

STUDIES OF INHERITANCE IN LOP-EARED RABBITS

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IN 1909 CASTLE published some observations on the behavior of ear length in crosses between lop-eared and ordinary varieties of rabbits, describing the inheritance as blending. Shortly thereafter LANG (1911) applied to these observations the multiple factor hypothesis which had been formulated by NILSSON-EHLE on the basis of his studies of quantitative characters in oats and wheat. Since then, numerous studies of quantitative characters in animals and plants have served to establish firmly the multiple factor hypothesis. But no further study has been made of the peculiar ear character found in lop-eared rabbits. CASTLE has meanwhile shown that among other varieties of rabbits there is a close correlation between general body size and ear length, skull length, and leg length. During development, the body as a whole and its various parts grow faster lengthwise than transversely. So the general body form, and that of all elongated organs, becomes more slender as the absolute size increases. Accordingly, other things being equal, the larger the rabbit, the longer proportionally are its ears, its skull, and its legs.

Lop-eared rabbits are one of the oldest recognized varieties of domestic rabbits and have undoubtedly attained their present excessive ear length as a consequence of long-continued selection. Other breeds of rabbits, for example Flemish Giants, exceed them in size of body, but none in length, width, and softness of the ears. This last characteristic (softness) they owe to a deficiency of cartilage in the ear, which makes it pliable and lumpy and incapable of erection, as are the ears of ordinary rabbits. The body size of standard bred lop-eared rabbits is large, and that is one reason why their ears are long; but their ears are much longer than the ears in other breeds of rabbits of substantially the same body size. This shows that some additional agency operates to make the ears of lop-eared rabbits long. That it is a genetic agency there can be no doubt, for lop-eared rabbits are known to be true breeding, and their peculiar character in crosses is transmitted equally through male and female individuals in the blending manner generally recognized as indicating the operation of multiple genes.

In the light of what has been learned about heredity in the last highly fruitful quarter century, it has been thought desirable to make new observations on the results of crossing lop-eared rabbits with ordinary breeds of rabbits. To this end, in March 1932, a trio of purebred lop-eared rabbits was obtained from Mr. T. Corbishly, Secretary of the Lop-Eared

Rabbit Club of England, through arrangements kindly made by Mr. E. C. Richardson.

The results to be described in this paper were obtained by (a) crossing the lop-eared male with females of other breeds; (b) raising an F_2 generation from F_1 parents; (c) backcrossing F_1 females to the lop-eared male; or (d) backcrossing F_1 individuals to the other parental (short-eared) stock.

METHODS AND STOCKS EMPLOYED

It has been our endeavor to grow the experimental rabbits under optimum conditions. To this end a mother has not been allowed to suckle more than 4 or 5 young at a time, the remainder of the litter, if any, being entrusted to foster mothers. The young have been weaned, as a rule, when one month of age. At that time each animal was weighed, and measurements were made of its ear length and ear width. Thereafter the animals were weighed and had their ears measured once every two weeks until they were four months old. At this age growth of the ears is nearing completion, although growth of the body may continue to the age of a year, or even longer.

As a basis for comparing individuals of different generations or litters, an estimate was made of the weight and ear measurement of each individual at the age of 120 days. Ear lengths were measured with a thin ruler from the base of the ear to its tip, the ear being held vertical and slightly stretched. Three or four independent readings were made at each measuring to minimize observational errors. At 120 days rabbits of small to medium body size will have practically completed their ear growth. The ears of rabbits of larger body size will continue to grow at a steadily diminishing rate for a few weeks longer, but the proportional change will be small and may safely be disregarded for statistical purposes. The lop-eared male was said to be about ten months old when we received him in March 1932. He then weighed about 4,000 grams, and his ear length was 25.5 cm. At four months old he probably had an ear length of about 24.0 cm, judging by the growth rates of our $3/4$ blood lop rabbits. We shall accordingly rate him as a 24.0 cm rabbit.

He was mated with females of several different breeds, such as Blue Beveren, New Zealand Red, and the synthetic English-Dutch race of CASTLE. These range in body weight between 3,000 and 4,000 grams and in ear length from 11.0 to 13.5 cm. He was also mated with rabbits of smaller size, Himalayan and Polish derivatives. These ranged in weight from 2,000 to 3,000 grams and in ear length from 10.0 to 10.9 cm.

THE F_1 GENERATION

Eleven females in matings with the lop-eared male produced a total of 65 F_1 young, which were reared to maturity. The ear length of these in

Ear length in cm of the F₁ animals at age 4 months in relation to ear length of their mothers

MATING	BAR LENGTH OF MOTHER	11.5	12.5	13	13.5	14	14.5	15	15.5	16	16.5	17	17.5	18	18.5	19	19.5	NO.	MEAN	S.D.	C.V.
A	10.0	I			I	2	3	I										8	14.57	1.17	8.0
B	10.2				I	6												7	15.15		
C	10.4				2	I		I										4	15.25		
D	10.4						2	2	I	I								6	16.48		
E	10.9					I	I		I	2								5	16.66		
Total (A-E)		I		I	5	11	4	3	2	3		2	3					30	15.53	1.22	7.8
F	11.5						I	I	3	2								6	17.21		
G	11.8					I	I		I	I	I	I	I					6	16.70		
H	12.2						2	3	4	I								10	16.85		
I	12.0						I	2	I	I	I	I	I	I				4	17.50		
J	13.4								I	I	I	2						4	17.87		
K	13.5								I	I	I	I	I	I				5	17.98		
Total (F-K)					I	I	6	3	11	5	5	2	2	2				35	17.23	.95	5.5

TABLE 2
Variation in ear length of the F₂ animals at age 4 months

MATING (SEE TABLE 1)	12.5	13	13.5	14	14.5	15	15.5	16	16.5	17	17.5	18	18.5	19	19.5	20	NO.	MEAN	S.D.	C.V.
♀ A × ♂ A	I	2	I			2	3										9	14.61		
♀ E × ♂ A				I	I		3				I						6	16.10		
♀ D × ♂ D						I		I		I							4	15.67		
Total	I	2	3	I	3	7	7		I	I	I						19	15.16	1.33	8.8
♀ Q and E × ♂ H					2	4	5	I	3	3	I						19	16.48		
♀ H × ♂ H		I	I	I	I	5	11	5	11	3	6	I	I				47	16.72		
♀ I and J × ♂ H				I		I	3	2	2	5	I	I	I	I			17	17.46		
♀ C × ♂ I					2	3	I	2	2	3	I	5	I				20	17.24		
♀ E × ♂ I						3	I	2	2	5	I	I	I				15	17.64		
♀ F-K × ♂ I					I	I	3	5	8	2	5	3					28	17.75		
Total	I	I	2	5	14	4	14	23	21	20	13	7	7	I			146	17.17	1.18	6.8

relation to that of their mothers is shown in table 1. In general, the greater the ear length of the mother, the greater the ear length of the offspring, all having the same father, the lop-eared male with an ear length of 25.5 cm when full grown. One F_1 individual was peculiar in having ears only slightly longer than those of its mother and not at all lopped. This animal (♀ 2994) at 4 months of age had an ear length of 11.6 cm, at which measurement it remained permanently. The mother of ♀ 2994 came of a purebred Himalayan family, and the seven sibs of the peculiar individual were very uniform in ear length (see table 1, Mating A); but this one aberrant individual had singularly short ears and transmitted that peculiarity to her offspring, as we shall see.

In general the ear length of the F_1 animals is nearer to that of the small races. This is not a matter involving superior maternal influence, since in a litter produced by the reciprocal cross (lop-eared ♀ \times normal ♂) the F_1 young had similar ear length.

THE F_2 AND BACKCROSS POPULATIONS

An F_2 population was produced consisting of 165 individuals. Of these, 19 resulted from matings within the first group of F_1 individuals (matings A-E). Their variation in ear length is shown in the first section of table 2, the mean being 15.16 cm. The mean for the 146 F_2 individuals classified in the second section of table 2 is 17.17 cm. As compared with the 19 F_2 individuals of the first section of table 2, these are larger animals and have longer ears, as might be expected from their ancestry.

A backcross of F_1 females to the pure lop male (their father) produced a population of 68 animals which are listed in table 4 as $3/4$ lop. Twenty-three of these, descended from a small-sized grandmother (matings A and E, table 1), had an average ear length of 19.20 cm. The remaining 45 were descended from larger mothers (matings F-H, table 1). They had an average ear length of 20.07 cm.

Backcrosses of F_1 animals to the maternal parent stock produced the 239 rabbits listed in table 4 as $1/4$ lop. The peculiar F_1 female (2994) which had an ear length of only 11.6 cm, produced 18 backcross young. They form a compact group, varying closely about a mean of 10.98 cm, which is intermediate between the ear length of their mother (11.6 cm) and that of their Himalayan father (9.9 cm). The litter mate sisters of this female, likewise from mating A but having ears close to 15 cm long, produced 71 backcross young. They vary about an average of 12.09 cm, which again is intermediate between the ear lengths of the respective parents, 15 and 9.9 cm. The peculiar short ear character of ♀ 2994 would not appear to have been due to a single inhibiting or modifying factor derived from her mother, for in that case her backcross young should show a bimodal dis-

tribution owing to segregation on the part of the inhibiting factor. But in reality her backcross young are less variable than the young of her sisters (row 2, table 4), since their standard deviation was only .56 cm and their coefficient of variation 5.1; whereas her sisters' young had a S.D. of .76 cm and a C.V. of 6.2.

All backcrosses to the smaller Himalayan race, when combined, show an average ear length of 11.86 cm; all backcrosses to larger females show an average ear length of 14.42 cm. The coefficient of variation for the two groups is substantially the same (see table 4).

DISCUSSION

The F_1 young of small race mothers are more variable in ear length than the F_1 young of large race mothers, the former having a coefficient of variability of 7.8, whereas that of the latter group is 5.5. This indicates that the small mothers were less homogeneous than the large ones in regard to factors influencing ear length. The F_2 generation bears out this interpretation. The F_2 group from small mothers has a C.V. of 8.8, whereas the group from large mothers has a C.V. of 6.8. The backcross to the pure lop-eared male has a similar implication. The young descended from small mothers have a C.V. of 6.6; the corresponding group derived from large mothers has a C.V. of 5.7. CASTLE (1922) has shown that among ordinary (non-lop) rabbits a close correlation exists between body weight and ear length ($.836 \pm 0.011$). In the present investigation body weights and ear measurements were taken of 67 adult individuals as diverse in size as could be found in the laboratory at that time, ranging in weight from 1,400 to 4,700 grams. In this case also a fairly high correlation was found between body weight and ear length, namely, 0.76 ± 0.03 . This indicates that among ordinary rabbits variation in ear length occurs chiefly as a consequence of variation in general body size. The genetic agencies which produce large body size automatically produce long ears and *vice versa*. But the case is very different with lop-eared rabbits. Here a body size of 4,300 grams, which among ordinary rabbits would be associated with an ear length of about 13.5 cm, is found associated with an ear length some 12 cm greater, an increase of 90 percent. We are concerned with investigating what genetic agency has caused this remarkable change.

It might be expected that so great a change in the size of the ear would be attended also with some change in its shape, but this apparently is not true. The relation of ear width to ear length remains about the same, irrespective of the absolute size of the ear. In the 67 adult individuals of various races, the ear length of which we measured, the ratio of ear length to ear width varied closely about a mode of 56 percent, regardless of absolute size (table 3). In a group of twelve $3/4$ blood lop rabbits, the group,

of all those raised by us, having maximum ear size, the variation was very similar in character and the mean identical at .554.

TABLE 3
Ratio, ear length to ear width

	.51	.52	.53	.54	.55	.56	.57	.58	.59	.60	Mean
Frequency, mixed group	3	4	5	7	12	19	10	3	2	2	55.4
Frequency, 3/4 lop group			1	2	3	3	3				55.4

In the growth of the ear, as well as in its completed state, the relation of length to width changes very little from one month of age to maturity. Previous to one month, change in ear shape is more noticeable.

The twelve 3/4 blood lop individuals whose length-width ratios are recorded in table 3, gave the following average ratios at earlier ages.

Age in months	1	1 1/2	2	3	4	5	6
Mean ratio	59.03	58.03	57.60	57.10	56.32	56.34	55.91

The change in the shape ratio was small and gradual between the ages of 1 and 6 months, amounting in all to only 3 percent. If, instead of calculating such ratios, ear lengths are directly plotted against ear widths on a logarithmic scale for the period between one and six months of age, lines apparently perfectly straight are obtained. Both methods indicate that no genes affecting shape independently of size are in evidence during the period of maximum growth.

It would seem that all races of ordinary rabbits, irrespective of body size, would be equally available for crossing with pure lop-eared rabbits in a study of the genetic agencies responsible for the lop character, since all show a similar relation between body size and ear length. The genetic agency responsible for the added ear length of lop rabbits seems entirely lacking in ordinary rabbits, which differ in ear length chiefly because they differ in body size. If, accordingly, we can devise a means for equalizing the body weights of all rabbits studied, we can estimate what corresponding ear length each would be expected to have.

The regression of ear length on body weight was calculated for the 67 adult non-lop rabbits already mentioned. It was found that ear length increases one millimeter for each increase in weight of one hundred grams. The average body weight for the population of F₁ lop rabbits at four months of age was 2,400 grams. If all animals listed in table 4 had this same body weight, their ear lengths would be directly comparable. Accordingly an ear length was calculated for each individual on this basis, by use of a

TABLE 4
Actual ear lengths at four months of age of the various populations produced by crossing ordinary rabbits with a lop-eared individual

MATING	10	10.5	11	11.5	12	12.5	13	13.5	14	14.5	15	15.5	16	16.5	17	17.5	18	18.5	19	20	20.5	21	21.5	22	NO.	MEAN	S.D.	C.V.	
F ₁ , A-E			I						I	5	II	4	3		2	3									30	15.53	1.22	7.8	
F ₁ , F-K									I	I	I	6	3	II	5	5	2	I							35	17.23	.95	5.5	
F ₂ , A-E			I					2	3	I	3	7		I											19	15.16	1.33	8.8	
F ₂ , C-K								I	I	2	5	14	22	14	22	19	19	14	7	I					146	17.17	1.18	6.8	
1/4 Lop, A	2	6	6	3	I																				18	10.98	.56	5.1	
♀ 2094																													
1/4 Lop, sisters of	2	II	19	17	13	5	3	I																	71	12.09	.76	6.2	
♀ 2094																													
1/4 Lop, F-K			2	3	15	29	34	26	17	15	7	2													150	14.42	.92	6.3	
3/4 Lop, A-E														3	I	I			6	4	5	3			23	19.20	1.28	6.6	
3/4 Lop, F-K														I		3	2	7	6	6	II	5	I	3	45	20.07	1.15	5.7	

TABLE 5
Calculated ear lengths at four months of age of the populations of Table 4, if all had the same body weight, 2,400 grams

	10.5	11	11.5	12	12.5	13	13.5	14	14.5	15	15.5	16	16.5	17	17.5	18	18.5	19	20	20.5	21	21.5	22	TOTAL	MEAN	S.D.	C.V.	
P ₁ , Parents A-E		4	I																						5	11.10		
P ₁ , Parents F-K			I	I	I	2	I																		6	12.58		
F ₁ , Matings A-E			I						3	12	5	4	I	2	2										30	15.36	1.08	7.0
F ₁ , Matings F-K										2	4	7	9	7	5	I									35	16.99	.74	4.4
F ₂ , A-E				I				4	2	3	4	2	I	I	I										19	15.45	1.36	8.8
F ₂ , C-K									I	I	4	8	25	17	19	23	19	9	I						146	17.16	1.14	6.6
1/4 Lop, ♀ 2094, Mating A			3	9	5	I																			18	11.11	.39	3.5
1/4 Lop, sisters of ♀ 2094			3	10	17	19	14	5	2	I															71	12.42	.73	5.9
1/4 Lop, Matings F-K			4	9	20	41	27	25	12	10	2														150	14.41	.85	5.9
3/4 Lop, Matings A-E														2	2	I	I	3	5	9					23	19.13	1.01	5.3
3/4 Lop, Matings F-H														I		2	2	5	6	8	II	5	4	I	45	20.01	1.04	5.2

conversion factor of one mm for each hundred grams of weight. The observed ear length was increased if the animal weighed less than 2,400 grams and decreased if the animal weighed more than 2,400 grams. Thus were obtained the calculated results shown in table 5. As thus treated, the F_1 populations become less variable, and the difference between the progeny of small mothers (Matings A-E) and the progeny of large mothers (Matings F-K) becomes less. The former group still has the greater C.V. (5.5 as compared with 3.7), but this difference is due, principally, to the very aberrant individual produced in Mating A which had an actual ear length of 11.6 cm and a calculated ear length of 14.0 cm (table 5). Nevertheless, the mean and mode for the ear length of the F_1 progeny of small mothers remain lower than those for the F_1 progeny of larger mothers (Matings F-K). They differ by almost two centimeters. This indicates that the two groups differ by more than body size alone. The small mothers apparently carry certain genes which tend to make the ears short, irrespective of body size. But it may be that this apparent difference is due, in part at least, to the known earlier maturity of rabbits of racially small body size. The earlier the maturity of a rabbit, the more nearly would it have completed its growth at four months of age. The amount by which it falls below standard size would thus be *underestimated*, and the added ear length computed would fall below what it would be if all individuals had, at four months old, completed the same proportion of their full growth.

The F_2 populations show a relation similar to that shown by the F_1 populations. Those from small and short-eared mothers (Matings A-E) have ears over a centimeter shorter than those derived from Matings F-K. Both groups are more variable than the F_1 groups from which they were derived. The C.V. for the F_1 groups were 7.0 and 4.4 respectively; for the corresponding F_2 groups the values are 8.8 and 6.6 respectively. Note, however, that the variation in F_2 , as well as in F_1 , is slightly less when corrected or "equivalent" values are taken (table 5) than when uncorrected values are taken, as in table 4.

The $1/4$ blood lop populations produced by backcrossing F_1 to the short-eared parent races, as calculated in table 5, cover the range between the ear length of ordinary rabbits (non lops) and that of the F_1 populations. There is still the same difference between the derivatives of Matings A-E and the derivatives of Matings F-K, the former being shorter in ear length by two centimeters, either because of the presence of special genes for short ear in the small races, or because their earlier maturity results in under correction, or for both reasons. The variability (C.V.) is the same in both groups of $1/4$ blood lops (5.9). It is less than in the F_2 groups, but greater than in the F_1 groups, as we should expect on the multiple factor hypothesis.

Similar differences between the derivatives of Matings A-E and the derivatives of Matings F-K are found among the $3/4$ blood lops (last two rows of table 5). The former are shorter eared by almost one centimeter. Their variability (C. V.) is substantially the same, but is somewhat less than that of the $1/4$ blood lop populations. This again is what we should expect, as the lop-eared male which sired all the $3/4$ blood lop individuals was purer, racially, than the mothers of the $1/2$ blood lop populations. His race had been long selected for maximum ear length. The mothers in matings A-K and in the backcrosses which produced the $1/2$ blood lop populations, were from races largely unselected as regards ear length. The equivalent ear lengths of the $3/4$ blood lops do not quite cover the range between F_1 and the pure lop-eared ancestor.

On the whole, there is nothing in the results of these experiments at variance with the accepted multiple factor theory of inheritance, which supposes that an apparently blending inheritance results from the action of numerous genes located in many different chromosomes and so segregating independently.

However, we can not ignore the possibility that cytoplasmic, as well as gene, influences may be involved in producing an altered ratio between body weight and ear length, as, for example, in the peculiar short-eared F_1 female, 2994. She is similar in body size to her sibs, and yet has much shorter ears. It would seem, accordingly, that she must possess one or more genes which inhibit the action of the lop-ear genes inherited from her sire. If so, she should be more highly heterozygous for genes affecting ear length than her more normal sisters. For, like them, she would have inherited from their common sire (the purebred lop male) a full set of lop-ear genes, but from their mother she would have inherited *more* than their equipment of short-ear genes. Hence she would be more highly heterozygous than her sisters, and her gametic output would be potentially more variable. In reality, however, when mated to a purebred Himalayan male, she produced a group of 18 offspring which were *less variable* than the 71 offspring produced by her sisters mated to the same male.

A possible alternative explanation, in terms of genes, would be to suppose that a mutation had occurred in the gamete contributed by the lop-eared male to produce ♀ 2994, so that it carried less than the normal equipment of lop-ear genes. The zygote, in that case, (1) would have a lower (somatic) ear length than her sibs of identical parentage, and (2) would be less heterozygous than they for genes affecting ear length, as is indicated by the $1/4$ lop population (table 4).

A more orthodox Mendelian explanation is equally possible, it being assumed that an extreme minus variant coming from the lop-eared parent happened to combine with an extreme minus variant from the short-eared

parent, the result being a zygote somatically extremely low in ear length but with only normal variability in the next generation about a lowered (intermediate) mean.

The blending or intermediate character of the inheritance of lop-ears, both in F_1 and in the backcrosses, shows that the genes which differentiate pure lop-eared rabbits from ordinary ones must be numerous and cumulative in their action. How numerous they are, it is impossible to say. Application of the CASTLE-WRIGHT formula (CASTLE 1921) to the F-K matings (table 6) indicates that the lop race differs from the F-K non-lop parental animals by about 22 genes for ear size, if it be assumed that each of these genes exercises the same quantitative influence as every other such gene. Since this assumption is of doubtful validity, the estimated number, 22, is probably too high.

A study of the range of variability of F_2 and backcross generations often allows one to estimate the number of important genes affecting the expression of a quantitative character. Possibly both parental types (short and lop-ears) would have been regained in the F_2 , had a sufficiently large generation been raised. In the backcross to the parental race with short ears, 20 out of 150 of the backcross young had ears as short as those of the short-eared parents (table 4). The parental range was also regained when the F_1 animals were backcrossed to the lop race. Were there as many as 10 factor differences (all equal and additive in their action) between short and lop-ears, we should expect to regain the parental type of factor combination in only one out of 1,024 animals. Actually we regained the parental type in about one out of every 10-50 animals, which allows us to conclude that the number of important factor pairs differentiating the lop race from ordinary rabbits is probably less than ten.

If genes located in particular chromosomes are responsible for the greater ear size of lop-eared rabbits, the question arises, is it possible to identify such chromosomes by means of linkage studies? We have a certain amount of data bearing on this question, but its indications are wholly negative.

1. In backcrosses to the short-eared Himalayan race employed in Mating A, there were produced 48 colored young having a mean ear length of 14.91 cm; also 34 Himalayans having a mean ear length of 14.60 cm, a non-significant difference indicating no linkage between short ears and albinism.

2. The dominant English coat pattern was introduced into certain of the F_1 individuals in Mating H. Among the $1/4$ lop animals derived from this cross there were 79 English individuals having an estimated ear length of 16.78 cm, and 51 non-English with an average ear length of 16.62 cm, an insignificant difference.

3. The agouti factor was introduced into certain F_1 individuals by the non-lop parent. Among the $1/4$ lop animals derived from Matings F-K there were 34 agouti individuals with an average ear length of 16.86 cm, and 24 non-agoutis with an ear length of 16.73 cm, a difference devoid of significance.

4. The lop-eared male was a sooty yellow. All F_1 individuals which were black pigmented consequently carried yellow as a recessive character which should show coupling with lop-ear. Back-crosses of such F_1 black females with their father produced, among the $3/4$ lops, 29 sooty yellows and 32 blacks. The former had an average ear length of 19.63 cm; the blacks had an ear length of 20.04 cm. There is thus seen to be no difference in ear length favoring the yellow young.

These findings, inconclusive though they are, on account of the small numbers observed, give no indication of the presence of genes for lop-ear in the four chromosomes which harbor the genes for albinism, English, agouti, and yellow, respectively. It is true that these are only four of the 22 chromosome pairs of the rabbit, and it is possible that genes affecting ear length are located in the 18 other chromosome pairs. It is also true that if a single gene for lop-ear were present in one of these chromosomes, yet had by itself only a minor influence on ear length, this influence might well be masked by the influence of other genes present in undetermined combinations.

We have seen that ear size is influenced by general body size, which, in turn, is influenced by rate of development of the fertilized egg. But there must be also in lop-eared rabbits an especial accelerated development in the head region, which makes the ears of lop-eared rabbits, or lop-eared crossbred derivatives, noticeably larger at birth than the ears of ordinary rabbits. The persistence of such an initial difference would account satisfactorily for the subsequent greater ear length of lop-eared rabbits. We can not assume that the supposed accelerated development in the head region is due to a special localized organization of the cytoplasm of the egg, since we know that the sperm is equally capable of inducing it.

The case of the short-eared mouse shows us that a single gene may be responsible for retarded development of the ear, which makes its ultimate length less. We know definitely that the gene in this case is located in the same chromosome with the gene for dilution. It seems reasonable to suppose that, in the case of the rabbit, a series of gene mutations having an opposite effect on ear length has taken place; that each of these, considered separately, has only a minor effect, but cumulatively they make all the difference between the lop-eared and ordinary rabbit. Yet the initial mutation or chance coincidence of mutations which formed the starting

point for human selection must have been sufficiently obvious to attract attention, after which new mutations having a like effect would be incorporated and retained in the selected race. There is reason to think that mutations having a contrary effect also occur among rabbits as well as among mice. The breeders' standard for Polish rabbits insists that the ears be as short as possible. This shortness is secured, in part, by keeping the body small, but to some extent also by special shortening genes. For it will be observed, in tables 4 and 5, that in our Mating A-E, in which mothers of small racial size were used, the progeny have shorter ears than the derivatives of mothers of larger racial size, even when correction is made for the differences in body size among the progeny. This indicates that in the rabbit, although there is (other things being equal) a strong correlation between general body size and ear size, there are also special genes influencing ear size, and chance mutations in these have been utilized in the production of lop-eared rabbits in large-bodied races and of notably short-eared rabbits in small-bodied races. This conclusion is in harmony with WRIGHT'S (1932) finding, based on a statistical examination of CASTLE'S size inheritance data, that although the various parts of the body form a harmonious system varying in unison and controlled by general body size, nevertheless to a minor extent variation in one part takes place independently of other parts.

SUMMARY

1. A renewed study of the inheritance of ear length in crosses between lop-eared and ordinary short-eared rabbits supports the multiple factor interpretation first applied to the case by LANG.

2. Ear length among ordinary breeds of rabbits is closely correlated with general body size. A similar influence of body size on ear length is found also among lop-eared rabbits, but special mutated genes in the case of purebred lop-eared rabbits nearly double the ear length as compared with that of ordinary rabbits of like body size.

3. The increased size of the ears in lop-eared rabbits has not been attended by any change in the shape of the ear. The ratio of ear length to ear width is nearly the same in all breeds of rabbits and at all ages between one month and maturity. It varies closely about a modal value of 0.56.

4. There are indications that mutations decreasing the size of the ears in relation to that of the body have also occurred among rabbits, and that such mutations have been incorporated in such small-bodied and short-eared breeds as Polish.

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