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PHYSIOLOGIC AND GENETIC STUDIES OF CROOKED KEELS IN CHICKENS



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TABLE OF CONTENTS

	Page
PRACTICAL SIGNIFICANCE	5
PHYSIOLOGIC STUDIES	6
Age at appearance of deformity.....	6
Direction of crookedness.....	10
D-avitaminosis and crooked keels.....	12
Crooked keels in relation to growth and fecundity.....	16
Sex and crooked keels.....	17
Hatching season and crooked keels.....	18
Influence of roosting conditions.....	19
GENETIC STUDIES	23
Selection results	24
Differences in unselected strains.....	26
F ₁ generation of crosses between strains selected for presence and absence of crooked keels.....	28
Back crosses	29
DISCUSSION	31

SUMMARY

1. In most instances, birds developing crooked keels will do so before maturity. Most of the keel deformities appear between the 6- and 12-week age.
2. The bend in the keel occurs slightly more frequently to the right than to the left.
3. Chemical analyses of the breast and leg showed that the breast bones of 8-week-old crooked keeled birds have a lower percentage of dry ash than do the breast bones of straight keeled birds. No difference was found in the ash content of the leg bones of the two groups of birds.
4. Crooked and straight keeled birds of the same breeding showed no difference in rate of growth or in fecundity.
5. Males showed both a slightly higher incidence of crooked keels and a greater degree of deformity.
6. The season of hatching seemed not to influence the tendency to develop crooked keels.
7. The age at which chicks started to roost, the sharpness of the perches, and the degree to which the chicks used the perches all influenced the expression of the heritable differences in tendency to develop crooked keels.
8. The tendency to develop crooked keels was definitely shown to be inherent but the expression of the inherent qualities was found to be determined largely by the early roosting conditions.

PHYSIOLOGIC AND GENETIC STUDIES OF CROOKED KEELS IN CHICKENS¹

D. C. WARREN

PRACTICAL SIGNIFICANCE

The sternum is that part of the skeleton forming the floor of the thoracic cavity. The blade-like portion of the sternum which is set between the heavy breast muscles in the bird is called the carina or keel, and its external edge is referred to as the sternal crest. The sternal crest may readily be traced by passing the hand along the ventral surface of the thorax.

In passing the hand over the sternum in the living bird, the sternal crest normally may be traced as forming a straight line between the hypocleidium forming the tip of the clavicle and the zyphoid process of the sternum. It is, however, a matter of common knowledge among poultrymen that the breast bone frequently shows considerable deformity in shape.

With an increasing interest in the factors influencing quality in market poultry in this country, the problem of deformities of the breast bone becomes one of considerable practical significance. Badly deformed breasts detract from the appearance of the dressed bird and this condition is already meeting a market discrimination in the sale of both live and dressed birds. Figure 1 is a photograph of a group of White Leghorn cockerels showing the degree to which the crooked keel may deform the bird.

Very little study has been made of the factors responsible for deformities of the keel although the opinion prevails rather generally among poultrymen that crookedness of the keel is due to nutrition and roosting conditions during growth. The belief that nutrition of the bird is an important factor in producing crooked breast bones has probably arisen from the observations in studies on D-avitaminosis, where the crookedness of the keel was one of the diagnostic features of rickets in chickens. The fact that the crooked keel frequently occurs in flocks of chicks reared on adequate diets would indicate that nutrition cannot be the major factor in the production of deformities of the breast bone.

From 1926 to 1935 studies of physiologic and genetic factors responsible for the crookedness of the keel of chickens have been carried out at the Kansas Agricultural Experiment Station. Most of the studies have been with the White Leghorn breed, although a few others have been given consideration.

1. Contribution No. 99 from the department of Poultry Husbandry.

PHYSIOLOGIC STUDIES

AGE AT APPEARANCE OF DEFORMITY

In most of the data here presented, the condition of the keel at 6 months of age was the basis of classification. It will be



FIG. 1.—A group of White Leghorn cockerels showing the deformities resulting from crookedness of the keels.

shown that some birds developed crooked keels after this age, but the percentage not showing the deformity until after they were 6 months old was small. The difficulty of satisfactorily holding large numbers of males after this age was the decisive factor in the termination of the examinations at the 6-month age in most of the experiments.

STUDIES OF CROOKED KEELS IN CHICKENS

In 1931, 90 chicks from the strain being selected for the presence of crooked keels were examined at 1 day and 5, 8, 12, 16, 20, and 24 weeks of age for the condition of the keel bones. Eighteen died before the study was completed and 19 showed no deformity of the keels during the period. None of the 53 individuals which later developed crooked keels showed any evidence of the deformity as day-old chicks and the 5-week description was not found dependable since classification was difficult and the condition at this age seemed to bear little relationship to the adult condition. In Table I, the results of the study are given. For this group of birds, those developing deformed keels did so in the first 20 weeks. In each sex, over half of those eventually showing crooked keels did not develop the

TABLE I.—Age at development of crookedness of the keel.

Sex	Number having deformed keels at:					Number having straight keels
	8 wks.	12 wks.	16 wks.	20 wks.	24 wks.	
Female	4	6	14	16	16	13
Male	9	13	35	37	37	6

deformity until after 12 weeks of age. In addition to an increase in the percentage of crooked keels, there was also an accompanying change in the degree of the deformity, the crookedness frequently becoming more evident with age up to maturity.

In other groups of females, the changes in the condition of the breast bone were followed between 2 and 18 months and between 2 and 10 months of age. Because of the difficulty of holding large numbers of mature males without heavy losses from fighting, these observations were restricted to females.

The data in Table II are the result of examinations of five groups of hens at various ages. At six months of age, Leghorn females are approximately sexually mature. The data in the table give the number and percentage of straight keeled birds in the various groups at the different ages and also the number and percentage of birds showing the various degrees of the deformity. The decreasing percentage of straight keels as the birds age indicates the age at which the deformity appears. The increasing percentage of very crooked keels at the later examinations indicates the tendency for the degree of deformity to become greater with age.

It is believed that the differences in the percentage of crooked keels in the groups of birds recorded in Table II have an hereditary basis. A considerable number of the birds developed the deformity of the keel after 2 months of age in some of the groups

and in the case of the unselected stock there was an increase in percentage of crooked keels after 6 months of age. It is noted that in the stocks selected for the presence of the crooked keeled condition most of the deformities had developed before the age of 2 months.

Any changes which took place with age were usually in the

TABLE II.—Age and degree of development of crooked keels in females.

Source of Stock	Straight keel		Slightly crooked keel		Crooked keel		Very crooked keel	
	Num-ber	Per-cent	Num-ber	Per-cent	Num-ber	Per-cent	Num-ber	Per-cent
Stock unselected for keel condition, 1930:								
2 months old	40	67.8	6	10.2	9	15.3	4	6.8
6 months old	32	54.2	11	18.6	12	20.3	4	6.8
18 months old	26	44.1	6	10.2	18	30.5	9	15.3
Straight keel selection, 1930:								
2 months old	35	92.1	1	2.6	2	5.3	0	0.0
6 months old	37	97.4	0	0.0	1	2.6	0	0.0
18 months old	34	89.5	0	0.0	4	10.5	0	0.0
Stock unselected for keel condition, 1931:								
2 months old	232	92.4	10	4.0	8	3.2	1	0.4
6 months old	212	84.5	11	4.4	18	7.2	10	4.0
18 months old	191	76.1	8	3.2	35	13.9	17	6.8
Crooked keel selection, 1931:								
2 months old	47	78.3	2	3.3	9	15.0	2	3.3
6 months old	3	5.1	2	3.4	18	30.5	36	61.0
7 months old	0	0.0	0	0.0	20	38.9	39	66.1
10 months old	0	0.0	0	0.0	15	25.9	43	74.1
Straight keel selection, 1931:								
2 months old	31	93.9	0	0.0	2	6.1	0	0.0
6 months old	33	100.0	0	0.0	0	0.0	0	0.0
7 months old	32	97.0	0	0.0	1	3.0	0	0.0
10 months old	25	92.6	2	7.4	0	0.0	0	0.0

direction of increased degree of crookedness or increased percentage of birds showing crooked keels. Occasionally a bird would show a crooked keel at one description and later fail to show the deformity, but in these instances the previous description usually indicated that the crookedness was only slightly developed. The condition of the bird would cause some variation in the classification of the degree of crookedness, since the development of heavy muscular tissue on the breast would tend to obscure slight deformities. In no case did a keel showing a pronounced crookedness ever become straight.

The recording of relatively few birds developing crooked keels after 6 months of age does not agree with the report of the Wisconsin Agricultural Experiment Station.² It was reported that over 50 percent of females receiving no fish liver

2. Annual Rep. of Director of Wis. Agr. Expt. Sta. for 1932-1933. Bul. 428: 50-51, 1934.

oil or irradiated yeast were found to have developed crooked keels after October 1. In other lots where vitamin D was supplied, the percentage of crooked keels developing after this date was considerably higher than reported in Table II. The birds supplying the data in Table II were kept in open front houses and fed 1 percent cod liver oil in the ration during the winter.

There exists considerable variability as to the age of development of crooked keels, although a large majority of those showing the deformity will do so by the time they are 6 months old. As is later indicated in this discussion, the early roosting condition is an important factor.

In figure 2 are shown the breast bones of several chicks at 8 weeks of age. At this age, the bones are largely cartilaginous in structure. Very little calcification of the keel had taken place, but some breast bones shown in the figure were much deformed.



FIG. 2.—Keels of representative 8-week-old chicks from the crooked keeled strain (top row) and the straight keeled strain (bottom row) when reared on a vitamin D deficient diet.

It therefore would seem that the factor responsible for the deformity of the keels may have its effect before much calcification of the bone takes place, while in other birds the keels are largely in the adult condition before the crookedness appears.

DIRECTION OF CROOKEDNESS

It will be shown later that the crooked keels probably are the result of a combination of early roosting conditions and inherent tendencies. Thus, the deformity is probably the result of the pressure of the roost on a breast bone which is inherently deficient in its structure. With these conditions, it would seem probable that the direction of the bend in the keel would be entirely the result of chance.

In Table III, a summarization is made of the direction of the crookedness of the keels of birds from several types of matings. The terms right and left as used here are based upon the relationships of the bends to the right and left side of the body of the chicken. In some birds, there may be more than one bend in the keel which results in doubt as to how the record should be made. However, in most cases, the crook is definitely in one direction as is shown in figures 2 and 3.

TABLE III.—Direction of the crookedness of the keels.

Type of mating	Number of right crooks	Number of left crooks	Number straight	Percentage right crooks
Selection matings	482	334	516	59.07 ± 1.16
Hybrid crosses	95	95	271	50.00 ± 2.45
R. I. Reds	224	103	370	68.50 ± 1.73
Back-crosses	289	133	466	68.48 ± 1.53
Total	1090	665	1623	62.11 ± 0.78

The results show that there was a tendency in most matings for the bend more frequently to be to the right. The deviation from a 1 to 1 ratio was statistically significant in most of the calculations. In some of the groups given in Table III the preponderance in favor of the crook to the right was as much as 68 percent and 32 percent to the left, when 289 birds were considered in one case and 224 in another. In a total of over 1,000 birds, the percentage having the bend to the right was 62.11 and to the left 37.89. The writer has no satisfactory explanation for this tendency. The only plausible clew is that it in some way might be associated with roosting positions. If the lighting conditions in the brooder houses were such that many

birds would place their breasts on the perches at a more or less oblique angle, the difference might result. However, the direction of the source of light with respect to the location of the perches was so varied in the brooder houses, that this explanation would seem improbable.

The tendency of the crookedness to be in one direction more frequently may be of the same nature as the asymmetry of poly-



FIG. 3.—Sterni of four adult chickens showing the extent and nature of crookedness of the keel.

dactyly. A number of workers have noted that the extra toe may appear only on one foot, and if this is the case, the right foot is more frequently the one where the fifth toe is missing.

D-AVITAMINOSIS³ AND CROOKED KEELS

D-avitaminosis frequently results in deformities of the keel bone. This fact early led to the consideration of the idea that crooked keels observed in this study were in some way associated with defective calcium metabolism even though the ration was adequate. It early was recognized that the tendency toward crooked keels was heritable but it was thought that the heritable condition might be a defective calcium metabolism.

A number of tests were carried out to determine whether the strain having a high percentage of crooked keels showed any less efficient calcium and phosphorus metabolism than did the strain relatively free from crooked keels.

In 1927, analyses were made of the pooled blood from 5 adult laying females, with and without crooked keels, to determine whether the calcium and phosphorus content would differ in the two types of birds. The amount of phosphorus and calcium in the blood was practically normal and identical in the two groups. The analyses showed 3 mg. of phosphorus and 21 mg. of calcium in 100 cc. of plasma for the crooked keeled females and 3 mg. of phosphorus and 20 mg. of calcium for those with straight keels. Thus it cannot be said that the analyses showed any evidence of defective calcium or phosphorus metabolism in the birds with crooked keels.

A more critical test was carried out in the fall of 1932, when analytical studies were made of the skeleton and blood of 8-week-old straight and crooked keeled strain chicks reared on a rachitic and an antirachitic diet.

The rachitic ration used was that proposed by Hart, Kline and Keenan⁴ and the adequate ration was the one regularly used for rearing chicks at Kansas State College in 1932. The two rations were:

Rachitic		Percent	Adequate		Percent
Yellow corn		59	Yellow corn		48
Standard wheat middlings		25	Wheat bran		15
Crude casein		12	Oat groat meal		15
Common salt		1	Meat cracklings		5
Calcium carbonate		1	Dried buttermilk		10
Dried yeast		1	Alfalfa leaf meal		5
Cod liver oil		0.2	Common salt		1
			Cod liver oil		1

The chicks were kept in batteries and allowed no direct sunlight. Fifty-one chicks from the crooked keeled strain and 60 from the straight keeled strain were used. These two strains had been selected during 5 generations for crooked and straight

3. All chemical analyses were secured through the cooperation of Dr. J. S. Hughes of the Department of Chemistry of Kansas State College.

4. Hart, E. B., Kline, O. L., and Keenan, J. A. A ration for the production of rickets in chicks. *Science* 73: 710-711. 1931.

keels, respectively. The chicks were individually pedigreed, each hen's chicks being equally divided between the two rations, rachitic and adequate. Thus, 30 chicks from the crooked keeled strain and 30 from the straight keeled strain each were placed on the vitamin D-deficient ration and 21 and 30 chicks from the crooked and straight keeled strain, respectively, were started on the vitamin D-adequate ration. After 4 weeks feeding, no evidence of rickets was seen in the lots fed the D-deficient ration and in order to bring on the desired condition more rapidly, all cod liver oil was removed from the supposedly rachitic ration. After 2 weeks on this ration, several of the chicks developed the unsteady gait characteristic of rickets and at the 6-week age, the keel condition and the rachitic characteristics were recorded. The 0.2 percent cod liver oil was again added to the rachitic ration at the 6-week age and the D-deficient groups were fed that ration until the 8-week age. The intention was to keep the chicks on a ration near the border line between rachitic and nonrachitic. At 8 weeks, the analytical studies were made using the leg and breast bones and pooled blood of 5 birds in each analysis. An approximately equal representation of the sexes was included in each lot. The results of the analytical studies are given in Table IV. Since among the chicks of the crooked keeled strain, both straight and crooked keeled individuals were found at 8 weeks on each of the rations, the four groups were analyzed separately. The straight and crooked keeled chicks from the straight keeled strain reared on the rachitic diet were also analyzed separately as were the straight keeled individuals of this strain on the D-adequate ration. Keels from chicks from both strains reared on the rachitic ration are shown in figure 2.

Considering first the percentage of ash in the leg bones (Table IV) there is a striking difference between those reared

TABLE IV.—Blood and bone analysis of crooked and straight keeled chickens reared on adequate and rachitic diets.

Ration	Strain	Condition of keel	Percent ash dry extracted		Mg. Ca. in 100 c. c. serum	Mg. inorganic phosphorus in 100 c. c. of blood	P. x Ca.
			Leg bone	Breast bone			
Rachitic diet	Straight	Crooked	37.9	19.9	11.5	4.4	50.6
	Crooked		38.9	16.8	12.5	3.5	43.8
	Straight	Straight	39.7	27.8	12.6	5.0	63.0
	Crooked		38.5	24.7	10.2	5.2	53.0
Normal diet	Straight	Straight	51.5	37.8	12.8	5.8	74.2
	Crooked	Crooked	48.6	32.9	13.1	5.2	68.1
		Straight	50.0	38.6	12.0	4.9	61.7

on the D-deficient and D-adequate diets. Among the different groups on each of these diets, however, no significant differences were found in the percentage of ash in the leg bones. The analyses of leg bones of chicks from the two strains were very similar.

The analyses of breast bones gave quite different results from those of leg bones. As in the case of the leg bones, the breast bones of the chicks on the D-deficient diet showed a much lower percentage of ash than did those of the D-adequate diet. Also, the keels of the chicks from the two different strains but on the same diet gave rather widely differing analytical results. The keel bones of crooked keeled rachitic-diet chicks of the straight keeled strain contained 19.9 percent ash, while the corresponding bones of crooked keeled chicks from the crooked keeled strain on the same diet contained only 16.8 percent ash. A similar difference was found between the straight keeled chicks from the two strains when on the rachitic diet. Those from the crooked keeled strain had 24.7 percent ash in the breast bones while those from the straight keeled strain had 27.8 percent.

In those birds on the D-adequate diet, the crooked keeled chicks from the crooked keeled strain showed considerably less ash in the breast bones than either the straight keeled chicks from the crooked keeled strain or the straight keeled individuals from the straight keeled strain.

The analyses of the blood for calcium and phosphorus are in fairly good agreement with the ash analysis of breast bones. The product of the calcium and phosphorus content of the blood has frequently been used in the diagnosis for rickets, and is given in the last column of Table IV. In general, the straight keeled chicks showed a higher content of calcium and phosphorus than did those with crooked keels, when the two were kept on the same diet.

The results in Table IV may be interpreted as follows: The ash analyses of the leg bones show no evidence of defective calcium metabolism in the crooked keeled strain. Analyses of the breast bones indicate a defective calcium deposition in this portion of the skeleton of birds of the crooked keeled strain when compared with those of the straight keeled strain. This fact was especially well brought out when the chicks were reared on a rachitic diet. The analyses of the breast bones of chicks on the rachitic diet also indicated rather strikingly that those from the crooked keeled strain possessing crooked and straight keels at the 8-week age differed rather widely in the ash content of their breast bones. The same was true of the chicks of the straight keeled strain and although practically all of the chicks of this strain would have had straight keels when on an adequate diet, many, when on a rachitic diet, developed crooked

keels, which, when analyzed, showed a lower ash content than did their straight keeled sibs. The question may be raised whether the crooked keeled condition in the straight keeled strain chicks on the rachitic ration is comparable to the crooked keeled condition in the crooked keeled strain chicks reared on an adequate diet. It would seem, however, that the rachitic diet acts as an indicator in bringing out genetic differences in the straight keeled strain which would not be noted when on an adequate diet.

These results may be taken to indicate that although selection has made the straight and crooked keeled strains to differ genetically, neither strain is homozygous for the genetic factors involved. The straight keeled bird appearing in the crooked keeled strain, although differing some in ash content of its breast bone from a straight keeled bird of the straight keeled strain, also shows an ash content differing from that of the crooked keeled bird of its own strain.

An examination of 6-week-old chicks on the rachitic diet was made to determine the rate at which the crooked and straight keeled strain came down with rickets. In the straight keeled strain, 12 showed the characteristic unsteady rachitic gait while 13 appeared normal. In the crooked keeled strain, 6 exhibited the rachitic gait and 22 were normal. It was thought that if the calcium metabolism of the crooked keeled strain was defective, chicks of this strain would be more susceptible to the effects of a D-deficient diet and quickly develop rickets. The observed difference, which is probably not significant, would indicate that the outward signs of rickets are no more easily developed in the crooked keeled strain than in the straight keeled strain. It is known, however, that the unsteady gait is not a critical test for the rachitic condition.

At the 8-week age, 17 of the chicks of the crooked keeled strain on the rachitic diet had crooked keels and 10 had straight keels, and 9 of the chicks of the straight keeled strain had crooked keels and 14 had straight keels. Of the chicks on adequate diet, 8 of the crooked keeled strain had crooked keels and 9 had straight keels. The straight keeled chicks on the adequate diet all had straight keels except one which showed a slight crookedness.

Earlier tests had shown no significant differences in the total calcium content of the blood of adults from the crooked and the straight keeled strains. The possibility was considered that although the blood of the two strains might carry the same amount of calcium, there might be a difference in that available for bone formation. Therefore, a comparison was made of the percentage of diffusible calcium in the blood of the two strains. Individual analyses were made for diffusible calcium in the blood of 5 six-month-old cockerels from the crooked keeled

strain and 5 from the F_1 generation of the cross of crooked by straight strain. The incidence of crooked keels differed widely in these two groups but the percentage of diffusible calcium was very similar. The mean percentage of diffusible calcium for the cockerels of the crooked keeled strain was 59.8 and for the F_1 generation cockerels was 55.5. This difference is probably non-significant and is in the direction opposite the expected one, if the available calcium were the limiting factor in the production of straight keels.

The general results of this phase of the study are that blood analyses show no evidence of a defective calcium metabolism in the crooked keeled adults. Insofar as superficial characteristics of rickets are indicative, the crooked keeled strain chicks are no more susceptible to rickets than are those of the straight keeled strain. The breast bones of crooked keeled chicks did show a lower rate of calcification than did those of chicks with straight keels.

CROOKED KEELS IN RELATION TO GROWTH AND FECUNDITY

It seems probable that the tendency to develop crooked keels although inherent, is due to a defective execution of those physiological processes associated with bone formation. If this be true, then it is possible that development in general might be inferior in the crooked keeled individuals.

Comparisons were made of the growth of chicks at 8 weeks in four strains where both crooked and straight keels were found at maturity. All chicks being compared were hatched at the same time and reared under as nearly identical conditions as was practical. Since some of them did not develop crooked keels until after the 8-week age, it was not known at the time of weighing how they would be classified as to keel condition. Individual weights were taken and results on males were not included since they were sold at the 8-week age at which time they could not be classified accurately with respect to keel condition.

The data on growth of four strains of White Leghorns are given in Table V. These strains differed with respect to the incidence of crooked keels. It is seen that in all four strains the crooked keeled females averaged heavier than did those having straight keels. The data certainly provide no support for the view that the factor responsible for the crooked keels in any way handicaps the chick in growth. In fact, the strain 2 showed a significant difference in favor of the crooked keeled birds. The other differences are too small to be statistically significant.

Asmundson⁵ had previously found that there was no relationship between straightness of the keel and total egg production. He did state, however, that there was some evidence

5. Asmundson, V. S. The relation of keel bone to egg production. *Scien. Agr.* 1: 30-33, 63-67. 1921.

STUDIES OF CROOKED KEELS IN CHICKENS

TABLE V.—Comparison of weight at 8 weeks and pullet year fecundity in crooked and straight keeled females of the same strain.

Relation to Growth					
Stock	Females having straight keels		Females developing crooked keels		$\frac{D}{E}$
	Number	Mean wt. (grams)	Number	Mean wt. (grams)	
Strain 1	95	445.5±5.2	73	448.3±5.7	.4
Strain 2	162	339.4±3.4	21	406.0±8.3	7.4
Strain 3	177	436.6±3.6	71	444.7±6.6	1.1
Strain 4	167	406.4±4.1	38	421.1±8.9	1.5

Relation to Fecundity					
Stock	Number	Eggs produced in pullet year		$\frac{D}{E}$	
		Number	Eggs produced in pullet year		
Strain 1	24	206.7±6.3	15	200.0±8.8	.6
Strain 2	78	199.5±3.4	10	200.0±11.4	.0
Strain 3	54	224.4±4.1	22	218.2±6.2	.8
Strain 4	65	229.0±3.0	16	215.0±8.2	1.6

that crooked keeled females started to lay earlier than did those with straight keels. Patterson and Quisenberry stated that straight keeled females laid better than females either with slightly or decidedly crooked keels. They also found that birds with decidedly crooked keels did not lay so well as did those with slightly crooked keels. Patterson and Quisenberry did not, however, present any data in support of their statements. In Table V, also will be found data on the influence of crooked keels on the pullet year fecundity. Only those females having a full year's production were considered. The annual egg production of pullets of the same strain with and without crooked keels was very similar. None of the differences in fecundity between the straight and crooked keeled pullets were statistically significant, indicating that egg production is not influenced by the possession of a crooked keel by a bird. The results in Table V would seem to indicate that the factors responsible for crooked keels have no deleterious effects on the birds growth or fecundity.

SEX AND CROOKED KEELS

The data under the heading of the genetic nature of crooked keels were summarized to determine the influence of sex on the tendency to develop the deformity. A comparison was made of the percentage of crooked keels in individuals of the two sexes

6. Patterson, C. T. and Quisenberry, T. E. Observations made and lessons learned from the Missouri National Egg Laying Contests. Mo. State Poultry Expt. Sta. Bul. 10: 1-43. 1915.

from several types of matings. These results given in Table VI show that in most of the matings the males showed a higher percentage of crooked keels than did the females. In some cases, the difference in favor of the males was statistically significant.

Not only did the males in the same matings show crooked keels more frequently than did the females, but there was also a greater degree of deformity in the males showing crooked keels. In some matings, the birds were placed into three arbitrary classes, slightly crooked, crooked, and very crooked. In 945 birds so classified, the ratio of very crooked to slightly crooked keels was approximately 3 to 1 in the males and 2 to 1 in the females. These results and those in Table VI would indicate that there is a slight sexual dimorphism with respect to the expression of crooked keels in the chicken, the males showing the greater tendency.

TABLE VI.—Influence of sex on expression of crooked keels.

Type of mating	Females		Males		D E
	Num. birds	Percent crooked	Num. birds	Percent crooked	
Selection matings	740	65.7±1.18	640	63.1±1.29	1.5
Strain crosses	802	25.8±1.04	729	33.3±1.78	4.8
F ₁ generation	523	45.3±1.47	487	50.5±1.53	2.5
Back-cross generation	442	44.1±1.59	448	50.9±1.58	3.0

Schroeder⁷ has shown that there is a significant sexual dimorphism in the calcification of shaft bones in chicks. His work indicated that males had a lower rate of calcification of the leg bones than did females. This fact might account for the males showing a greater tendency to develop the deformed keels, since a lower rate of calcification might make them more susceptible to the deforming influence of the perches.

HATCHING SEASON AND CROOKED KEELS

Inasmuch as it was found that there was considerable variability in the incidence of crooked keels, the data for the matings in which there was selection for crooked keels were arranged to determine the influence of the month of hatching. In Table VII, the data from the crooked keeled matings for 1927 to 1931 were segregated on the basis of the month of hatching. Since management conditions varied somewhat from year to year, dependable comparisons probably can only be made of chicks hatched in the different months of the same year. The range of

7. Schroeder, Carl H. Sexual differences in calcification of chicks and the effect on assays. Poultry Sci. 12: 256-260. 1933.

months during which hatching was done was not the same for all years. It cannot be said that the data in Table VII show any consistent trends with respect to the incidence of crooked keels. There was rather wide variability in the monthly percentages of crooked keels, but some of this may be due to the fact that

TABLE VII.—Effect of season of hatch upon incidence of crooked keels.

Year	Hatches in the month of—							
	February		March		April		May	
	Number chicks	Percent crooked keels	Number chicks	Percent crooked keels	Number chicks	Percent crooked keels	Number chicks	Percent crooked keels
1927			46	74	51	84	16	44
1928	26	81	36	39	40	50		
1929			41	49	67	48	21	76
1930	30	80	201	84	289	46		
1931	61	79	243	75	322	64		

the data for the two sexes were not segregated. It may be stated that the variations in season of hatch insofar as they are represented in the data presented, do not appear to influence the incidence of crooked keels.

INFLUENCE OF ROOSTING CONDITIONS

Although the idea has been rather generally accepted that too sharp perches would cause crooked keels, very little published information is available to substantiate the opinion. Platt⁸ reported that chicks placed in battery cages at 3 weeks of age with and without perches differed widely as to the incidence of crooked keels. Two lots without perches had no crooked keels, while three lots provided with perches showed 66, 64 and 44 percent crooked keels when 8 weeks old. Platt⁹ also reported that the width of the perch was a factor influencing the incidence of crooked keels.

It had been found in this study that under uniform roosting conditions, the incidence of crooked keels differed rather widely in different strains. However, it also was observed that the incidence of crooked keels varied considerably in the same strains and it was believed that the roosting conditions might be a factor.

Chicks With and Without Perches. — Experiments were planned to test the influence of roosting conditions on the in-

8. Platt, C. S. Early roosting as a cause of crooked keels in S. C. White Leghorn cockerels. (Abstract) Poultry Sci. 11: 362. 1932.

9. Platt, C. S. Crooked keels in relation to width of perch. (Abstract) Poultry Sci. 12: 333. 1933.

cidence of crooked keels. In Table VIII, are given the results of rearing chicks under the two extremes of roosting conditions. In one group, the chicks were provided with low sharp edged perches (1 inch by 1 inch) at 2 weeks of age. In the other group, no perches were provided during the period of the experiment, and all equipment upon which chicks might roost was removed from the pen in which they were confined. In the two experiments, the data for which are given in Table VIII, the chicks were all reared in a battery brooder with no perches for the first 2 weeks. The chicks were individually pedigreed and each hen's chicks were equally divided between the sharp-roost- and no-roost-pens. In the 1932 experiment, the chicks were kept in small pens (4 x 8 feet) with hardware cloth floors, while in 1933 the chicks were placed in larger pens with concrete floors covered with straw. It is difficult to get chicks to make use of perches until they are 3 or 4 weeks old.

In the 1932 experiment (Table VIII), it will be seen that at the 16-week age, chicks of the crooked keeled strain (5 generations of selection) had 100 percent crooked keels when reared in a pen carrying sharp roosts. Chicks of the same parentage but reared without any roosts were almost 100 percent with straight keels. Under the same conditions, chicks from the F_1 generation of crossing the straight and crooked keeled strains gave 27 percent crooked keels when provided sharp roosts and 100 percent straight keels when kept without roosts.

In 1933, a comparison was made of chicks with and without roosts, from the crooked and straight keeled strains (after 6 generations of selection). The percentage of crooked and straight keels was recorded at the 12- and 24-week age. The only difference between the conditions here and those in the 1932 experiment was that the chicks here were on concrete floors instead of hardware cloth and the pen was considerably larger. Being allowed more room, the chicks spent less time on the perches during the day and thus the incidence of crooked keels was reduced.

The difference between the incidences of crooked keels in the roost and non-roost lots in the crooked keeled strain is less striking than in the previous experiment. The roosting conditions here were not such as to give nearly so high a percentage of crooked keels in the crooked keeled strain at either the 12- or 24-week age. At 12 weeks of age, most of the non-roost chicks had straight keels, but many of them developed crooked keels between the 12- and 24-week age, although no perches were provided in that period. The chicks of the straight keeled strain remained 100 percent straight at the 24-week age whether kept on sharp perches or without perches.

Age at Starting Roosting. — In order to determine at what age chicks were most susceptible to the effect of sharp perches in

TABLE VIII.—Influence of roosting conditions on the development of crooked keels.

Type of mating	Age in weeks	Sharp perches provided at two-weeks age				No perches provided			
		Number chicks	Number crooked	Number straight	Percent crooked	Number chicks	Number crooked	Number straight	Percent crooked
1932 Experiment: Crooked keeled strain	16	15	15	0	100	15	1	14	7
F ₁ (straight x crooked)	16	51	14	37	27	45	0	45	0
1933 Experiment: Crooked keeled strain	12	22	14	8	64	23	3	20	13
Crooked keeled strain	24	20	14	6	70	20	12	8	60
Straight keeled strain	12	27	0	27	0	24	0	24	0
Straight keeled strain	24	27	0	27	0	21	0	21	0

producing crooked keels, chicks were placed on 1 x 1 inch roosts at varying ages. The stock used was the strain selected six generations for the presence of crooked keels. The data for this strain in Table VIII show a high percentage of crooked keel developing in the birds when sharp perches were provided at the 4-week age and very few crooked keels when roosting was not permitted. The results of the experiment on the influence of age are given in Table IX. All chicks were kept in a wire floored battery with no perches until 4 weeks old, after which they were moved to 4 x 8 foot pens with wire floors. When the chicks reached the age desired, each hen's offspring were equally divided between the roost- and non-roost pens. The roosts were made of 1 x 1 inch material placed across low upright supports. At the 12-week age, all chicks were moved to a larger room with a straw covered concrete floor and the roosting groups were again provided with 1 x 1 inch perches. These conditions were maintained until the birds were 24 weeks old when the data given in Table IX were taken. These data show a very definite trend toward a smaller percentage of crooked keels the later in life the chicks were provided sharp perches. When the chicks were placed on sharp perches at the 4-week age, over 90 percent of the chicks developed crooked keels while they showed 20 percent or less when not allowed roosts until 12 weeks old. Although showing considerably less crooked keels than when allowed perches at 4 weeks of age, it did not seem to make much difference whether they were provided at 6 or 8 weeks of age. There was a rather sharp drop-off in percentage of crooked keels when perches were withheld until the chicks were 10 to 12 weeks old. Although the data in Table IX are somewhat meager, they do indicate rather definitely that the incidence of crooked keels, in a strain having a tendency to develop crooked keels, can be controlled largely by modification of the roosting conditions.

In Table X, data are recorded as to the incidence of crooked keels in two strains (unselected for keel condition) when groups

TABLE IX.—Effect of providing chicks of the crooked keeled strain with sharp perches at varying ages. Records taken at 24 weeks of age.

Perches provided at the age of—	Num. of females with—			Num. of males with—		
	Crooked keels	Straight keels	Percent crooked	Crooked keels	Straight keels	Percent crooked
4 weeks	8	1	90	15	1	94
6 weeks	12	8	60	12	4	75
8 weeks	15	9	63	13	2	87
10 weeks	2	16	11	8	8	50
12 weeks	0	9	0	3	12	20

from each strain were maintained under slightly differing conditions. All chicks were kept in battery brooders without perches until 4 weeks old and then transferred to pens provided with sharp perches (1 x 1 inch). From each strain, one group was placed in a small wire floored pen (4 x 8 feet) and another in a larger (8 x 10 foot) pen with a straw covered concrete floor. The restricted conditions in the small wire floored pen caused the chicks to spend considerably more of the day-time period on the perches. In Table X, the wire floored pens are referred to as restricted quarters and the concrete floored pens as less restricted quarters. Although the numbers are too small for the exact percentages of crooked keels secured to have much significance, the data are in agreement in pointing to the conclusion that crowding may be a factor increasing the incidence of crooked keels.

These results seem to indicate that, in stocks having a tendency to produce crooked keels, the incidence of the deformity will vary widely, depending upon the age at which perches are provided and the crowding of the chicks in the pen. It should be kept in mind that the perches utilized were much sharper than normally would be used.

GENETIC STUDIES

In the foregoing study, we have shown that the early roosting conditions are of considerable importance in the expression of the crooked keeled condition. However, evidence was se-

TABLE X.—Effect of crowding when chicks of crooked keeled strain were provided sharp perches at 4 weeks of age.

Records taken at 24 weeks of age.

Strain and rearing conditions	Num. of females with—			Num. of males with—		
	Crooked keels	Straight keels	Percent crooked	Crooked keels	Straight keels	Percent crooked
Strain A: Sharp perches and restricted quarters	3	3	50	8	1	89
Sharp perches but less restricted quarters	8	12	40	13	8	62
Strain B: Sharp perches and restricted quarters	6	2	75	4	1	80
Sharp perches and less restricted quarters	3	11	21	11	8	58

cured early pointing strongly to the view that the inherent constitution of the bird also was of importance.

SELECTION RESULTS

In 1926, it was first observed that families of White Leghorns carried at the Kansas Agricultural Experiment Station varied greatly in the incidence of crooked keels. In 1927, the first generation of selection for the presence and absence of crooked keels was initiated. The mating of crooked keeled males by crooked keeled females from a family showing a tendency toward crooked keels gave 49 crooked keeled offspring to 12 straight keels. A mating of straight keeled individuals from a family giving few crooked keels gave 49 straight keels and 2 crooked keels. Since the management of the two lots of offspring was identical, these rather marked differences in the first generation of selection could be attributed only to genetic differences in the parent stock used in the two matings. In Table XI, are given the data for later generations of selection between the years 1928 and 1932. In each generation of the crooked keeled strain, the crooked keeled individuals from the families having the highest incidence of crooked keels were mated and the same procedure was followed in selecting for straight keels. The 5 generations of selection accomplished virtually nothing in the straight keeled strain. There was little opportunity for bringing about any change in the strain since the percentage of crooked keels was never more than 13 in either sex in any generation. There was an increase in percentage of crooked keels in the crooked keeled strain, but the higher incidence cannot be attributed entirely to selection since in the earlier generations of selection the influence of roosting conditions was not fully appreciated and the care was not exercised to get the chickens to make use of the perches as soon as possible. For any one year, the roosting conditions were the same for the two strains, the chicks of each hatch of the two strains being reared in the same brooder rooms. During the years 1928 and 1929, the chicks were all started in 10 x 12 foot brooder houses and in later years they were kept in battery brooders for the first 4 weeks and then transferred to a brooder house with a straw covered floor and low perches carrying 2-inch strips. It is quite possible that the increase in incidence of crooked keels in the later generations of the crooked keeled strain was due to the change in management. Under the discussion of the influence of roosts, it was shown that after six generations of selection the crooked keeled strain could be varied from near 0 to near 100 percent of crooked keels depending upon the roosting conditions. In Table VIII, it is shown that when the chicks from the straight keeled strain were placed on sharp roosts at 2 weeks of age, the keels remained straight at 24 weeks of age. Unfortunately, it was not possible to carry

TABLE XI.—Successive generations of selection for the presence and absence of crooked keels.

Crooked keel selection										
Year	Females with—					Males with—				
	Straight keels	Crooked Keels			Percent crooked in any degree	Straight keels	Crooked Keels			Percent crooked in any degree
		Slightly crooked	Crooked	Very crooked			Slightly crooked	Crooked	Very crooked	
1928	33	6	12	4	40	18	4	18	12	65
1929	35	4	19	4	44	39	6	19	2	41
1930	85	16	60	55	61	71	14	45	46	60
1931	88	57	97	94	74	102	30	88	74	65
1932	13	3	30	25	82	6	0	28	18	88
Straight keel selection										
1928	69	0	0	2	3	68	5	4	1	13
1929	32	1	0	0	3	32	1	0	0	3
1930	40	1	5	0	13	Not recorded—				
1931	124	3	3	2	6	Not recorded—				
1932	25	1	0	0	4	28	0	1	0	3

the straight keeled strain beyond 1933. The deleterious effects of inbreeding resulting from the type of matings necessary in selection virtually eliminated the strain. It was, therefore, not determined whether the straight keeled strain would remain relatively free from crooked keels even when placed on sharp perches early and kept under crowded conditions, thus causing the chicks to spend much of the daytime period on the perches. It seems to be well demonstrated by the data in Table XI that under the usual management conditions, the crooked and straight keeled strains differed widely in the incidence of crooked keels. A few crooked keels usually appeared in each generation of the straight keeled strain and the crooked keeled strain gave approximately only 75 percent crooked keels unless kept in crowded quarters with sharp roosts from an early age.

DIFFERENCES IN UNSELECTED STRAINS

In addition to the matings between the selected straight and crooked keeled strains, certain other stocks were mated which also indicated the heritability of the tendency to grow crooked

TABLE XII.—Results of reciprocal matings of Leghorn strains differing in the incidence of crooked keels.

Strain	Keel condition of daughters			Keel condition of sons		
	Number straight keels	Number crooked keels	Percent crooked keels	Number straight keels	Number crooked keels	Percent crooked keels
Strain A	94	74	44	78	79	50
Strain C	161	21	12	128	35	21
St. A male x C female	175	74	30	135	88	39
St. C male x A female	165	38	19	145	41	22
Strain A	97	65	40	Not recorded		
Strain B	129	8	6	Not recorded		
St. B male x A female	116	17	13	Not recorded		
St. A male x B female	137	18	12	Not recorded		

breast bones. In Table XII, are given the first generation results of matings among three strains of White Leghorns carried at the Kansas Agricultural Experiment Station. The two pure strain chicks, A and C, were compared with the offspring of reciprocal matings between the two strains. It is seen that

strain A gave a much higher percentage of crooked keels in both males and females than did strain C and that the F_1 generation offspring were somewhat intermediate between the two parental strains with respect to the incidence of crooked keels. The fact that the female offspring from the mating of strain A males by strain C females showed a higher incidence than did the reciprocal cross might be taken as evidence for sex-linked factors being involved. However, the males of this mating also showed more crooked keels than did those of the reciprocal mating, thus indicating that the difference between the reciprocal crosses was due to genetic differences in the parental stock used rather than to sex-linked factors. The slight difference in incidence of crooked keels in the female offspring of reciprocal matings of strains A and B (bottom of Table XII) is in the direction opposite of that found in the matings of strains A and C, thus indicating that sex-linked factors are probably not responsible for the differences in keel condition between the strains crossed. The keel condition of the males is not recorded in the matings of strains A and B since the males were disposed of when 8 weeks old, before the keel condition could be accurately classified.

The results shown in Table XII indicate rather definitely that the differences in incidence of crooked keels in the three strains, A, B, and C, are heritable. These three White Leghorn strains were mated to the same strains of Barred Plymouth Rocks in another investigation and the incidence of crooked keels was recorded in the hybrids. No data were available on the tendency toward crooked keels in the Barred Plymouth Rock strain. Six breeding pens were made up carrying one Barred Rock male and 4 females from each of the three White Leghorn strains. Thus, the hybrid offspring from the three groups of White Leghorn females were half sisters. The keel condition of the male offspring was not recorded since they were sold before being old enough to classify. After producing hybrids for a few weeks, the Leghorn females were mated to males of their respective strains giving pure strain chicks to be compared with the hybrids. The management and roosting conditions were the same for all chicks listed in Table XIII. The rank of the three groups of hybrids with respect to incidence of crooked keels is the same as that of the three pure strains of Leghorns giving rise to them. The rank of the three groups of pure Leghorns in Table XIII is the same as that shown in Table XII. The data given in Tables XII and XIII were secured in two successive years but in each case the rank of the three strains of Leghorns was in the order of A-C-B with respect to incidence of crooked keels. Even though the genetic constitution of the Barred Plymouth Rock males with respect to keel condition is unknown, the incidence of crooked keels among the three

groups of hybrids indicates that the differences in keel condition in the three Leghorn strains have an inherent basis. The Leghorn strain B here listed was the straight keel selection line.

TABLE XIII.—Results of mating females from three different White Leghorn strains to males of their own strain and to Barred Plymouth Rock males.

Dam's strain	*Daughters from mating to males of their own strain			Daughters from mating to Barred Rock males		
	Straight keels	Crooked keels	Percent crooked	Straight keels	Crooked keels	Percent crooked
Dams from Leghorn strain A	30	34	53	39	28	42
Dams from Leghorn strain B	40	6	13	51	20	28
Dams from Leghorn strain C	17	9	35	43	27	39

*Sons not recorded since they were sold at the 8-week age when keel description is not reliable.

F1, GENERATION OF CROSSES BETWEEN STRAINS SELECTED FOR PRESENCE AND ABSENCE OF CROOKED KEELS

In Table XIV, are given the results of reciprocal crosses between the strains selected for straight and crooked keels after 6 and 8 generations of selection. Under the heading 1932 matings, the data on the incidence of crooked keels in the two selected strains being crossed are given along with the results of the reciprocal matings. In 1932, the chicks were all encouraged to use perches at 4 weeks of age, but the perches were 2-inch strips instead of 1-inch ones as were used in 1934. The 1934 chicks were also more crowded than were the 1932 chicks. The percentage of crooked keels among the chicks of the F₁ generation in 1932 is more like that of the straight keeled strain while in 1934 the F₁ generation chicks showed an incidence of crooked keels similar to that of the crooked keeled strain. The difference in roosting conditions in 1932 and 1934 is probably responsible for the variation of dominance in the F₁ generation. In each case, the F₁ generation showed an incidence of crooked keels intermediate between that of the two strains being crossed. The results of the reciprocal matings of the two selected strains offer no support for the view that sex-linked factors are responsible for the differences in keel condition of the straight and crooked keeled strains.

STUDIES OF CROOKED KEELS IN CHICKENS

TABLE XIV.—F₁ generation results of crossing selected straight and crooked keeled strains.

Type of mating	Females with—			Males with—		
	Straight keels	Crooked keels	Percent crooked	Straight keels	Crooked keels	Percent crooked
1932 matings						
Straight male x straight female	25	1	4	28	1	3
Crooked male x crooked female	13	58	82	6	46	88
Straight male x crooked female	125	64	34	89	86	49
Crooked male x straight female	94	31	25	94	32	25
1934 matings						
Crooked male x straight female	29	83	74	24	81	77

BACK CROSSES

In Table XV, are given the data from back crosses of F₁ generation females to males of the straight and crooked keeled strains. These matings were made in 1933 and the F₁ generation females were secured from the matings given in Table XIV. Since both straight and crooked keeled females were produced in the F₁ generation, both kinds were used in the back crosses. The chicks listed in Table XV were provided 1 x 1 inch perches at 4 weeks of age, but under less crowded conditions than the 1934 F₁ generation chicks. The back crosses to the crooked keeled strain males gave a higher percentage of crooked keeled offspring than the back crosses to the straight keeled strain males as would be expected if the tendency to develop crooked keels were inherent.

It is of interest to note that in the back crosses to the crooked and straight keeled strain males (Table XV), the crooked keeled F₁ generation females gave a higher percentage of crooked keeled offspring than did the straight keeled females from the same generation. The crooked and straight keeled F₁ generation females were mated to the same males, thus the two groups of offspring being compared were half brothers and sisters. These results may be interpreted to indicate that the crooked and straight keeled birds in the F₁ generation had a different genetic constitution and that observed differences were not due to differences in the environment encountered by individual birds. When the influence of roosting condition on the expression of crooked keels was demonstrated, it was at first

thought that the few crooked keels in the straight keeled strain and the few straight keels in the crooked keeled strain after several generations of selection might be due to differences in roosting habits of the exceptional birds. The differences in the reaction of crooked and straight keeled F_1 generation birds indicate, however, that after six generations of selection, the straight and crooked keeled strains were not homozygous for the genetic factors conditioning crooked keels. The results of chemical analyses given in Table IV also show that these crooked and straight keeled birds in the same strain differed physiologically as expressed by differences in ash content of breast bones.

TABLE XV.—Back cross of F_1 generation females from crossing the straight and crooked keeled strains to males from each of the parental strains.

Type of mating	Females			Males		
	Straight keels	Crooked keels	Percent crooked	Straight keels	Crooked keels	Percent crooked
Back cross of straight keeled F_1 generation females to males from crooked keeled strain.	56	91	61.9	46	87	65.4
Same except crooked keeled F_1 generation females were used.	50	60	54.5	28	72	72.0
Back cross of straight keeled F_1 generation females to males from straight keeled strain.	69	12	14.8	84	30	26.3
Same except crooked keeled F_1 generation females were used.	72	32	30.8	62	39	38.6

This view is further supported by a test of the few straight keeled birds appearing in the crooked keeled strain after six generations of selection. Such straight and crooked keeled sisters were mated to the same crooked keeled male, the former giving 73 and 59 percent crooked keels in daughters and sons, respectively, while the latter gave 79 and 73 percent crooked keels.

In view of the failure after six generations of selection to make the two strains homozygous for the factors controlling the chick's ability to grow a straight keel when permitted to roost at an early age, it would seem that the inherent tendency

had more than a monofactorial basis. Since the roosting conditions play such an important part in the expression of the genes favoring the development of crooked keels, it seems unwise to attempt to place the crooked keeled condition on a specific factorial basis. It is believed that the data here presented demonstrate that the tendency to develop crooked keels during growth is inherent but requires early roosting on sharp perches to bring the genes into full expression. It is to be expected that a condition which probably has its basis in the mineral metabolism of the bird would have a complicated genetic foundation.

DISCUSSION

The crooked keeled condition usually develops during the growth of the chick, although a few birds do not show the deformity until after reaching sexual maturity. Males show a slightly higher incidence of crooked keels than do females. This sexual dimorphism may be a result of a slower rate of calcification of the skeleton in the male chicken. Schroeder¹⁰ reported that sexual differences in rate of calcification were present in the growing chicks. Statistical treatment of the available data also indicates that the keels are more frequently bent to the right than to the left.

The tendency to develop crooked keels probably has its basis in a defective calcium-phosphorus metabolism. This view is supported by the finding that the ash content of the breast bones of crooked keeled chicks is less than that of straight keeled chicks. The leg bones of the same two groups of chicks fail to show any difference in ash content. However, crooked keeled strain chicks do not appear to be any more susceptible to rickets than do straight keeled chicks, when kept on a rachitic diet. Blood analysis also fails to reveal any rachitic tendencies in crooked keeled birds.

The apparent deficiency of mineral deposition in the keels of crooked keeled chicks does not seem otherwise to have a deleterious influence on the bird. Both growth and egg production tendencies appear to be uninfluenced by the presence of crooked keels. The fact that leg bones of crooked keeled chicks are normal for ash content while the breast bones are deficient would indicate that the deformity is due to an insufficiency of mineral deposition in the one portion of the skeleton rather than a generalized deficiency in the birds' metabolism. Since the effects are so localized, crooked keels could not be expected to influence the birds in a deleterious manner.

The studies on the influence of roosting conditions show that there is in crooked keels an excellent example of the interaction of heredity and environment. The expression of the genes responsible for the tendency to develop crooked keels is

10. loco citato.

influenced greatly by the type of roosting conditions provided the chick. To state it in another manner, it may be said that the chick's resistance to the deforming tendency of perches is inherent, but the degree of resistance is dependent upon the severity of the roosting conditions encountered. Two factors found to have an influence are age at starting roosting and the amount of time spent on the perches. The latter is conditioned by the amount of crowding to which the chicks are subjected. Platt¹¹ also found that the sharpness of the perches is a factor of importance. The character here studied is similar to the abnormal abdomen in *Drosophila* which requires a special moisture environment for its expression. In the case at hand, the tendency to develop crooked keels requires a certain combination of factors such as age at starting, amount of time spent on perches, and the sharpness of perches, to permit its expression. This favorable combination of environmental factors, combined with a deficiency of deposition of minerals in the breast bone, results in the deformity being studied.

It is to be expected that such a complicated set-up would present a complex genetic problem. The dominance or recessive relationship of the crooked keeled condition seems to be influenced by the type of roosting conditions provided. It is shown that by variation of the roosting conditions, the strain selected for the presence of crooked keels could be made to vary from 0 to practically 100 percent for the incidence of crooked keels. The fact that after six generations of selection and progeny testing for crooked keels, the few appearing straight keeled birds seemed to be of a genetic constitution differing from that of the crooked keeled individuals in the strain, is evidence that the mode of inheritance is not simple.

In view of the many complicating factors, it seems unwise to attempt to place the inheritance of the tendency to develop crooked keels on a definite factorial basis. The fact that under normal roosting conditions the crooked keeled strain would show an incidence of 60 to 80 percent crooked keels and the straight keeled strain an incidence of less than 10 percent is satisfactory evidence that the tendency is inherent.

Under practical conditions, in strains where the tendency to develop crooked keels is prevalent, selection against the tendency should be exercised. The prevention of roosting too early in life and the provision of wide roosting poles will also materially aid in controlling the tendency.

11. loco citato.