showed rather greater variation in length, which was probably caused by the additional action of the genomes from the unknown grandfathers of the drones. The distribution of testis length in haploid drones produced by each queen had a single well defined peak, and each mean was significantly different from the other two (Table 1).

The African daughter queens, each of which mated with one brother, produced diploid drones with testes 1.6–4.6 mm long (Table 3); the mean length was 3.3 mm, significantly less than the length for haploid drones in the previous group. The lengths of testes of drones from any given queen showed a distribution with a single well defined peak (Table 3). The difference between the highest and lowest means (diploid drone progeny of queens 141 and 128) was statistically significant, and these means were also significantly different from the other four means in this group (Table 1). However, the differences between these four means (from queens 182, 146, 37, 21) were not significant, although the differences between alternate means (i.e. diploid progeny of queens 182 and 37, 146 and 21) were significant. The African diploid drones could not, therefore, be divided into two definitive groups corresponding to two combinations of sex alleles (X_4X_4 and X_5X_5). But they could be arranged in groups of successively increasing length of testes.

The original Italian queen no. 7 produced haploid drones with significantly longer testes ($P < 0.05$) than those of the haploid drones produced by the original African queen no. 63. A statistical comparison of the mean testis length in all the haploid African drones (4.92 mm) with that in all the haploid Italian drones (4.95 mm), however, showed no significant difference (Table 4). A group of haploid Italian drones (from queen no. 155) was also reared by the method for producing diploids (Tables 1, 2), and their mean testis length was significantly greater, by 0.36 mm; data from this special group were not included in any other comparison.

The sibling-mated Italian daughters of queen no. 7 produced diploid drones whose mean testis length was highly significantly less than that of the African diploids (2.17 and 3.34 mm, respectively, Tables 1 and 5). This difference makes the two

TABLE 1. Mean lengths and volumes of testes from haploid and diploid drones (1 day old) from different crosses. In column 2, F = female, M = male.

Drones	Matings		Mother no.	No. testes	Length		Mother no.	No. testes	Volume		
	F	M			Mean \pm SE (mm)	SE (mm)			Mean \pm SE (mm)	SE (mm)	
<i>African</i>											
1n	Af	63	63	50	4.99 \pm 0.027 ⁻		63	50	12.59 \pm 0.143**		
1n	63	128	128	50	5.08 \pm 0.053**	4.92	128	50	11.30 \pm 0.212**	11.20	
1n	63	141	141	50	4.89 \pm 0.037**	\pm 0.02	141	48	10.59 \pm 0.141**	\pm 0.12	
1n	63	146	146	30	4.57 \pm 0.037		146	28	9.59 \pm 0.217		
2n	63 x 63	141	141	50	3.82 \pm 0.046**		141	50	5.67 \pm 0.200**		
2n	63 x 63	182	182	46	3.47 \pm 0.052 ⁻		182	46	4.32 \pm 0.161 ⁻		
2n	63 x 63	146	146	50	3.42 \pm 0.052 ⁻		146	50	4.17 \pm 0.161 ⁻		
2n	63 x 63	37	37	50	3.25 \pm 0.072 ⁻	3.34	37	50	4.02 \pm 0.195 ⁻	4.14	
2n	63 x 63	21	21	50	3.20 \pm 0.088**	\pm 0.03	21	50	3.91 \pm 0.224**	\pm 0.10	
2n	63 x 63	128	128	40	2.79 \pm 0.069		128	40	2.40 \pm 0.133		
<i>Italian</i>											
1n	It	7	7	50	5.09 \pm 0.038**		7	50	13.23 \pm 0.238**		
1n	7	144	144	50	4.90 \pm 0.034 ⁻	4.95	144	50	11.35 \pm 0.223**	11.92	
1n	7	155	155	50	4.85 \pm 0.046**	\pm 0.03	155	50	11.18 \pm 0.145	\pm 0.14	
1n	7	155+	155+	36	5.21 \pm 0.048		155+	36	13.39 \pm 0.191		
2n	7 x 7	144	144	50	2.72 \pm 0.064**		144	50	2.65 \pm 0.118**		
2n	7 x 7	103	103	50	2.15 \pm 0.067 ⁻	2.17	103	40	1.80 \pm 0.137**	1.82	
2n	7 x 7	155	155	40	2.14 \pm 0.068**	\pm 0.04	103	50	1.65 \pm 0.116**	\pm 0.07	
2n	7 x 7	154	154	50	1.66 \pm 0.042		154	50	1.19 \pm 0.060		
<i>F₁</i>											
1n	120 x 63	48	48	50	4.79 \pm 0.042		48	50	9.78 \pm 0.288		
<i>Backcross</i>											
1n	7	167	167	50	5.12 \pm 0.041**		167	50	12.50 \pm 0.221**		
1n	7	125	125	50	4.86 \pm 0.055 ⁻	4.93	125	50	11.49 \pm 0.178 ⁻	11.76	
1n	7	131	131	50	4.82 \pm 0.046	\pm 0.03	131	48	11.27 \pm 0.220	\pm 0.13	
2n	7 x 4	131	131	50	2.96 \pm 0.060 ⁻		131	50	3.28 \pm 0.117**		
2n	7 x 2	44	44	28	2.84 \pm 0.082 ⁻	2.74	44	26	2.85 \pm 0.178 ⁻	2.76	
2n	7 x 4	125	125	50	2.79 \pm 0.050**	\pm 0.04	125	50	2.79 \pm 0.100**	\pm 0.07	
2n	7 x 48	167	167	50	2.41 \pm 0.062		167	50	2.17 \pm 0.108		

Next generation of backcross	122	44	2.73 ± 0.069 ⁻	2.47	122	44	2.99 ± 0.153 ⁻
2n 131 × 131	122	44	2.73 ± 0.069 ⁻	2.47	122	44	2.99 ± 0.153 ⁻
2n 125 × 125	97†	50	2.71 ± 0.092 ⁻		97	50	2.74 ± 0.180 ⁻
2n 125 × 125	205	14	2.51 ± 0.130 ⁻		78	38	2.36 ± 0.164 ⁻
2n 125 × 125	78	38	2.49 ± 0.077**	±0.36	205	14	1.96 ± 0.209 ⁻
2n 125 × 125	79	44	2.25 ± 0.056 ⁻		46	50	1.87 ± 0.129 ⁻
2n 125 × 125	46†	50	2.18 ± 0.079		79	44	1.82 ± 0.102

+ Haploid drones were reared by the method for diploid drones

† Queen no. 97 mated with 2 drones and no. 46 with 3 drones

- Difference between this mean and subsequent one not significant

* Difference between this mean and subsequent one significant (P < 0.05)

** Difference between this mean and subsequent one highly significant (P < 0.01)

TABLE 2. Frequency distribution of length of testes of haploid drones 1 day old*

Group	Mother of drone (queen no.)	Length (mm ³)												
		4.0	4.2	4.4	4.6	4.8	5.0	5.2	5.4	5.6	5.8	6.0	6.2	
African	63			2	18	19	11							
	128			5	4	7	8	5	6	1				
	141			4	10	14	6	1	1					
	146		5	10	9	6								
Italian	7		1	2	2	11	12	18	4					
	144	1		4	10	17	11	5	2					
	155	1	3	5	10	12	9	1	1					
	155+			1	1	6	9	13	3	2	1	1		
F ₁	48	3	7	12	13	9	4	2						
Backcross	167		1	2	9	15	13	6	3					
	125	2	6	9	14	7	7	1	2					
	131	1	2	8	10	13	9	5	1	1				

* Bold figures show the modal value.

+ Haploid drones reared by the method for diploid drones.

TABLE 3. Frequency distribution of length of testes of diploid drones 1 day old*.

Group	Mother of drone (queen no.)	Length (mm)																		
		1.0	1.2	1.4	1.6	1.8	2.0	2.2	2.4	2.6	2.8	3.0	3.2	3.4	3.6	3.8	4.0	4.2	4.4	4.6
African	141											1	3	6	9	14	8	7	2	
	182								1	3	5	7	16	7	5	3	1			
	146							1	4	7	11	3	15	11	3				2	
	37						2	3	1	2	8	9	14	2	4	4				
21						2		5	3	4	11	8	7	4	4					
128						4		7	6	9	6	6	1	1	1					
Italian	144				1	4	2	5	4	4	9	14	7							
	103		2	2	5	10	9	7	4	4	4	2	1							
	155		2	1	6	2	11	7	5	2	2	1	1							
	154	1	5	11	19	4	8		2											
Backcross	131						3	2	6	2	10	10	8	8		1				
	44					2			4	7	4	5	4		2					
	125							3	12	12	7	7	4	5						
	167				5	3	6	7	15	6	3	1	3	1						
Next generation of backcross	122						5	6	7	2	3	12	6	2						
	97†			3	4	1	2	6	2	7	7	6	2	5	5					
	205					1	1	6	2			2	1	1						
	78				3	3	4	5	6	4	4	7	2							
79					8	7	10	6	7	2	1	1								
46†		4	2	6	4	10	7	5	3	3	3	2	1							

* Bold figures show the modal value.

† Queen no. 97 mated with 2 drones and no. 46 with 3 drones.

TABLE 4. Differences between the mean size of testes of haploid drones of various groups (t-test).

Group	Length (mm)			Volume (mm ³)		
	Italian 4.95	Backcross 4.93	African 4.92	Italian 11.92	Backcross 11.76	African 11.20
Italian		0.02 ⁻	0.03 ⁻		0.16 ⁻	0.72**
Backcross			0.01 ⁻			0.56**

⁻ Not significant ($P > 0.05$)

** $P < 0.01$

TABLE 5. Differences between the mean size of testes of diploid drones of various groups (t-test).

Group	Length (mm)				Volume (mm ³)			
	African 3.34	Back- cross 2.74	Next generation 2.47	Italian 2.17	African 4.14	Back- cross 2.76	Next generation 2.33	Italian 1.82
African		0.60**	0.87**	1.17**		1.38**	1.81**	2.32**
Backcross			0.27**	0.57**			0.43**	0.94**
Next generation				0.30**				0.51**

** $P < 0.01$

racess useful for crosses and genetic studies. Like the African diploid drones, the Italians could be arranged in a series of increasing testis length. Similarly, the highest and lowest means were significantly different, as were differences between these and the intermediate means.

The mean length of 50 testes of haploid drones originating from one F_1 queen was 4.79 mm, within the range found in the four groups of African haploid drones, but slightly lower than any of the three Italian haploid means (Table 1). However, the distribution of lengths was similar in all three groups (Table 2) and, therefore, no heterosis was detected here.

Backcrosses to the Italian strain were made with single drones produced by various F_1 queens (Fig. 1, Table 1). Italian queens 125, 131 and 167 were crosses with drones produced by the F_1 queens, and they produced haploid drones with testes identical or very similar to those of haploid drones originating from the Italian sister queens 144 and 155 used previously for the sibling matings. No significant difference between the means for the two groups was found (Table 4). The length of testes of diploid drones originating from different queens could be arranged in populations with successively decreasing size. Differences between alternate means in Table 1 were statistically significant. Table 5 shows that the mean testis length of diploid drones resulting from the backcross matings was significantly less than that of the African group and greater than that of the Italian group; the mean length in the diploids was marginally less than the mid-point between the African and Italian diploids.

The next generation of queens resulting from the backcross was sibling mated. The length of testes of diploid drones originating from queens 97 and 46 inseminated with two or three drones did not create populations with two peaks, as expected on the basis of the different additivity of the X -alleles, though the variability and the

range of testis length resulting from matings with several drones were greater than in populations from matings with one drone (Table 3). The diploid drones from different queens could, as before, be arranged in populations according to decreasing length of testes. Only two successive means differed significantly. Differences between all alternate means in Table 1, apart from those relating to queens 122 and 205, and to queens 97 and 78, were significant or highly significant. The testes of the diploid drones produced by sibling-mated daughters of queen no. 125 (Table 1: next generation of backcross) were shorter than those of diploid drones produced by their mother, queen no. 125 (Table 1: backcross). Table 5 shows that the average for the next generation backcross was significantly lower than that for the backcross diploid group and for the African diploid group, and significantly higher than that for the pure Italian diploid group. The mean testis length of the whole next generation group was intermediate between that of drones originating from the fundator queen no. 125 and that of the pure Italian diploids.

Volume of testes

The distribution of testis volume was very similar to that of length (Tables 1, 6, 7). Great variations occurred in testes of diploid drones produced by any particular African queen, but in most cases the distribution of volume in siblings had a single well defined peak (Table 7). The highest and lowest mean values in the diploid group differed statistically from those in the intermediates (Table 1), but no difference was found between the four intermediate means. (In results for testis length, differences between alternate means *were* significant.) Thus the diploid testes could perhaps be arranged, on the basis of volume, in three groups.

Table 4 shows that the mean testis volume for haploid Italian drones was significantly higher than that for the African haploids. Differences between all the means for Italian diploid drones were highly significant (Table 1).

The haploid drones of the group backcrosses to the Italian queens had testes whose volume did not differ statistically from the Italian group (Table 4) as the length did. The significance of differences between mean volumes in the diploid backcrossed drones is shown in Table 1. Table 5 shows that the mean volume of diploid testes resulting from the backcross was significantly lower than that from African drones and significantly higher than that from Italian diploids; the mean volume for the backcross diploids was, however, closer to that of the Italians than it was to the Africans.

Differences between alternate mean testis volumes of diploid drones produced by particular queens of the next generation of the backcross (Table 1) were significant, except that between queens 205 and 79. The mean for the group (2.33 mm^3) was less than that for the fundator queens 131 and 125. Table 5 shows that the mean volume for this group differed significantly from the means for all other groups.

Discussion

Any honeybee queen produces haploid drones of which 50% have one *X*-allele and 50% have another. The distributions of length and volume for populations of testes of haploid drones produced by different queens in the present experiments had only one peak, suggesting that the influence of the different *X*-alleles on testis size in haploid drones either was absent or had little effect.

The testes of diploids are much smaller than those of haploids, but the mean sizes of testes of haploid and diploid drones originating from the same queen were not

TABLE 6. Frequency distribution of volume of testes of haploid drones 1 day old.*

Group	Mother of drone (queen no.)	Volume (mm ³)																			
		7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0	
African	63				1		1	1	2	8	7	13	10	4	1	2					
	128				3	11	5	5	7	3	4	1	5	5	1						
	141			1		2	11	10	9	1		3	1								
	146			2	5	1	4	8	2	2	2										
Italian	7	1		1				2	3	1	4	5	11	3	9	5	3	2			
	144						6	8	12	5	4	3	2	1							
	155				2	5	5	3	5	7	9	3	3	1	2	1					
	155+									1	3	6	5	3	6	6	3	2	1		
F ₁	48	2	4	3	7	6	6	3	3	1	2	4	4	1	1	2					
Backcross (48 measurements, not 50)	167				3	4	3	7	6	1	10	3	4	3	2	2					
	125						4	3	2	3	5	7	10	4	1	2					
	131				1	1	5	7	6	6	9	4	8	2							

* Bold figures show the modal value.

+ Haploid drones reared by method for diploid drones.

TABLE 7. Frequency distribution of volume of testes of diploid drones 1 day old.*

Mother of drone (queen no.)	Volume (mm ³)																			
	0.00	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5
African	141						1	2	2	4	6	9	10	5	2	2	4	1	1	1
	182				2		1	9	8	8	4	8	3	1	2					
	146 (48 measurements)			2	1		6	4	5	9	13	4	1	2	1					
	37			2	3		3	5	11	8	5	4	2	3	1	1				
	21		2	2	2		2	6	8	8	3	4	4	3	1	1				
	128		2	2	9		8	5	2	2										
Italian	144	1	3	8	8	14	8	5	3											
	155	6	8	16	4	3	1	1	1											
	103	2	11	9	9	4	4													
	154	18	23	6	3															
Backcross	131			3	8	8	8	13	7	3										
	44		2	1	6	7	6	2		1	1									
	125			7	11	14	11	3	4											
	167	2	7	12	16	7	2	3	1											
Next generation of backcross	122			9	9	6	5	7	4	3	1									
	97†	7	1	7	7	8	6	4	4	5	1									
	78	1	5	12	4	5	6	4	1											
	205		4	6	1	1	1	1												
	46†	2	5	12	9	3	5	1	2											
	79	3	10	16	5	7	3													

* Bold figures show the modal value.

† Queen no. 97 mated with 2 drones and no. 46 with 3 drones.

there is no segregation of gametes produced by a father. Genetic segregation occurs only in the gametes produced by the mother. When the gametes of a population produced by one daughter-queen are all fertilized with the (genetically identical) gametes from the father, the resulting new population will show a change in one direction. Gametes of a similar population produced by a second daughter-queen and fertilized by gametes from another father will result in a population showing a change in another direction, or in the same direction but to a different extent. By these means, different populations can be changed in different ways.

The fact that the mean volume of the diploid testes of the backcross generation was lower than the mid-point between the means of the African and Italian diploids was to be expected on the polygene theory. The diploids of the backcross generation received the size-reducing Italian genome in all genes from the mother and in half those from the F_1 father. Thus, the frequency of the Italian genes was 0.75, and that of the African genes 0.25, and the testes of diploids reared from the backcross were changed in the Italian direction.

The mean volume in the backcross diploids was not as low as predicted on this theory, but it is possible that the single father of all the F_1 queens, which in turn produced haploid drones for the backcross, passed on genes for rather larger testes than the mean for the African population.

Testes of diploid drones of the next generation of the backcross were of an intermediate size between those of the diploid drone progeny of the fundator queen no. 125 mated to an F_1 drone (from whom all daughter queens except one originated) and those of Italian diploids. This, again, would be expected on the polygene hypothesis. Queen no. 125 produced pure Italian drones transmitting small testes in diploids, as well as queens having only some of the genes resulting in large testes in Africans. Therefore, the resulting diploids had characters midway between those of both parents (Italians and backcross) and were much closer to Italians than to Africans.

Conclusions

Homozygosity of X -alleles diminishes the size of testes of diploid drones. The small testes of these drones may possibly be a female-like character. But the size of their testes does not follow the X -allele composition of the individual. Thus the different additive ability of various X -alleles was not detected here.

An increase of the heterozygosity of other loci than X does not decrease the size of testes of diploid drones, which is contrary to the multiple heterozygous loci hypothesis.

The inheritance of the size of testes in diploid drones is in accordance with the additive action of special polygenes. Thus breeding diploid drones should be carried out on the basis of polygene action.

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