THE MORPHOGENETICAL VALUE OF THE WEIGHT OF RABBITS AT BIRTH.

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(With Four Text-figures.)

CONTENTS.

Introduction.

As stated before, the weight of rabbits at birth is governed by two different sets of factors. Firstly, by "external" conditions of the growing foetus, such as the age and the nourishment of pregnant females, the duration of the gestation period (Kopeć (12)) and the size of the litter (Kopeć (12), Hammond (7)), and secondly by internal genetic agencies, the action of which was demonstrated by methodical crosses between breeds differing in size (Kopeć (11)). The simultaneous action of both these kinds of factors was most clearly demonstrated in my former experiments on the offspring of Himalayan does mated to a Himalayan and a Silver buck during one and the same rutting time, the latter belonging to a heavier breed (Kopeć (10)). According to genetical differences, the weight of new-born hybrids in these cases was usually greater than that of Himalayan youngsters. But, at the same time, probably by an introduction of specific substances through the body of the doubly mated female from foetuses of one physiological type to foetuses of the other type, the Himalayan born from these matings were as a rule heavier than the normal young of the breed. The hybrids from heterogeneous gestations weighed also more than the F_1 new-born from normal crosses.

The problem now arises, whether and to what extent the influence of both kinds of factors specified above, determining the weight of the new-born rabbits, can be detected during growth and in the adult animals. To this end, the morphogenetical value of the weight of new-born mam-

mals should be taken into consideration. The genetic aspects of the above question have not been, as far as I know, worked out till now. The opinions of breeders concerning the significance of the weight of different domestic animals at birth are still very contradictory. The ultimate solution of this question has also considerable theoretical interest. For if it could be made evident that the weight of the newly born is correlated with the weight of the adult, then my method of studying the inheritance of birth-weight could successfully replace the method hitherto employed of working with full-grown mammals, a considerably more expensive and in some respects less exact method (cf. Kopeć (11), pp. 243–244).

According to MacDowell (14) and also to Punnett and Bailey (15) there is no significant connection between the size of the litter, the age of the doe, the season of birth and the weight of the full-grown rabbits. Castle (2) emphasises that rabbits weighing more on the 29th day of life than others can in the course of time become lighter than others and *vice versa*. But such a possibility, according to my opinion, excludes in no way the existence of an essential positive correlation between the weight of the new-born rabbit and that of the fully developed adult. On the contrary, a distinct positive connection between the weight of growing animals and the weight of young ones may be inferred from other observations. Dunn (3), in her investigations on 7 albino rats, stated that individuals weighing the most on the 14th day of life were also the heaviest on the 66th day of life. King (9) comes to the conclusion that 11 albino rats maintained as a rule on the 150th day the same order as at birth, in respect to their body-weight. Analogical inferences can be drawn from the data collected by Gärtner (5) as to the monthly weights of 65 calves, during their first 6 months of life. My own calculations concerning the above material give the following coefficients of correlation between the birth-weight and the weight of growing animals in separate months: $+ 0{\cdot}530 \pm 0{\cdot}089$, $+ 0{\cdot}588 \pm 0{\cdot}081$, $+ 0{\cdot}422 \pm 0{\cdot}102$, $+ 0{\cdot}471 \pm 0{\cdot}097$, $+ 0{\cdot}510 \pm 0{\cdot}092$ and $+ 0{\cdot}497 \pm 0{\cdot}093$ respectively. The ratio of the coefficient to its probable error being always larger than the obligatory number 3, the above correlation may be regarded as biometrically significant[1].

The last volume of facts is of course of great importance for the

[1] The relation between the weight of calves at birth and the mature height at withers was studied by Eckles and Swett (4). The biometrical proof of the recorded data compels me to agree with these authors' opinion that little, if any, relation in this respect can be stated in Holsteins and Jerseys. Of comparable observations on birds only the investigations of Goldschmidt (6) referring to 21 Peking ducks are known to me. No relation between the weight of hatched ducklings and the weight of full-grown birds is found by this author.

problem of the morphogenetical value of the birth-weight in mammals. But, in all cases the animals had not ceased to grow before the observations were finished. Consequently the problem discussed is not entirely solved by the investigations quoted, especially as the authors mentioned have not considered separately the "external" and genetical agencies involved. Hence it follows that the conclusions drawn from the above data may require further verification. The following study is presented here as an attempt to solve these difficulties.

MATERIAL AND METHODS.

The material employed in my study consisted of 60 rabbits forming an F_2 generation from two Himalayan does sired by a Silver buck. The F_2 animals were obtained from 15 F_1 females, four years old when mated with their brothers. The food of the rabbits consisted of hay, oats, beets and boiled potatoes and was always administered with a certain excess. The F_2 young, born in the period from 5 May to 18 July, 1923, were supplied with fresh green stuff during the first three months of their lives. They were weaned at six weeks and helped through with goat milk. Six weeks later they were penned in separate cages. At the same time the supplementary feeding with goat milk was discontinued. The conditions of light, space and temperature in separate cages were made as uniform as possible.

As pointed out above, the age of F_1 females, as well as the quality and the quantity of food administered to each doe during the gestation period, was always identical. The only "external" factor, that could not be accurately controlled was the size of the different litters which is known to be negatively correlated with the weight of newly born rabbits. The duration of pregnancy being inversely correlated with the litter-size need not be considered separately here (cf. Kopeć (12))[1]. Only litters ranging from 4 to 9 young were taken into consideration. In order to rear the youngsters in possible uniform conditions from the very beginning, only 4 individuals were reared in every litter, all others being immediately killed. Exceptionally light or exceptionally heavy individuals, weighing less than 30 grm. or more than 60 grm. were all removed as I am convinced that the former die before maturity, while the latter

[1] The respective coefficient of correlation amounted to $-0{\cdot}586 \pm 0{\cdot}073$ in Himalayan does mated with a Himalayan or a Silver buck, being $-0{\cdot}421 \pm 0{\cdot}124$ in F_2 ex ♀ Himalayan × ♂ Silver. On the contrary, Hammond (8) in his most valuable monograph on reproduction in rabbits found no relation between the litter-size and the duration of the gestation period. As this author probably used in his studies material not genetically uniform the above discrepancy may be only apparent.

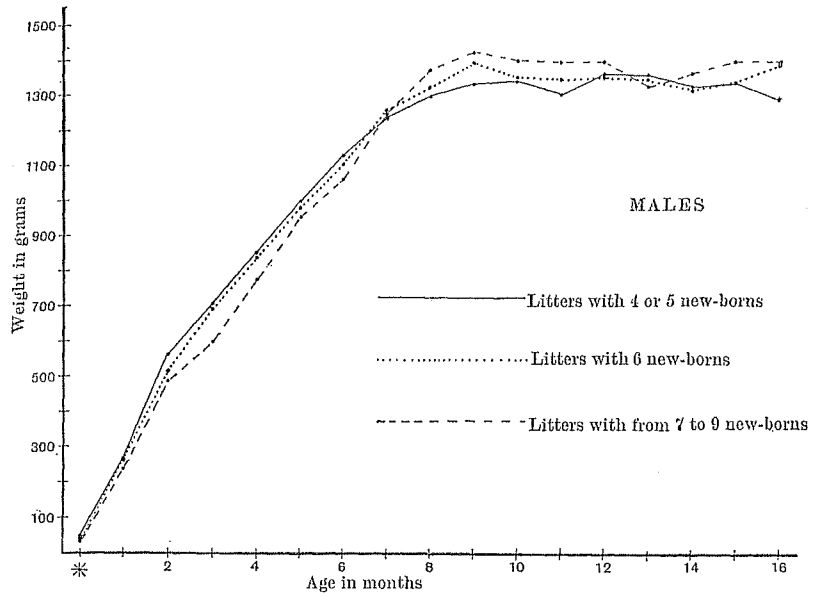
hinder the further development of their brothers in marked degree. As the number of such exceptionally heavy or light specimens was only 5 in the whole series, the general results cannot in any way be influenced by them. No other selection was made. I have further considered only such litters where the young did not die before weaning.

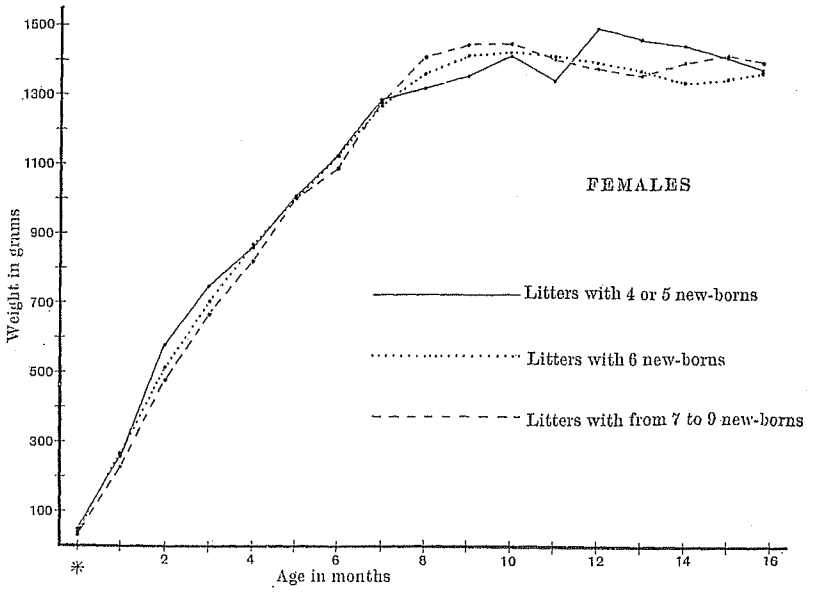
Thirty males and the same number of females were reared to maturity. None of them were sexually active during the time of observations. The newly born were always weighed before their first suckling, between the second to the sixth hour after birth (cf. Kopeć (10), p. 372). The weight of the growing rabbits was calculated for each month, from three weighings on successive days, made in the morning before feeding the animals: the last day of the preceding month and the first and second day referring to the month taken into consideration. Fragments of grams were considered as full grams except in the case of the new-born. The whole material of males and of females was twice segregated into special groups according to the litter-size or to the weight differences due to genetical factors (cf. below). In both cases the average weight of all animals of each discriminated group was determined and used for curves (Figs. 1–4). The observations lasted 16 months, *i.e.* much longer than the animals grew, growth being completed as a rule during the 9th and 10th month of the rabbits' life.

The Weight of Rabbits and the Birth-weight Differences due to Different Litter-sizes.

In order to ascertain whether and to what extent the weight of the growing and of the adult rabbit is influenced by the size of the litter I have divided the males and the females of my material into three groups according to the size of the respective litters. The groups were formed of litters ranging from 7 to 9, 6, and 4 to 5 young respectively. The average values for the groups amount to 8·4, 6·0 and 4·6 new-born for males and 8·3, 6·0 and 4·3 for females. The average weights of young at birth were 40·8, 42·3 and 45·9 grm. for males and 38·5, 42·7 and 48·6 grm. for females, a further proof of the negative correlation present between the size of a litter and the new-born's weight. In the corresponding groups 8, 9 and 13 males and 6, 17 and 7 females were examined.

The curves of Figs. 1 and 2 show that though the weight of the growing animals stands, in the beginning, as a rule in a direct proportion to its weight at birth, yet, starting from the 7th month in males and from the 4th in females, the regular increase mentioned becomes less noticeable. From the 8th till the 12th and from the 14th till the 16th month





Figs. 1 and 2. Curves of absolute growth of rabbits, in dependence on different litter-size. The day of birth is marked by an asterisk.

in males, as well as from the 8th till the 10th and from 15th till 16th in females, the former relation may be completely reversed, *i.e.* the lightest rabbits from the largest litters became the heaviest. Hence it follows that the differences of weight at birth, due to different litter-sizes, have no connection with the weight of the growing and full-grown rabbit. When looking through the items of Table I containing the monthly

TABLE I.

Monthly Coefficients of correlation between the litter-size and the weight of separate rabbits during growth.

Data referring to F_2 specimens ex ♀ Himalayan × ♂ Silver.
$r \pm E_r$, the coefficient with its probable error; r/E_r, ratio of the coefficient to its probable error; n, number of specimens.

	Males			Females		
Month	$r \pm E_r$	r/E_r	n	$r \pm E_r$	r/E_r	n
1	$-0{\cdot}443 \pm 0{\cdot}099$	4·5	30	$-0{\cdot}287 \pm 0{\cdot}113$	2·5	30
2	$-0{\cdot}373 \pm 0{\cdot}106$	3·5	,,	$-0{\cdot}301 \pm 0{\cdot}112$	2·7	,,
3	$-0{\cdot}506 \pm 0{\cdot}092$	5·5	,,	$-0{\cdot}329 \pm 0{\cdot}110$	3·0	,,
4	$-0{\cdot}275 \pm 0{\cdot}114$	2·4	,,	$-0{\cdot}068 \pm 0{\cdot}123$	0·6	,,
5	$-0{\cdot}126 \pm 0{\cdot}121$	1·0	,,	$-0{\cdot}116 \pm 0{\cdot}121$	1·0	,,
6	$-0{\cdot}295 \pm 0{\cdot}112$	2·6	,,	$-0{\cdot}155 \pm 0{\cdot}120$	1·3	,,
7	$-0{\cdot}094 \pm 0{\cdot}122$	0·8	,,	$-0{\cdot}086 \pm 0{\cdot}122$	0·7	,,
8	$+0{\cdot}154 \pm 0{\cdot}120$	1·3	,,	$+0{\cdot}060 \pm 0{\cdot}123$	0·5	,,
9	$+0{\cdot}224 \pm 0{\cdot}117$	1·9	,,	$+0{\cdot}060 \pm 0{\cdot}123$	0·5	,,
10	$+0{\cdot}092 \pm 0{\cdot}122$	0·8	,,	$-0{\cdot}052 \pm 0{\cdot}123$	0·4	,,
11	$+0{\cdot}138 \pm 0{\cdot}121$	1·1	,,	$-0{\cdot}010 \pm 0{\cdot}123$	0·1	,,
12	$+0{\cdot}045 \pm 0{\cdot}123$	0·4	,,	$-0{\cdot}244 \pm 0{\cdot}116$	2·1	,,
13	$-0{\cdot}135 \pm 0{\cdot}121$	1·1	,,	$-0{\cdot}238 \pm 0{\cdot}116$	2·1	,,
14	$+0{\cdot}072 \pm 0{\cdot}123$	0·6	,,	$-0{\cdot}192 \pm 0{\cdot}119$	1·6	,,
15	$+0{\cdot}130 \pm 0{\cdot}121$	1·1	,,	$-0{\cdot}048 \pm 0{\cdot}123$	0·4	,,
16	$+0{\cdot}162 \pm 0{\cdot}120$	1·4	,,	$-0{\cdot}068 \pm 0{\cdot}123$	0·6	,,

coefficients of correlation between the weight of each individual and the size of the litter, we may observe that the independence mentioned can also be demonstrated by biometrical methods. As the ratio of the coefficients to their probable error is here, as a rule, considerably smaller than the obligatory number 3, the correlation must be considered as fortuitous, especially as the sign of the coefficient was not in all cases negative.

Table II gives supplemental data for two litters derived from the same Himalayan doe sired by an Albino buck of unknown origin. The number of young in these litters was 3 and 8 respectively. Three young, all females, were reared in both these litters. From the recorded data it follows that, in these cases also, the negative correlation between the number of young in a litter and their initial weight is totally obscured after the 10th month of the rabbits' life.

TABLE II.

Average weight of rabbits during growth in grams in relation to the litter-size.

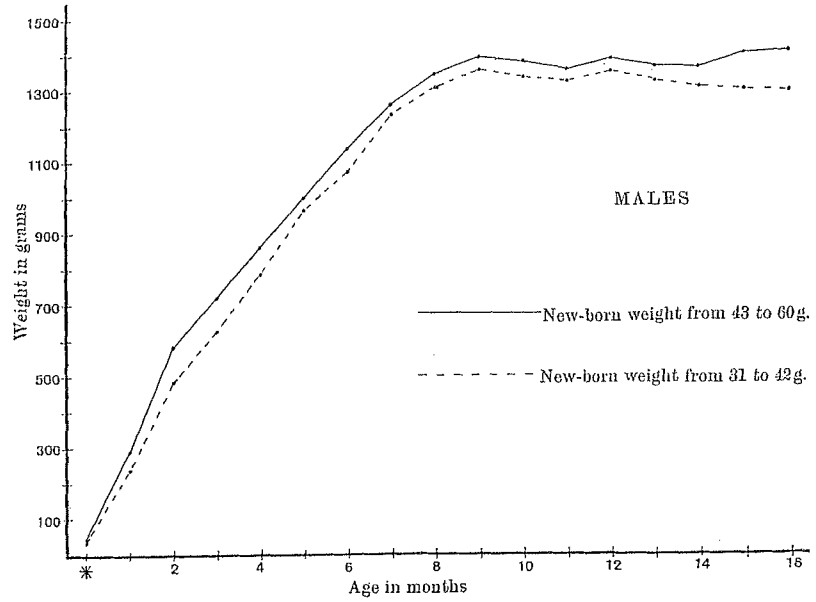
Data referring to females ex ♀ Himalayan × ♂ Albino.

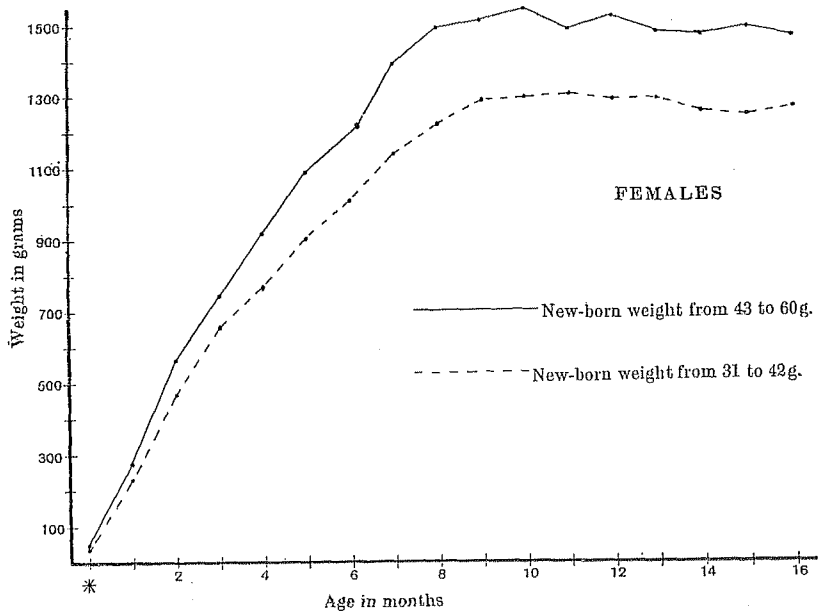
Month	Litter-size: Three new-borns	Litter-size: Eight new-borns	Month	Litter-size: Three new-borns	Litter-size: Eight new-borns
*	55·7	37·0	8	1609	1541
1	307	167	9	1798	1710
2	526	419	10	1854	1872
3	897	612	11	1970	2050
4	1069	909	12	2017	1931
5	1163	1012	13	1951	1976
6	1237	1221	14	1986	2026
7	1418	1338	15	1956	2053

THE WEIGHT OF RABBITS AND THE BIRTH-WEIGHT DIFFERENCES DUE TO GENETICAL FACTORS.

Quite different results were obtained when the genetics of the weight differences were taken into account. Dividing the newly born into two groups according to the new-born weight, regardless of the litter-size, we get two distinct groups, one ranging from 31 to 42 grm., the other from 43 to 60 grm. The averages for each group lie at 39·1 and 47·8 grm. for males and 36·4 and 49·3 grm. for females, the corresponding differences between both the groups amounting to 8·7 grm. in males and to 12·9 grm. in females. (The number of males examined was 15 in each group, of females 14 for the first and 16 for the second.)

The question arises now, whether the above differences have a genetical basis, or whether they are due to different sizes of litters in the two discriminated groups. (Other "external" agencies, which have an influence on the new-born weight being made uniform in this study, must not be considered here.) It should be at once admitted that the average size of the respective litters proved to be somewhat different for both groups. The average in the first group was 6·5 young per litter in both sexes. In the second the averages were 5·5 for males and 5·7 young per litter for females. It is therefore true that the litters differed in size in the two groups, but the corresponding differences did not amount to more than 1·0 young in males and 0·8 young in females. These small differences cannot be regarded as decisive, for the averages of the weight of the new-born in both groups are more strongly pronounced. The point discussed here is much better emphasised in the preceding chapter, where all the rabbits were divided into three groups in relation to the





Figs. 3 and 4. Curves of absolute growth of rabbits, in dependence on different genetical weight at birth. The day of birth is marked by an asterisk.

size of the litter regardless of the weight of the newly born. The differences in the average litter-size amounted there to 8·4 — 6·0 = 2·4 young in males and to 8·3 — 6·0 = 2·3 in females for groups 1 and 2, whilst they reached 6·0 — 4·6 = 1·4 for males and 6·0 — 4·3 = 1·7 in females on comparison of groups 2 and 3. On the contrary the average weight of the new-born did not differ more than 42·3 — 40·8 = 1·5 grm. for males and 42·7 — 38·5 = 4·2 grm. in females or 45·9 — 42·3 = 3·6 in males and 48·6 — 42·7 = 5·9 in females when comparing the groups 1 and 2 or 2 and 3 respectively. It follows therefore that when grouping the material as to the litter-size into three different classes, we find that relatively large differences in the number of young are connected with comparatively small differences in their body-weight at birth. Consequently, the distinct birth-weight differences noticed between both the groups in the present chapter must be atributed first of all to the action of genetic factors.

Figs. 3 and 4 show that rabbits weighing at birth genetically much, so to speak, maintain their higher values in comparison with the lighter newly born. The respective curves do not in any month meet together. The same conclusion must be drawn, when the corresponding data are studied by biometrical methods. The coefficients of the mentioned correlation being always positive are, as a rule, greater than three times their probable error (cf. Table III). Consequently, there cannot be any

TABLE III.

Monthly coefficients of correlation between the weight of new-born (dependent on genetical factors) and the weight of separate rabbits during growth.

Data referring to F_2 specimens ex ♀ Himalayan × ♂ Silver.
$r \pm E_r$, the coefficient with its probable error; r/E_r, ratio of the coefficient to its probable error; n, number of specimens.

	Males			Females		
Month	$r \pm E_r$	r/E_r	n	$r \pm E_r$	r/E_r	n
1	+0·662±0·069	9·6	30	+0·463±0·097	4·8	30
2	+0·538±0·088	6·1	,,	+0·536±0·088	6·1	,,
3	+0·520±0·090	5·8	,,	+0·576±0·082	7·0	,,
4	+0·469±0·096	4·9	,,	+0·498±0·093	5·4	,,
5	+0·333±0·109	3·1	,,	+0·571±0·083	6·9	,,
6	+0·420±0·101	4·2	,,	+0·588±0·081	7·3	,,
7	+0·361±0·107	3·4	,,	+0·597±0·079	7·6	,,
8	+0·363±0·107	3·4	,,	+0·598±0·079	7·6	,,
9	+0·259±0·115	2·3	,,	+0·377±0·106	3·6	,,
10	+0·299±0·112	2·7	,,	+0·447±0·099	4·5	,,
11	+0·296±0·112	2·6	,,	+0·270±0·114	2·4	,,
12	+0·330±0·110	3·0	,,	+0·545±0·087	6·3	,,
13	+0·322±0·110	2·9	,,	+0·565±0·084	6·7	,,
14	+0·383±0·105	3·6	,,	+0·665±0·069	9·6	,,
15	+0·544±0·087	6·3	,,	+0·683±0·066	10·3	,,
16	+0·592±0·080	7·4	,,	+0·715±0·060	11·9	,,

doubt as to the essential positive correlation between the "genetical" weight of the new-born and the weight of growing and of full-grown rabbits. The above correlation seems to be higher in females than in males. As the latter varied less at birth, the figures being 36–55 grm., than the former, which weighed at birth from 31 to 60 grm., it is very possible that various external life conditions more easily bring about greater uniformity in the less variable male.

Conclusions and Summary.

The above investigations suggest that though both external and genetic agencies affect the weight of new-born rabbits, only the latter have a distinct influence upon the weight of growing and adult animals. In other words, a definite morphogenetical value of the weight of the new-born was ascertained irrespectively of distinct modifications caused by the one variable present in the above inquiries, viz. the litter-size. Consequently, the "genetical" weight of the new-born being related to the weight of the animal when adult, furnishes a satisfactory method for the study of the inheritance of weight. Granting that the important environmental conditions of the growing foetuses, such as the age of the dam, her nutrition, the size of the litter, etc., are sufficiently uniform, the weights of the newly born give a satisfactory clue as to the weight of the future adult, and allow us to obtain results in genetical studies with a considerable gain in time and cost, as compared with the usual method of studying the weight of mature animals only.

It seems that a certain explanation should be given here in relation to my former results, referring to the inheritance of the weight of new-born rabbits (Kopeć(11)). Though the variability of the weight of the F_2 new-born is much greater than that of the F_1 animals of the ♀ Himalayan × ♂ Silver cross, the average values are about the same in both generations, that of the F_1 being intermediate between the new-born weights of both parental breeds. The greatest weight recorded for full-grown Himalayan females amounted, as stated in my paper, to 1831 grm. on the average, that for mature Silver does to 2286 grm. Consequently, if the new-born weight can be related to the adult weight, an average of about 2050 grm. in full-grown F_2 females of this cross should be expected. In contrast to such supposition, the average of the greatest adult weights reached by the F_2 females of this cross was in the present study not greater than 1423 grm. The fact, that in my previous genetical investigations only the heaviest does were used for the calculation of the average adult weight of the breed, chosen for further breed-

ing, and that records were taken also during the period of gestation, readily can account for the above apparent discrepancy. In the present paper all the F_2 females were recorded without any selection in respect of the weight. The common increase of females' bodies during the gestation as well as after the first parturition is well known. Stress must be laid, therefore, on the fact that the females of the present investigations had never been pregnant before. Consequently the disagreement between my present and former results is readily explained.

As pointed out elsewhere, there is no correlation between the size of the litter and the course of growth in rabbits (cf. Kopeć (13)[1]). On the contrary a remarkable connection was observed between the genetically determined birth-weight of a rabbit and its course of growth. The smaller the "genetical" weight at birth, the larger as a rule the per cent. increase of the body-weight, and smaller the absolute increase. I think, therefore, that, in studies of the course of growth, attention should be paid to the initial weight at birth, as differences in the course of growth due to genetic causes can be easily and unjustly attributed to special experimental conditions, and faulty conclusions drawn.

It seems that the morphogenetical value of the birth-weight may also be of some practical importance. Though no breeder can distinguish, at first sight, which variations of the initial body-weight are genetic and which environic in nature, yet the existence of genes, working throughout the growing period, should not be forgotten. For the selection of animals from separate litters the following rule most likely holds good: the greater the initial weight at birth, the greater the weight of the adult. Identical conclusions were drawn from the extensive studies of Benjamin (1). This writer, working with Leghorn fowls, proved a significant correlation between the size of growing and mature birds and the size of eggs from which the respective individuals hatched.

From the foregoing inquiries the following summary may be given:

(1) No connection exists between the birth-weight differences, due to the different litter-sizes and the weight of growing and adult rabbits. These birth-weight differences must be regarded as common modifications due to "external" conditions of the growing foetus.

(2) An essential positive correlation is stated between initial differ-

[1] Data referring to the sexual differences in weight are also given in the cited paper. A certain predominance of the weight of females over the weight of males, stated by Punnett and Bailey (15) and by Castle (2), was as a rule confirmed, also in these cases, when the rabbits were divided into separate groups according to the litter-size or to the genetical birth-weight differences.

ences in weight that have a genetic origin and the weight of growing and mature rabbits.

(3) On account of this morphogenetical value of the body-weight at birth the genetics of weight inheritance may be well studied on new-born mammals.

The above investigations were carried out in part by means provided by the Department of Science of the Ministry of Instruction.

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