A GENETIC ANALYSIS OF THE CROOKED TOES DEFECT IN CHICKENS

by

Keith Geoffrey Hollands

B.A., University of British Columbia, 1953
B.S.A., University of British Columbia, 1954

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ABSTRACT

The crooked toes defect in chicken is an example of an aberrant polymorphic trait associated with inbreeding degeneration. The mechanism governing its expression is a property of balanced genotypes based on obligate levels of heterozygosity. Fixation of the trait was accomplished in California by a selection program combined with inbreeding in a Single Comb White Leghorn flock. The crooked toes line developed from this program was combined, in the present investigation, in crosses with genetically unrelated stock.

Strain and breed (New Hampshire) crosses to the crooked toes line were made reciprocally and carried through the F_1, F_2 and backcross generations. Offspring from each cross were mated from the F_1 generation to establish four lines based on reciprocal parental matings. Comparisons were then made to determine the levels of incidence, the degree of phenotypic expression, the association of the trait with fitness and the effects of sex-linkage, maternal environment and inbreeding.

Crooked toes were found to be a polygenic trait characterized by semi-dominance and variable penetrance. The trait is associated with a number of modifiers affecting fitness. Inbreeding per se increased incidence, and increased incidence was accompanied by increased expressivity. The behavior of matings between parents with varying degrees of crooked toe incidence was unpredictable. The appearance of the defect is determined to a considerable degree by the presence of a physiological threshold for its expression. An unsuccessful attempt was made to locate marker genes associated with aggregates of crooked toe determining loci.

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Department of Poultry Science,
The University of British Columbia,
Vancouver 8, Canada.

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INTRODUCTION

Crooked toes in chicken and turkeys is a morphological defect expressed as a persistent flexion (Fig. 1) of the plantar digits of the feet. In most cases onset of the defect is during the last eight days of incubation but may occur at any time prior to somatic maturity (Hicks, 1953). Due to reduction in growth of the flexor tendons of the feet, the digits are unable to achieve full extension.

The genetic characteristics of the crooked toes complex show that it is a polygenically determined trait which occurs in many poultry flocks at a low level of incidence (Hicks and Lerner, 1949). The trait is amenable to selection. It exhibits variability in phenotypic expression, shows semi-dominance, and incomplete penetrance. The incidence of the trait is greatly influenced by environmental conditions.

Crooked toes is similar in occurrence and genetic determination to a number of traits in other organisms which have been categorized as aberrant polymorphs. The nature of their genetic determination and wide distribution in populations of cross-fertilizing organisms indicates an association with adaptive potentials in those populations. The occurrence of the characteristics in populations at low frequencies is associated with disarrangements of balanced genetic systems which are oriented and maintained by natural selection.

The following study was designed to enlarge the understanding of the genetic mechanisms controlling crooked toes. A number of strain and breed crosses have been made to obtain data for the F_1, F_2, and backcross generations. The incidence of crooked toes is compared between different crosses and the effects of genetic and non-genetic factors that modify their expression are evaluated.

Figure 1. White leghorn chick with crooked toes.

LITERATURE REVIEW

During the development of the science of Genetics a number of heritable traits have been reported whose behaviour under selection had little apparent connection with a Mendelian interpretation of inheritance. Lerner (1954) has classed such traits as phenodeviants; others (Dubinin, 1948) have described them as aberrant polymorphism. One of the more detailed early investigations was made by Wright (1934a) on otocephaly in the guinea pig. He described it as a trait with variable manifestation involving the reduction of head parts from a very slight decrease in the size of the lower jaw to a virtual suppression of cephalization. It was found to be prevalent at a low incidence (.05%) in guinea pig populations and to be determined by a number of genes which lacked dominance. He concluded that complete dominance of the trait was not possible. In one line which reached a 27% level of incidence, he assumed a dominant mutant was present.

Wright (1934, b and c) found a similar genetic mechanism to exist in the control of polydactyly in guinea pigs. The trait was also prevalent at a low incidence and was characterised by: genetic determination by a number of genes none of which showed dominance; a variable response in crossing to different strains; the presence of physiological thresholds affecting its expression; and increased incidence of expression with unfavorable environmental conditions. He believed it was a polygenic trait exhibiting blending inheritance which was affected by physiological thresholds. A similar behaviour of polydactyly in mice was reported by Murray (1932), Holt (1945), Holt and Wright (1946), and Chase (1951). Murray postulated that genetic control was determined by a dominant gene and a number of modifiers. On the other hand, Chase considered the trait to be composed of several genes, none of them dominant, which were strongly influenced by a physiological threshold.

One of the more extensively studied genetic complexes in Drosophila melanogaster is that of abnormal abdomen (Sobel, 1952). This trait was present in a Dichaete strain which he established from a strain exhibiting asymmetrical abnormalities of the head, thorax, and abdomen during the pupal stage. During selection for abnormal abdomen some inbreeding was practised. In one strain, selection was able to increase incidence from 4.4% to 28 - 31%. This apparently was the selection limit. When reverse selection was practised, no reduction in incidence occurred. In another Dichaete strain, selection increased the incidence to 39%. Incidence was affected by temperature and time of hatching. When crossed into other stocks, the trait exhibited irregular dominance. He concluded that abnormal abdomen genes are present as balanced polygenic systems involving several chromosomes. The expression of the trait is increased in the presence of Dichaete. Selection can increase incidence when Dichaete is present, until homozygosity of the genes determining this trait is reached.

Another example in Drosophila is podoptera (Goldschmidt, Hannah, and Piternick, 1951). This trait has a polygenic basis and is found at a low incidence in many strains. The behaviour of this trait is similar to that of abnormal abdomen. Donald (1949) gives evidence of a complicated genetic structure for a tail abnormality, kinky tail, in pigs that is apparently the same in its major features as the above traits. There are also some interesting characters in plants such as rogue peas (Bateson and Pellew, 1920; Renard, 1930) whose genetic structure may be related to the above traits described in animals.

Two important studies of this type of characteristic, in widely divergent material, have resulted in essentially the same independently formulated interpretation of experimental data. The first of these studies was completed by Dubinin (1948) on extra wing venation in Drosophila. The trait was demonstrated to be widely distributed in a number of wild populations of D. melanogaster and three other species of Drosophila. Although

a seasonal cycle of fluctuation in incidence occurred, it remained at an average low level of 0.29%. Selection and inbreeding were effective in increasing the incidence and degree of expression of this trait. The majority of the selected lines showed the trait within five generations but in one line it did not appear until the twenty-second generation of brother-sister matings. When lines were crossed, the incidences in the offspring were unpredictable. Genetically, the trait was characterised by plastic semi-dominance, incomplete penetrance, and a polygenic system organised into gene blocks within the second chromosome.

The second investigation was on the crooked toes defect (CT) in chicken by Hicks (1953), and Hicks and Lerner (1949). This trait has the same essential features as that of extra wing venation. It is widespread at a low incidence and expression in poultry flocks; with selection the trait can be fixed; inbreeding in the absence of selection will increase CT incidence; it is variable in expression, so much so that the results of individual matings are unpredictable; as incidence of CT increases, so does the degree of expression; and it is a polygenic trait characterised by a varying threshold for expression, incomplete dominance, and incomplete penetrance.

The theoretical interpretation of the results of these experiments has received its fullest treatment by Lerner (1954) who incorporated the interpretations of Dubinin and Hicks into a larger and more speculative theory of genetic homeostasis. This theory assumes that a population of cross-fertilizing organisms has self-regulating properties which enable it to balance its genetic composition and to resist sudden changes in environment. These properties are not simply the substitution at individual loci of less favorable alleles by more favorable ones but include the integrative abilities of a population by shifting gene frequencies and gene arrangements to adapt to changing environmental conditions. These properties have evolved under natural selection. The genetic mechanism which best fits this theory involves an

an obligate degree of heterozygosity in most individuals.

In support of this theory, Lerner has drawn upon several other important lines of investigation that have been instrumental in demonstrating genetic properties in populations that transcend those in individuals. Waddington (1942) has demonstrated that cross-fertilizing organisms have the power of regulating their development (canalization) which produces a uniformity of phenotypic expression in a population in spite of genetic variability between individuals. The action of natural selection is to favor the average phenotype (stabilizing selection) with the elimination of extreme phenotypes (Schmalhausen, 1949). Heterozygosity best explains greater fitness in the average individual by regulating his ontogeny to remain within the normal bounds of development.

Organised and balanced systems of polygenes have been described by Mather (1941, 1943, and 1953; Wigan and Mather, 1942; Wigan, 1944) which require a heterogeneous condition for optimum fitness in natural populations. They are based on two types of balancing mechanisms, both controlled by natural selection. Internal balance refers to the organisation of genes along a chromosome. Crossing over and chromosomal aberrations such as inversions (Dobzhansky, 1947a) will develop and maintain desirable gene arrangements within a chromosome. Relational balance refers to interactions between homologous chromosomes and between chromosomes. This should be the most important balancing mechanism and is demonstrated repeatedly when inbred individuals exhibit greater phenotypic variability than crossbred individuals. An extensive study by Mather and Harrison (1949) who selected for high and low chaetae number in Drosopila melanogaster, indicated that selection with inbreeding upsets the genetic balance of polygenic systems and can be restored either by relaxing selection or by the adjustment of the polygenic systems to a new balance.

The theory with regard to phenodeviants rests on their properties as balanced polygenic complexes. Most individuals in a population possess balanced genotype and are, therefore,

phenotypically normal. Nevertheless, a few individuals in every generation fall below a threshold of obligate heterozygosity and through unbalance of the polygenic system are unable to regulate themselves along a normal developmental pattern.

MATERIALS AND METHODS

Birds from three lines of stock were used in the experiment. A small number of fertile eggs from the University of California CT line were shipped to the University of British Columbia in the early spring of 1954. This line was derived from the Single Comb White Leghorn (SCWL) production flock at that institution. The CT line has been a pure CT breeding line since 1950 (one chick out of 146 was classified as normal at time of hatch in 1953).

The second line came from the UBC SCWL production flock. This strain has been established for over 20 years and has been essentially closed since then as far as can be determined. The flock is reproductively inefficient and a mediocre producer. Selection in the SCWL flock has been toward improvement of the production index with some selection pressure for egg size. The third line came from the UBC New Hampshire (NH) production flock which was developed from a combination of several strains in the early mid-forties. The NH flock has been developed as a dual purpose strain, with approximately equal selection pressure applied for the improvement of both meat and egg production. The flock is reproductively efficient.

There was a very low incidence of CT (Table I) in the UBC production flock at the time of hatch in the first two years that the trait was recorded. Nevertheless, in the 1953-54 season there was a significantly greater incidence in the SCWL flock than in the NH flock. The differences are reduced in the following season although the SCWL flock again has a higher incidence of CT. While the effects of the two selection programs are difficult to assess regarding their effects on the CT complex, the broader heterogeneity and the cancelling effects of a dual selection program in the NH flock may conceivably lead to a better balanced flock genotype.

There were no CT birds present at hatch in the dam families from which birds were taken to mate with the California CT line. All matings made in the course of the experiment are

Table I

Incidence of CT among hatched chicks in the University of British Columbia production flocks.

Season	Breed	Chicks hatched	CT at hatch	% incidence
1953-54	SCWL	1547	29	1.87 **
	NH	1518	10	0.66 **
1954-55	SCWL	1470	4	0.27
	NH	1482	0	0.00

** The difference in CT incidence between breeds is statistically significant at the .01% level.

shown in Table II. Three breeding pens were made up with the parental birds in the fall of 1954, each headed by a sire from one of the lines used in the experiment. Each pen contained five dams (only four were available from the CT line) from each of the three lines. Where possible dams within a pen were unrelated but each dam had full sib in each of the other two pens.

Within a mating pen comparison of the results between mating categories was based on the difference between half-sib groups. Reciprocal matings occurred between each strain and breed crossed. Thus genotypic differences were minimized between mating categories permitting the maximum effect of the CT complex to be expressed. The mating design also would permit the detection of sex-linkage and maternal effects if these characteristics were present.

The CT line dams were socially dominated by the other birds in the parental matings to such an extent that they had to be housed separately if they were to survive. Similarily, the NH dams dominated the CT sire sufficiently to prevent successful matings. Consequently, the three sires were housed in individual cages and the parental matings were conducted with an artifical insemination program.

In the fall of 1955, four breeding pens were made up with F_1 birds, one from each of the reciprocal matings of the CT line with the SCWL line and the CT line with the NH line. Table II indicates the phenotype and the line of origin of the birds in each breeding pen. It will be seen that the mating structure of each pen was similar to that in the parental mating, that is, each male was mated with three categories of females with a maximum of five dams in each category. In these matings there were three shifts of males to each pen, so that each dam was mated to an F_1 straight toe (ST) sire, an F_1 CT sire, and a sire from one of the parental lines. Note that the backcross P_1 CT sire in group 12 (Table II) is the same sire as that in group 14.

Table II

Mating design of the CT experiment. Beneath each sire is the designation of each of the three classes of dams with which he was mated. In the F_1 matings, the parents of the birds are indicated by the numeral and letter in parenthesis.

Parental matings:

1. CT ♂	2. SCWL ♂	3. NH ♂
a. CT ♀♀	a. CT ♀♀	a. CT ♀♀
b. SCWL ♀♀	b. SCWL ♀♀	b. SCWL ♀♀
c. NH ♀♀	c. NH ♀♀	c. NH ♀♀

F_1 matings:

4. F_1 ST ♂ (1.b)	5. F_1 ST ♂ (2.a)	6. F_1 ST ♂ (1.c)	7. F_1 ST ♂ (3.a)
a. F_1 ST ♀♀ (1.b)	a. F_1 ST ♀♀ (2.a)	a. F_1 ST ♀♀ (1.c)	a. F_1 ST ♀♀ (3.a)
b. F_1 CT ♀♀ (1.b)	b. F_1 CT ♀♀ (2.a)	b. F_1 CT ♀♀ (1.c)	b. F_1 CT ♀♀ (3.a)
c. P_1 SCWL ♀♀ (2.b)	c. P_1 CT ♀♀ (1.a)[1]	c. P_1 NH ♀♀ (3.c)	c. P_1 CT ♀♀ (1.a)
8. F_1 CT ♂ (1.b)	9. F_1 CT ♂ (2.a)	10. F_1 CT ♂ (1.c)	11. F_1 CT ♂ (3.a)
Dams:- same as in 4a, b, and c.	Dams:- same as in 5a, b, and c.	Dams:- same as in 6a, b, and c.	Dams:- same as in 7a, b, and c.
12. P_1 CT ♂	13. P_1 SCWL ♂	14. P_1 CT ♂	15. P_1 NH ♂
Dams:- same as in 4a, b, and c.	Dams:- same as in 5a, b, and c.	Dams:- same as in 6a, b, and c.	Dams:- same as in 7a, b, and c.

1. In mating 5.c. one of the females is the dam of the males with which she is mated.

The incubated eggs which failed to hatch were broken open to determine the cause of death. In those embryos which died after the twelfth day of incubation, the sex and presence or absence of CT was recorded. Day old chicks were pedigreed and presence and grade of CT was recorded. At 10 weeks of age, all birds were again handled recording sex and presence and grade of CT. In the crosses to the NH line an attempt was made to identify color genes which might indicate linkage between a part of the CT complex and a single dominant gene. Birds dying before the tenth week were autopsied and cause of death and sex determined.

RESULTS

CROOKED TOE INCIDENCE

CT incidence has been measured by combining the incidence among embryonic dead (13-21 days of incubation) and hatched chicks. Embryos which died before thirteen days of incubation were not included because the development of the CT character is not expressed before that time (Hicks 1953). The combined incidence is probably the most reliable indicator of the true genetic picture since it includes more zygotes than either the embryonic dead or hatched chicks alone. Further, up to hatching time the zygotes have been living under the most uniform external conditions possible. Thus data obtained during this period of the life cycle are less subject to environmental modifications.

The incidence of CT in the parental lines and in the F_1, F_2 and backcross generations is presented in Tables III - V and Figs. 2 and 3. The data, summarized at the sire family level, illustrates one of the inherent difficulties as well as one of the important features characteristic of phenodeviants. This feature is the extreme variability between groups in the expression of the CT character. The variability is emphasized when the data are examined at the dam family level. A typical example of this in the F_2 generation is demonstrated in the sire family F_1 CT ♂ X F_1 ST ♀♀ from the parental mating CT ♂ X NH ♀♀. In this family of five dams, the CT incidence ranged from 14.7% in the progeny of the dam family with the lowest incidence of CT to 53.3% in the dam family with the highest incidence. Consequently, it has been desirable to combine the data into large groups (Table VI) for analysis. The four phenotypic classes in the F_1 matings from the same parental line (Table IV) illustrate a lack of correspondence between the phenotype of the parents and the phenotype of the offspring. In the mating of F_1 ST birds, the offspring had a CT incidence of 18.2% while that of F_1 CT birds had a CT incidence of 12.4%. The reciprocal F_1 CT X ST matings produced offspring with a CT incidence of 24 - 25%. Similar comparisons between the F_1 phenotypic classes derived from the other parental lines

Table III

Combined incidence * of CT and expressivity averages in the F_1 generation of crosses between CT, SCWL and NH lines.

Dams	CT sire			SCWL sire			NH sire		
	No. CT/ total	%	Expressivity	No. CT/ total	%	Expressivity	No. CT/ total	%	Expressivity
CT	42/46	91.3	3.65	30/52	57.7	1.70	7/40	17.5	1.15
SCWL	33/178	18.5	1.12	20/195	10.2	1.01	3/121	2.5	1.00
NH	5/178	2.8	1.01	0/175	0.0	1.00	2/80	2.5	1.00

* Combined incidence = incidence among dead embryos (13 - 21 days of incubation) + incidence among hatched chicks.

Table IV

Incidence of CT in the F_2 generation in reciprocal crosses of the CT line with UBC SCWL and NH lines.

CT X SCWL lines	CT ♂ X UBC ♀♀			UBC ♂ X CT ♀♀		
	No. CT/ total	%	Expressivity	No. CT/ total	%	Expressivity
Sire Dams						
F_1 ST X F_1 ST	34/93	36.6	1.87	33/114	29.0	1.57
F_1 ST X F_1 CT	20/54	37.0	1.65	19/84	22.6	1.36
F_1 CT X F_1 ST	50/102	49.0	1.54	55/98	56.1	2.14
F_1 CT X F_1 CT	43/71	60.6	2.07	45/97	46.4	1.96
CT X NH lines						
F_1 ST X F_1 ST	22/121	18.2	1.25	53/161	32.9	1.62
F_1 ST X F_1 CT	21/86	24.4	1.44	4/37	10.8	1.20
F_1 CT X F_1 ST	40/159	25.2	1.18	57/147	38.8	1.81
F_1 CT X F_1 CT	11/89	12.4	1.15	7/27	25.9	1.61

Table V

Incidence of CT in the backcross matings of F_1 birds with the parental lines.

CT X SCWL lines	CT ♂ X UBC ♀♀			UBC ♂ X CT ♀♀		
	No. CT/ total	%	Expressivity	No. CT/ total	%	Expressivity
		P_1 CT ♂			P_1 SCWL ♂	
F_1 ST ♀♀	70/93	75.3	2.81	14/85	16.5	1.12
F_1 CT ♀♀	59/60	98.3	3.61	25/97	25.8	1.12
		F_1 ST ♂				
P_1 SCWL ♀♀	1/109	0.9	1.02			
		F_1 CT ♂				
P_1 SCWL ♀♀	17/84	20.2	1.09			
CT X NH lines		P_1 CT ♂			P_1 NH ♂	
F_1 ST ♀♀	72/80	90.0	---	11/134	8.2	1.03
F_1 CT ♀♀	21/23	91.3	---	2/21	9.5	1.19
		F_1 ST ♂			F_1 ST ♂	
P_1 NH ♀♀	10/113	8.8	1.08			
P_1 CT ♀♀				5/6	83.3	4.00
		F_1 CT ♂			F_1 CT ♂	
P_1 NH ♀♀	10/110	9.1	1.06			
P_1 CT ♀♀				25/25	100	3.55

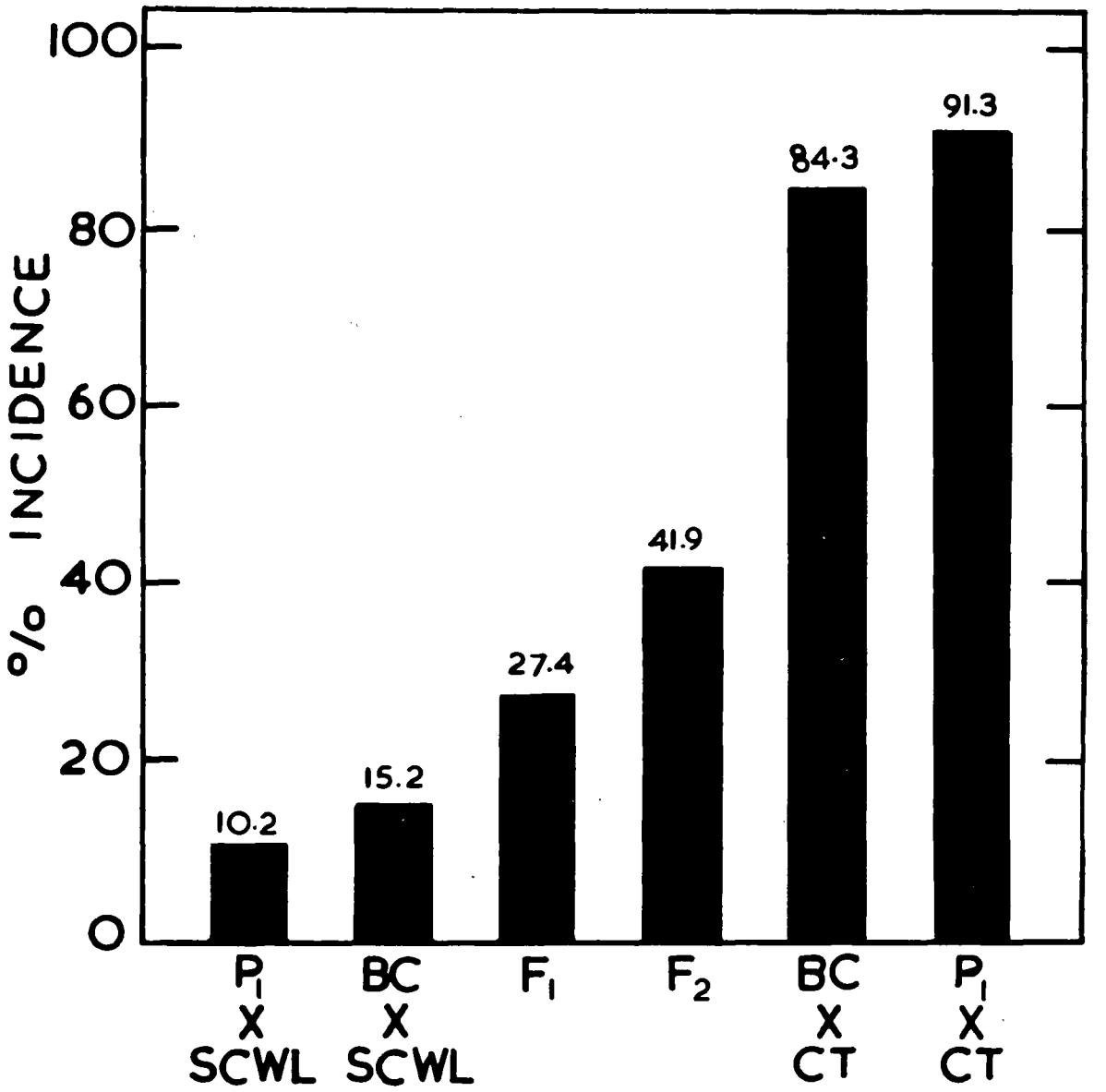

Figure 2. Incidence of CT in reciprocal CT X SCWL matings. Recorded in percent.

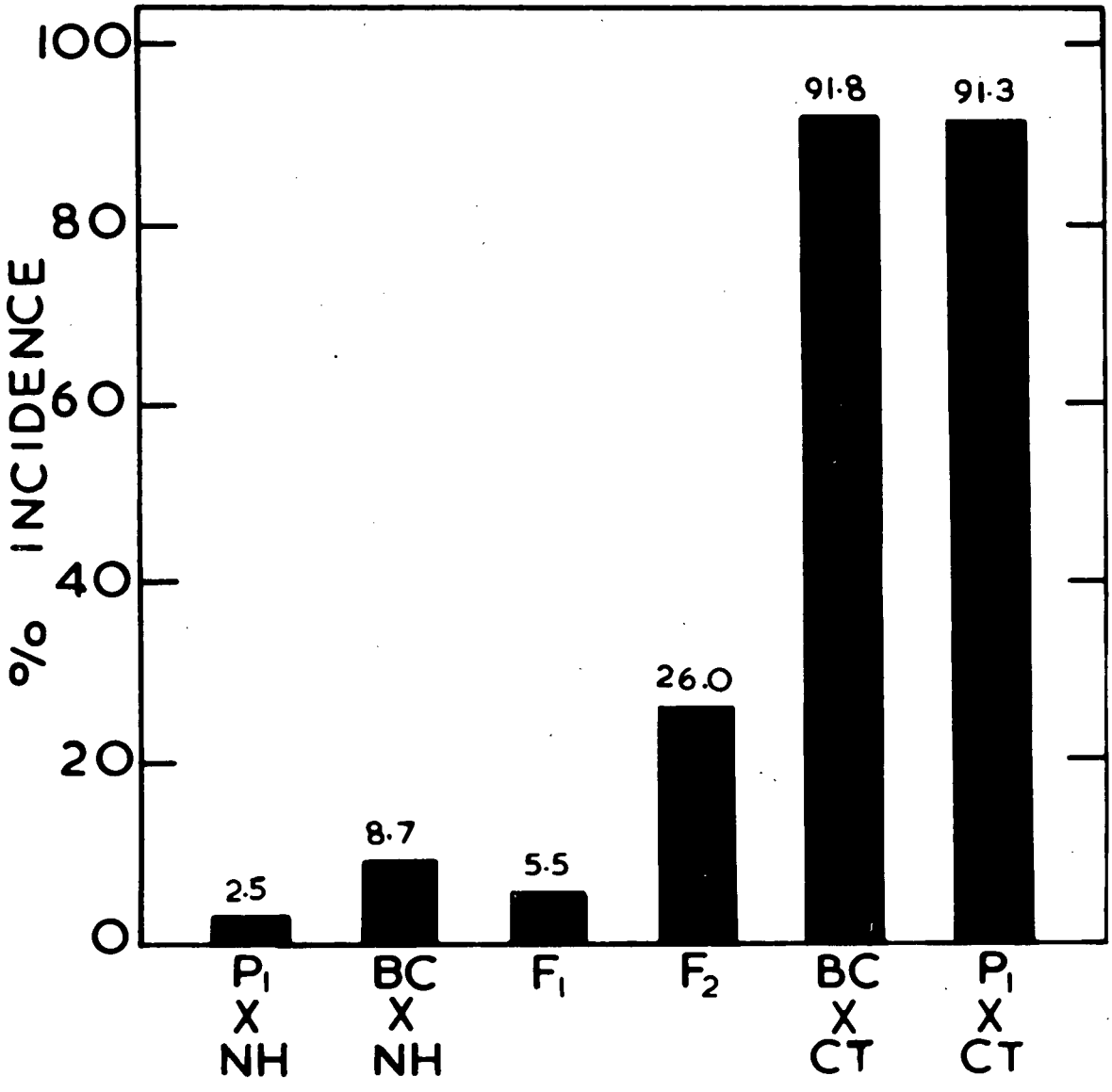

Figure 3. Incidence of CT in reciprocal CT X NH matings. Recorded in percent.

show a lack of correspondence between parent-offspring phenotypes.

The F_1 incidence of CT in the CT X SCWL crosses is intermediate between the two parental lines but approaches more closely the incidence in the SCWL line. A similar situation exists in the combined reciprocal crosses in the CT X NH lines where the incidence in the F_1 progeny is even more closely associated with that existing in the ST parents.

When the F_1 birds were mated interse, the incidence of CT increased in both the strain (CT X SCWL) and the breed (CT X NH) crosses. Although the F_2 incidence in the progeny from the SCWL lines remained higher than in the NH lines, there was proportionately a much greater increase in the latter group.

In the backcross matings of the F_1 progeny to the parental lines, progeny of these matings very nearly approach the CT incidence in the parental line to which they were mated. This tendency is carried to the greatest extreme in the CT X NH F_1 birds backcrossed to the CT parental line. In this case the backcross progeny equal the incidence of crooked toes in the CT line.

Sex-Linkage

Evidence of sex-linkage in the CT character (Hicks, 1953) was indicated for several generations during the development of the CT line in California. No evidence suggesting this relationship was found in the present experiment.

Maternal Effects

An examination of the data between reciprocal matings (Table VI) in the crosses to the SCWL and to the NH lines shows that in the F_1 generation there is a much higher CT incidence in the matings to CT line dams than in the matings to CT line sires. The higher incidence is statistically significant both in the CT X SCWL crosses (chi square = 28.709, $P = < .01$ with 1 d.f.) and in the CT X NH crosses (chi square = 10.874, $P = < .01$ with 1 d.f.).

When the two components, embryonic dead and hatched chicks are examined separately, they both exhibit a higher

incidence of CT in the crosses to the CT line dams (see below).

CT incidence in embryonic dead. F_1 generation.

SCWL ♂ X CT ♀♀	14/17	82.3%	NH ♂ X CT ♀♀	5/6	83.3%
CT ♂ X SCWL ♀♀	21/35	60.0%	CT ♂ X NH ♀♀	3/13	23.1%

CT incidence in hatched chicks. F_1 generation.

SCWL ♂ X CT ♀♀	16/35	45.7% **	NH ♂ X CT ♀♀	2/34	5.9%
CT ♂ X SCWL ♀♀	12/143	8.4% **	CT ♂ X NH ♀♀	2/163	1.2%

** Significant at 1% level

Failure to obtain statistically significant differences in the majority of comparisons is due to the small number of progeny in the separate categories. The evidence leaves no doubt that there is a strong maternal effect contributed by dams from the CT line toward the expression of the CT character in the F_1 generation. A high degree of inbreeding in the CT line (F = .55) is probably the cause of the maternal effect. This could occur provided the CT line dams were genetically unbalanced (relatively homozygous) producing unfavorable environmental conditions within the egg.

In the F_2 generation, progeny descendent from CT X SCWL matings do not exhibit a carry-over of maternal effects from the F_1 generation (Table VI). The progeny descendant from CT X NH matings continue to have a significantly higher CT incidence in the NH ♂ X CT ♀♀ line than in the CT ♂ X NH ♀♀ line (chi square = 14.983, $P = \angle .01$ with 1 d.f.). This difference between the reciprocal parental lines is not supported in the backcross matings where no differences in incidence occur in the backcrosses either to the NH line or to the CT line. Therefore, there may be a carry-over of maternal effects into the F_2 generation from the CT X NH breed crosses although the evidence is inconclusive.

Table VI

Incidence of CT in the P_1, F_1, F_2, and backcross matings in each of the four lines formed in the experiment. Combined data in percent.

Line	P_1 SCWL	BC to SCWL ♀♀	F_1	F_2	BC to CT ♂	P_1 CT
CT ♂ X SCWL ♀♀	10.2	9.3	18.5	45.9	84.3	91.3
		BC to SCWL ♂			BC to CT ♀♀	
SCWL ♂ X CT ♀♀	10.2	21.4	57.7	38.7	not made	91.3
	P_1 NH	BC to NH ♀♀			BC to CT ♂	
CT ♂ X NH ♀♀	2.5	9.0	2.8	20.6	90.3	91.3
		BC to NH ♂			BC to CT ♀♀	
NH ♂ X CT ♀♀	2.5	8.7	17.5	32.5	91.8	91.3

Inbreeding

There are two levels of inbreeding between progenies in the F_2 generation. Matings of the F_1 birds wherever possible were between half sibs which produced progeny with F = .194. In most sire families, however, it was necessary to place at least one full sister to the sire in the breeding pen to obtain a sufficient number of dams. Progeny from full sib matings had an inbreeding coefficient of .388.

Comparisons between dam families within sire families showed that in half the sire families (six out of 12) the progeny with the higher inbreeding coefficient were consistently higher in CT incidence than those with the lower inbreeding coefficient. When the sire families are combined for comparisons between the four classes of F_1 matings, the CT incidence is higher in the more inbred progeny in all lines except CT ♂ X NH ♀♀.

CT incidence in half sibs and full sibs in F_2 generation in percent.

	F = .194		F = .388		Weighted F
CT ♂ X SCWL ♀♀	83/214	38.8	64/108	59.2 **	.259
SCWL ♂ X CT ♀♀	72/183	39.3	16/29	55.2	.216
CT ♂ X NH ♀♀	63/290	21.7	31/165	18.8	.267
NH ♂ X CT ♀♀	39/131	29.8	71/177	40.1	.291
CT X SCWL (combined)	155/397	39.0	80/137	58.4 **	.237
CT X NH (combined)	102/421	24.2	102/342	29.8	.277

** Significant at 1% level.

The difference between the levels of incidence associated with the two degrees of inbreeding in the CT ♂X SCWL ♀♀ line is statistically significant. When the reciprocal parental lines are combined the CT incidence is higher in the full sibs in

both the strain cross and the breed cross. The differences in the CT X SCWL lines remains statistically significant.

If the higher CT incidence in the more highly inbred F_2 zygotes is a phenomenon of inbreeding degeneration, then it would be expected that a lowered hatchability would occur among these zygotes. This does not happen as is shown below.

Hatchability in half sibs and full sibs in F_2 generation.

	F = .194		F = .388	
CT X SCWL	232/318	73.0%	100/147	68.0%
CT X NH	366/450	81.3%	306/374	81.8%

Association with Sex

There was no association of CT incidence with sex evident in the data. Sex ratios were normal in combined data although considerable variation existed between dam families.

Secondary sex ratios in CT experiment, all zygotes combined.

Generation	Males	Females	Sex ratio
F_1	451	458	49.61
F_2	1063	1003	51.45

The relation between CT incidence and sex showed no differences between males and females.

Incidence of CT in:	Males	Females
F_1 generation	13.6%	14.8%
F_2 generation	32.3%	30.2%

In the dead embryos of the F_2 generation, 67.8% of the males were CT and 60.0% of the females were CT. At ten weeks of age, 69 CT birds had died (34 males and 35 females). The data suggest that the expression of CT acts equally on males and females.

Discussion

One of the most striking features of the data is the tremendous variability between the phenotypes of the dams and their offspring. This variability persists to a considerable extent even to the level of comparisons between sire families (note particularily the variability between sire families in Table IV). The performance of the parents gives but a slight indication of what to expect in the performance of the offspring with relation to the transmission of CT incidence (for example, no definitive segregation ratios). This characteristic of the CT trait provides strong evidence of a complex mechanism of inheritance, one that is not amenable to a simple Mendelian analysis.

The data (Table VI) indicate that breed differences exist at least during the first two generations after the combination of the CT genome with that of the UBC SCWL and NH breeds. The differences between the CT incidence in the strain and breed crosses may in part be attributed to different thresholds for the expression of the character. The wider cross to the NH line very likely provides a greater number of heterozygous loci in the F_1 generation. The consequence of this situation would be a tendency toward a higher threshold for CT expression as well as the expression of hybrid vigor. This hypothesis is supported by the relatively low incidence of CT in the F_1 generation of progeny from the reciprocal CT X NH matings (Figs. 2 and 3). Also, hybrid vigor is suggested by a greater hatchability in the reciprocal CT X NH F_1 generation (91.7%) than in the reciprocal CT X SCWL F_1 generation (76.6%).

That the trait is strongly subject to environmental modification is evinced by the effects of the maternal environ-

ment. The maternal effect has its primary influence on phenotypic expression and does not alter the zygotic genotypic potentials for CT expression, for example, the backcrosses in the CT X NH crosses. It reduces the threshold for CT expression so that more zygotes develop the defect than others with equivalent genotypes which develop under more favourable environmental conditions. It is probable that a lower CT incidence would prevail in the F_1 generation barring maternal effects. Even in the presence of maternal effects the F_1 incidence in the CT X NH crosses approaches very closely the incidence encountered in the NH parental strain. In fact, in the CT ♂ X NH ♀♀ cross the incidence in the F_1 generation was 2.8% (Table VI) which is almost identical with the incidence in the pure NH matings (2.5%). The evidence indicates that the CT genes condition different thresholds for expression of the defect. Thus a threshold which would not be exceeded in conditions of optimum environment may be triggered by a suboptimal maternal environment or other deleterious environments as occurred, for example, in the temperature experiments in the UBC Experimental lines. (Data unpublished).

The effect of temperature on CT incidence, in percent.

	High temperature 101.25°F		Low temperature 98.0°F	
	Embryonic	At hatch	Embryonic	At hatch
Inbred	41.8	4.2	13.0	0.0
Non-inbred	34.3	0.0	7.5	0.0
Crossbred	33.3	0.0	0.0	0.0

The effect of inbreeding is apparently to increase CT incidence independently of inbreeding degeneration. Statistical analysis of the data suggests that the assumption that chance fluctuation in gene frequencies of specific CT determining genes (genetic drift) alone is insufficient to account for the differences between different levels of inbreed-

ing. The evidence on this point is important in that it indicates that the CT character is influenced by homozygosity per se. Thus it is demonstrated that the expression of CT is not the result of inbreeding degeneration but rather both phenomena are the result of the same underlying cause. That is, both are influenced by increasing homozygosity in an organism that depends upon a highly heterozygous condition for optimum fitness.

The combined data (Figs. 2 and 3) for the F_1 and F_2 generations indicate the CT genes to be incompletely dominant. The maternal effect indicates a variable penetrance in the action of CT genes. Further evidence of this action may be found within the F_2 generation when all matings from the four parental crosses are combined on the basis of the parental phenotypes (see below).

F_1 ST X F_1 ST	142/489	29.0%
F_1 ST X F_1 CT	266/778	34.2%
F_1 CT X F_1 CT	106/264	40.2%

There is a rough correspondence between the phenotype of the parents and the CT incidence in the offspring but the high incidence in the ST X ST matings relative to that in the CT X CT matings indicates variable penetrance. A more striking example of variable penetrance occurred in the California CT line in 1949 when the progeny of ST representatives of the CT positive selection line had as high an incidence of CT as occured in the generation from which the ST parental birds came (Hicks, 1953).

The maternal and inbreeding effects indicate the incidence of CT is affected by varying threshold levels caused by gene-environment interactions and varying degrees of homozygosity. The fact that the incidence of CT in the F_1 generation (Figs. 2 and 3) lies between the incidence in the parental lines provides evidence of a partially quantitative genetic determination of the CT trait. If it is assumed that the higher level

of CT incidence in the F_2 generation is primarily due to a lower threshold resulting from segration and the production of a greater number of homozygous loci, then the quantitative characteristic of the trait becomes more evident. Further evidence is found in the backcross matings to the ST lines where the progeny exhibit a CT incidence intermediate to that in the parental lines. However, the CT incidence approaches more closely that in the parental ST lines.

The best hypothesis which fits the data is one which assumes a number of genes which condition the development of the extremities of the posterior limb. These genes, which may be recessive, are present in most if not all populations of chickens and they are amenable to selection with inbreeding. Thus, in each generation of a non-selected population there will be a certain number of individuals which have one or more loci in the homozygous state and which will exhibit the trait phenotypically. Selection for increased frequency of the genes leads to the accumulation of a greater proportion of homozygous loci and consequently to a higher incidence and expression of the phenotype.

Different populations may carry different constellations of genes at the CT loci. This would account for the variable incidences in the F_1 generations which were derived from different strain and breed crosses with the CT line. When these F_1 birds are backcrossed to a parental line with low incidence, it would be expected that the incidence would be approximately equal to that in the parental line because the backcross progeny would be homozygous only at those loci which received genes from the low incidence P_1 line.

Essentially the same line of reasoning can be applied to an explanation of the evidence in the backcross to the CT line. F_1 birds carry a large sampling of CT genes, a proportion of which are in the homozygous condition. When reintroduced into the CT genome, all of those loci which were homozygous will probably remain so and at least one half of the

loci which were heterozygous in the F_1 birds will become homozygous in the backcross zygotes. The presence of closely linked gene constellations with predominately CT genes which very likely occur in the CT parental line, will tend to increase the proportion of loci which become homozygous over that estimated above. Thus a considerably elevated incidence of CT will occur in such backcrosses.

The original hypothesis can be extended to account for more aspects of the data by certain assumptions relative to the quantitative aspects of the number of homozygous loci. During the course of the original selection for the increased incidence of CT (Hicks, 1953), the pattern of increases in the early generations followed a roughly quantitative response to selection (1945-46). The intermediate generations did not (1947-48). On the basis of the selection differential the increases due to selection in the intermediate generations were considerably greater than expected. Thus, as the number of homozygous loci is increased, the phenotypic expression of CT increases proportionately until a point is reached where the addition of still more homozygous loci produces a geometric increase in incidence. The backcross incidence in the F_1 X CT parental lines is amenable to such an explanation.

EXPRESSIVITY

The CT character was classified into four grades depending upon the degree of its expression, after the method of Hicks (1953). This classification is given below:

Classification	Grade	Curvature
Straight toes	1	none
Slight crooked toes	2	0-45°
Moderate crooked toes	3	45-90°
Severe crooked toes	4	over 90°

Bilateral asymmetry, which is very common in this material, was ignored when assigning a chick to a particular grade in that the foot with the greatest expression of CT was the criterion for classification.

The expressivity classifications were made at the time the chicks hatched. The matings in the F_1 generation (Table VII), with the exception of the CT X CT mating, show that the majority of birds fall within the low grade phenotypes. It is only in the matings where maternal effects are present that the severe CT phenotypes are present (see below).

Mating	No. of chicks in grade			
	1	2	3	4
CT ♂ X SCWL ♀♀	131	8	4	0
SCWL ♂ X CT ♀♀	19	11	1	4
CT ♂ X NH ♀♀	161	2	0	0
NH ♂ X CT ♀♀	32	1	0	1

On the other hand, in the CT X CT mating the greatest proportion of CT birds have severe phenotypes (85.7%). In the matings where the CT line birds were crossed with the UBC SCWL and NH line birds and the matings within the UBC lines, there is essentially

Table VII

Expressivity of CT trait. Chicks grouped according to grade of expression (see text). Includes all hatched chicks.

Mating category	Total No. chicks	No. chicks in grade 1	2	3	4	% chicks in grade 1	2	3	4
P_1 combined reciprocal									
CT X CT	28	2	1	1	24	7.1	3.6	3.6	85.7
CT X SCWL	178	150	19	5	4	84.3	10.7	2.8	2.2
CT X NH	197	193	3	0	1	98.0	1.5	0.0	0.5
SCWL X SCWL, SCWL X NH, NH X NH	460	459	1	0	0	99.8	0.2	0.0	0.0
F_1 combined recprocal									
CT X SCWL									
F_1 X F_1	552	354	58	44	96	64.1	10.5	8.0	17.4
F_1 X P_1 SCWL	307	297	1	3	6	96.7	0.3	1.0	2.0
F_1 X P_1 CT	130	22	18	17	73	16.9	13.8	13.1	56.2
CT X NH									
F_1 X F_1	714	563	54	22	75	78.8	7.6	3.1	10.5
F_1 X P_1 NH	342	328	9	2	3	95.9	2.6	0.6	0.9
F_1 X P_1 CT	99	8	21	24	46	8.1	21.2	24.2	46.5

a decreasing proportion of chicks with high grade phenotypes.

In the F_2 generation there is an increase in the proportion of birds with CT phenotypes. In the progeny from the reciprocal CT X SCWL parental matings, 15.7% of the F_1 chicks exhibited CT phenotypes compared with 35.9% in the F_2 generation while the weighted average expressivity increased from 1.22 to 1.78 (Fig. 4). A similar increase is present in matings of offspring from the reciprocal CT X NH parental matings (Fig. 5). It is interesting to note that the shift toward greater expressivity is apparently not progressive in this experimental material.

During the development of the CT line in California, the trait showed a progressive increase in CT incidence coupled with a progressive shifting in expressivity from low grade phenotypes, through the intermediate grades to the severe CT phenotypes. The lines from the strain and breed crosses show increased numbers of birds in the three grades representing phenotypic expression of the trait. Instead of the greatest proportional increase occurring in the intermediate phenotypes, it occurred in the severe CT phenotype.

This difference in the action of the CT gene complex in relation to expressivity may be explained if it is a polygenic system composed of groups of gene blocks or aggregates. During the development of the CT line, a gradual change occurred as the CT determining genes were increased so that a highly heterogenous system became at least relatively homogeneous for these genes. A number of generations were required for the processes of segregation, gene recombination, and selection, to accumulate within individuals enough CT genes for them to have a high transmitting ability. A further delay in obtaining CT genotypes with a high transmitting potential would occur if crossing over among closely linked gene aggregates was necessary. If this were the case, an important effect of crossing over under continued selection would be the gradual accumulation within closely linked gene aggregates of CT determining genes which would increase their CT potential relative to unselected birds.

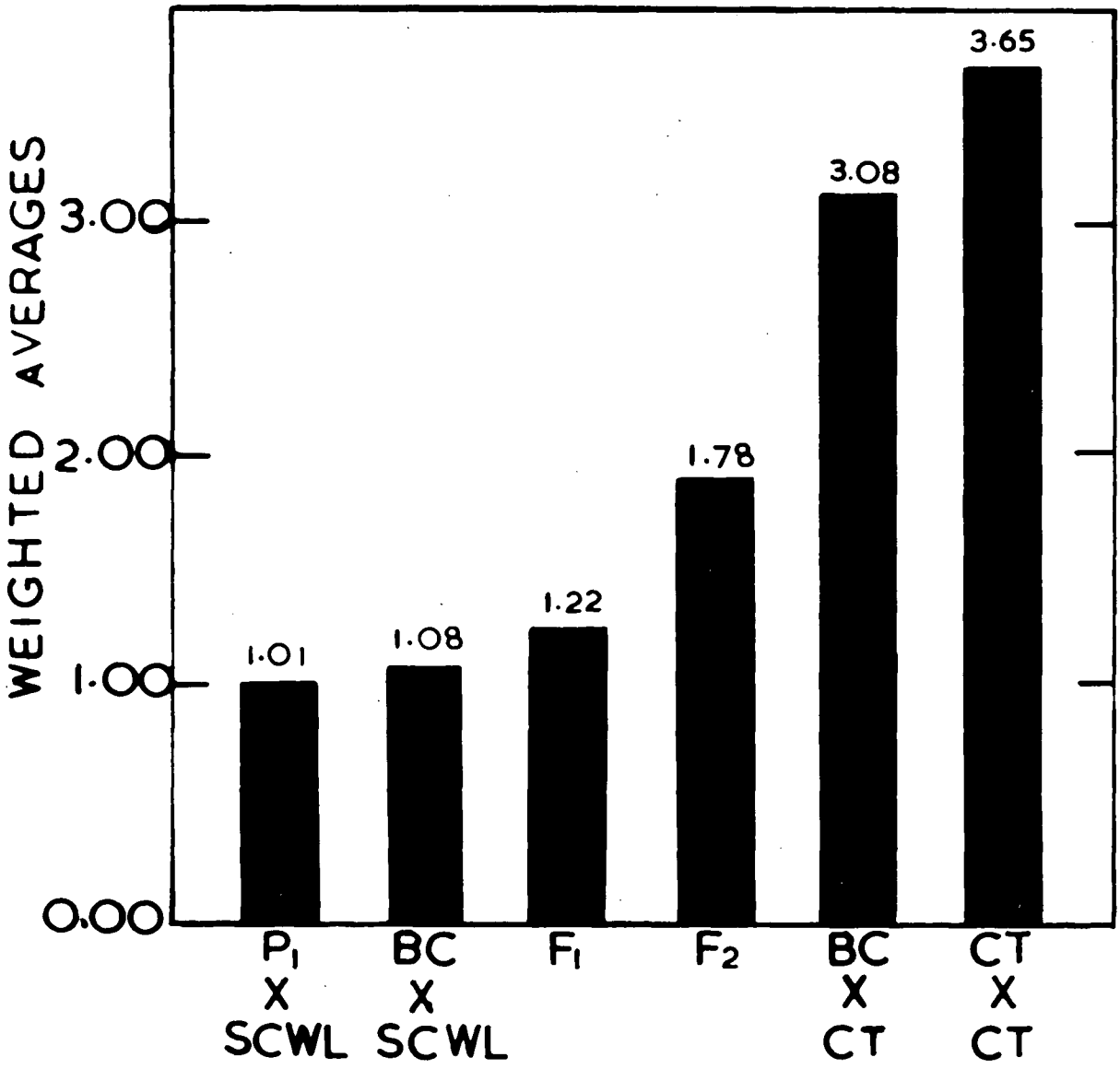

Figure 4. Expressivity in reciprocal CT X SCWL matings. Recorded as weighted average; see text.

Note: Value 1.00 represents ST phenotype.
Value 4.00 represents severe CT phenotype.

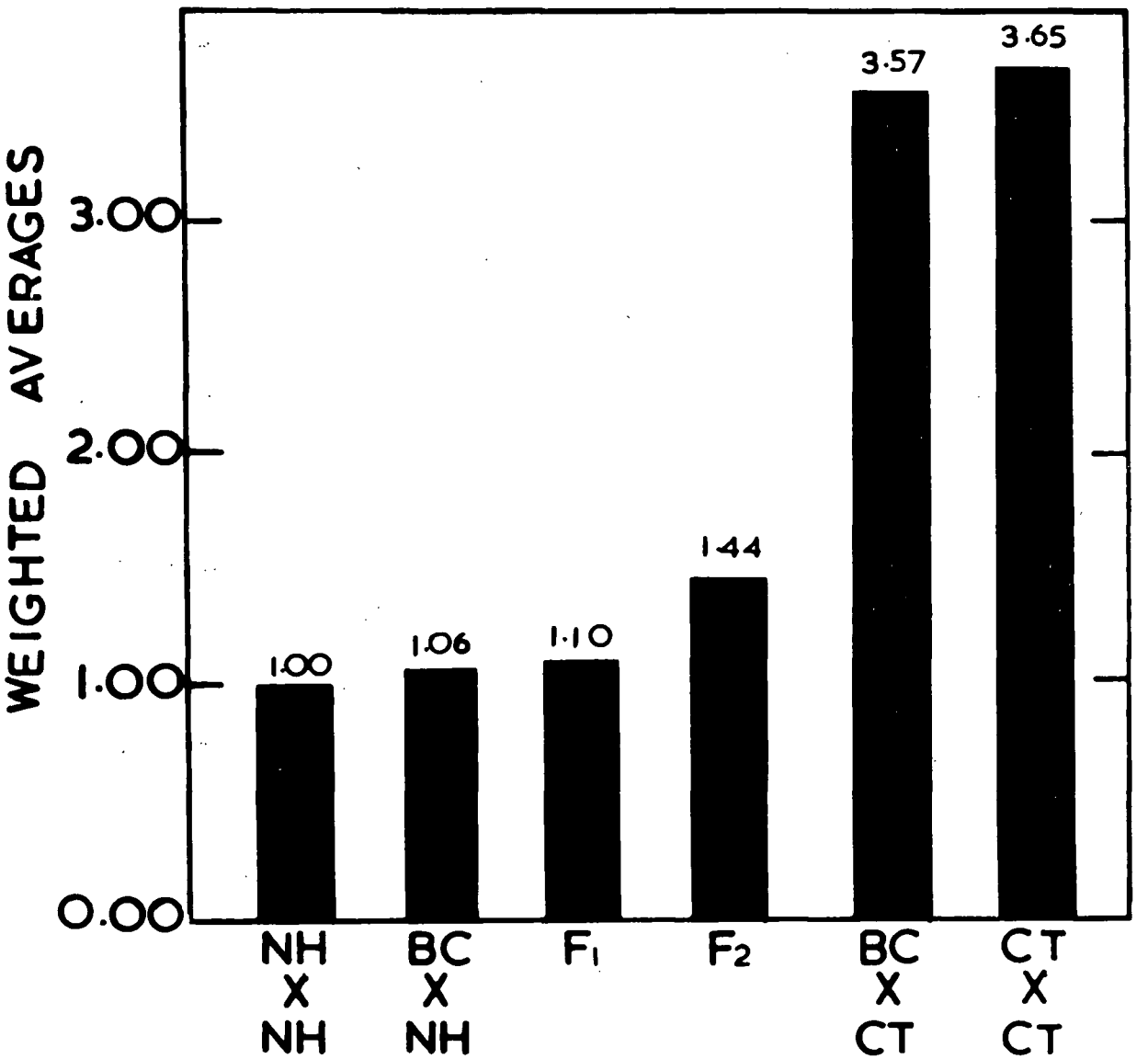

Figure 5. Expressivity in reciprocal CT X NH matings. Recorded as weighted average; see text.

Note: Value 1.00 represents ST phenotype.
Value 4.00 represents severe CT phenotype.

With the introduction of the CT line to UBC stock, a genome with a large number of CT determining loci was combined with one having few CT determining loci. In the F_1 generation, the heterozygosity resulting from strain and breed crosses produces a high threshold for CT expression and minimizes the number of phenotypes showing the trait. The threshold for CT expression is lowered in the F_2 generation by inbreeding and by segregation and recombination of homozygous genotypes which permits a greater incidence of CT phenotypes although the gene frequencies probably remain the same as in the F_1 generation.

The data were combined into a weighted average of the expressivity (Figs. 4 and 5) that permitted comparisons using only a single value to represent all the grades. This average was obtained using the formula:

$$\frac{\text{No. grade 1 chicks X 1 + No. grade 2 chicks X 2 + ... + No. grade 4 chicks X 4}}{\text{Total No. of chicks}}$$

Thus the weighted average value could range from 1.00 if all the chicks were straight toed, to 4.00 if all the chicks were in the severe CT class.

The classification of the expressivity data in Figs. 4 and 5 is the same as that of the CT incidence in Figs. 2 and 3. It was not possible to classify the degree to which dead embryos had developed CT because the expressivity of the CT character would vary from one developmental stage to another. Omission of the dead embryo component from the expressivity data would generally depress the values, particularly in those categories where expressivity is low, when they are compared with Figs. 2 and 3 (recall that embryonic dead and at hatch incidence are combined to give these values). It would not be expected that the omission of this component would seriously affect the relationships between the mating categories within Figs. 4 and 5. These relationships are the same as those in the incidence of CT. In general, there is a very close correlation of expressivity

with incidence. As the CT incidence increases, the expressivity shifts increasing the proportion of birds exhibiting the higher grade phenotype.

ASSOCIATION OF CT WITH FITNESS

Fitness is a very general term usually associated with factors such as fertility, family size, vigor, and survival ability. In chickens, hatchability of fertile eggs is one of the most useful single measures of fitness.

Co-adaptation

All the major mating categories were tested to determine the relation between the CT character and fitness. This was done by comparing the differential liveability of CT and ST zygotes on the basis of the proportion hatching against the proportion dying during incubation. If ST zygotes are considered co-adapted with fitness, and CT zygotes are compared with them, then the CT zygotes can be evaluated regarding co-adaptedness. If proportionately more CT zygotes die than ST zygotes, the evidence would indicate they were not co-adapted. If the proportions are the same, no relationship is evident unless they may be termed equally co-adapted. If proportionately fewer CT zygotes die, they would be considered co-adapted.

In the parental matings (Table VIII) there was evidence of co-adaptation of CT incidence with embryonic liveability in the CT X CT mating. This condition arose in the California CT line during the selection experiment (Hicks, 1953). On the other hand, in the SCWL X SCWL mating the CT incidence in the embryonic dead is significantly higher (chi square = 29.531, $P < .01$ with 1 d.f.) than that in the hatched chicks which indicates that in this case there is no co-adaptation of CT defect with embryonic liveability. In the NH X NH matings all the CT zygotes died during incubation but the number of CT zygotes was too small to obtain statistical verification that co-adaptation was not present in this mating.

The reciprocal parental strain and breed crosses to the California CT line (Table VIII) indicate no co-adaptation occurred between embryonic liveability and the CT character. In each cross the incidence of CT in the embryonic dead was significantly higher than in the hatched chicks.

In over half of the sire families from F_1 matings nine out of 16) a significantly higher CT incidence among embryonic dead occurred. Three of the remaining matings, (F_1 ST ♂ X F_1 ST ♀♀ and F_1 ST ♂ X F_1 CT ♀♀ from CT ♂ X SCWL ♀♀, and F_1 ST ♂ X F_1 CT ♀♀ from CT ♂ X NH ♀♀), had an equal or lower incidence of CT in the embryonic dead. These matings suggest that co-adaptation of CT incidence with embryonic liveability has occurred. If, however, the F_1 matings are combined so that all four classes of matings from each parental mating have a single value, then the F_1 X F_1 matings of CT ♂ X SCWL ♀♀ parental mating have a significantly higher CT incidence in the embryonic dead (chi square = 17.250, $P = < .01$ with 1 d.f.) than in the hatched chicks.

The backcross matings to the SCWL and NH lines (Table IX) give no indication of co-adaptation occurring. The embryonic dead have a consistently higher incidence that is statistically significant. This is contrasted in the backcross matings to the CT line where the embryonic dead either do not have significantly higher incidence of CT or have a lower incidence.

It seems likely that the CT trait is associated with a number of modifiers affecting fitness. In normal poultry flocks these modifiers are positively associated with ST phenotypes and negatively associated with CT phenotypes. A high embryonic mortality of CT zygotes in these flocks is indicated in the parental matings of the pure UBC lines (Table VIII). In the California CT line, fixation of the trait has resulted in a reorganisation of fitness modifiers so that they became positively associated with fitness. Positive association became possible with segregation and recombination recurring over a number of generations.

When the CT line was combined with the SCWL and NH lines,

Table VIII

Comparison of CT incidence in embryonic dead (13 - 21 days) with hatched chicks for evidence of co-adaptation of the CT character with fitness. F_1 and F_2 generations.

P_1 mating category		F_1 mating category		Embryonic dead		Hatched chicks	
Sire	Dams	Sire	Dams	No. CT/ total	%	No. CT/ total	%
CT	X CT			16/18	88.9	26/28	92.8
SCWL	X SCWL			17/73	23.3	1/121	0.8**
NH	X NH			2/10	20.0	0/70	0.0
CT	X SCWL			21/35	60.0	12/143	8.4**
SCWL	X CT			14/17	82.3	16/35	45.7*
CT	X NH			3/13	23.1	2/163	1.2**
NH	X CT			5/6	83.3	2/34	5.9**
CT	X SCWL	ST	X ST	2/15	13.3	32/78	41.0
		ST	X CT	1/3	33.3	19/51	37.2
		CT	X ST	30/37	81.8	20/65	30.8**
		CT	X CT	15/16	93.8	28/55	50.9**
SCWL	X CT	ST	X ST	15/35	42.9	18/79	22.8*
		ST	X CT	7/15	46.7	12/69	17.4*
		CT	X ST	18/22	81.8	37/76	48.7*
		CT	X CT	13/18	72.2	32/79	40.5*

Table VIII - continued

P_1 mating category		F_1 mating category		Embryonic dead		Hatched chicks	
Sire	Dams	Sire	Dams	No. CT/ total	%	No. CT/ total	%
CT X NH		ST X ST		4/10	40.0	18/111	16.2
		ST X CT		2/8	25.0	19/78	24.4
		CT X ST		31/45	68.9	9/114	7.9**
		CT X CT		6/17	35.3	5/72	6.9**
NH X CT		ST X ST		13/23	56.5	40/138	29.0**
		ST X CT		1/2	50.0	3/35	8.6
		CT X ST		6/8	75.0	51/139	36.7
		CT X CT		1/1	100	6/26	23.1

* Significant at the 5% level.
** Significant at the 1% level.

Table IX

Comparison of CT incidence in embryonic dead (13 - 21 days) with hatched chicks for evidence of co-adaptation of the CT character with fitness. Backcross matings.

P_1 mating category		Backcross mating category		Dead embryos		Hatched chicks	
Sire	Dams	Sires	Dams	No. CT/ total	%	No. CT/ total	%
CT X SCWL		F_1 X P_1 SCWL		14/20	70.0	4/173	2.3**
		P_1 CT X F_1		21/23	91.3	108/130	83.1
SCWL X CT		P_1 SCWL X F_1		33/48	68.8	6/134	4.5**
CT X NH		F_1 X P_1 NH		10/20	50.0	10/203	4.9**
		P_1 CT X F_1		23/25	92.0	70/78	89.7
NH X CT		P_1 NH X F_1		9/16	56.2	4/139	2.9**
		F_1 X P_1 CT		9/10	90.0	21/21	100.0

** Significant at the 1% level.

the zygotes from each of these crosses showed a negative association with fitness. Apparently, in the F_1 generation, a haploid set of chromosomes from the CT line does not contain sufficient modifiers to maintain a positive association of CT with fitness. However, segregation and recombination in the F_1 matings should enable the system of modifiers from the CT line to be largely recovered in some of the families. This is possibly indicated in the progeny of three F_1 sire families.

The backcross matings provide further information about these modifier systems. Whereas in the F_1 matings, on the average, half of the chromosomes in each offspring came from one of the parental lines, in the backcross matings, on the average, three fourths of the chromsomes in the progeny will come from the parental line. Clearly, in these matings a large part of the modifier system in the parental line will be recovered in the backcross progeny. Therefore it would be expected that the progeny from these matings would exhibit the same association of CT with fitness as that in the parental line used in the backcross. The associations of CT with fitness presented in Table IX support this hypothesis.

Correlation of CT Incidence with Hatchability

A comparison of the hatchability of the fertile eggs from the parental matings with that in the UBC production flocks shows that it was much lower in the experimental material.

Hatchability in: (%)	UBC production flock, 1954.	CT experiment, P_1 matings, 1955.
SCWL X SCWL	76.2	58.7
NH X NH	86.8	76.3

These values suggest that stress conditions were present in the experimental material. The hatchabilities in the highly inbred (F = .55) CT X CT mating (50.9%) and the reciprocal UBC breed crosses NH X SCWL (85.8%), indicate that the stress factors could

be acting equally on all the experimental material. Hence it should be safe to assume that uniform external conditions were acting on all the experimental material during development.

The hatchability of F_1 zygotes (Table X) indicate an inverse relationship between hatchability and incidence of CT. The relationships between matings are complicated by the maternal effect which will tend to exaggerate differences and by hybrid vigor in strain and breed crosses which will tend to reduce differences due to CT incidence.

Data from the F_2 generation were subjected to a regression analysis of dam family hatchability on CT incidence. This was made on all F_2 zygotes combined, and on the combined total from each of the reciprocal P_1 lines (see below).

	Regression coefficient	"t"	d.f.
Combined total F_2 zygotes	-0.6238	4.53**	62
CT ♂ X SCWL ♀♀	-0.5449	1.90	16
SCWL ♂ X CT ♀♀	-0.9080	3.93**	16
CT ♂ X NH ♀♀	-0.5050	1.26	14
NH ♂ X CT ♀♀	-0.5749	1.73	10

** Significant at 1% level.

A significant negative regression was present in the combined F_2 data. However, only one line showed a statistically significant regression. There was, however, a consistently negative relationship between the two variables which means that as the CT incidence increases, there is a decrease in hatchability.

The backcross matings to both parental strains in the CT X NH lines (Table XI) provide evidence supporting the regression analysis of the F_2 zygotes. Using chi square analysis,

Table X

Hatchability and liveability (10 weeks) to show association of CT gene complex with fitness. F_1 and F_2 generations.

P_1 mating category		F_1 mating category		CT incidence$_1$		Hatchability		Liveability	
Sire	Dams	Sire	Dams	No. CT/ total	%	No. chicks/ total embryos	%	No. birds/ total chicks	%
CT	CT			42/46	91.3	28/55	50.9	17/23	73.9
SCWL	NH			3/295	1.0	266/310	85.8	218/231	94.4
NH	SCWL								
CT	SCWL			33/170	19.4	143/188	76.1	119/128	93.0
SCWL	CT			30/52	57.7	35/65	53.8	22/28	78.6
CT	NH			5/178	2.8	183/199	92.0	136/139	97.8
NH	CT			7/40	17.5	19/31	61.3	24/27	88.9
CT	SCWL	ST	ST	34/93	36.6	78/98	79.6	73/78	93.6
		ST	CT	20/54	37.0	53/56	94.6	49/51	96.1
		CT	ST	50/102	49.0	65/104	62.5	64/65	98.5
		CT	CT	43/71	60.6	57/82	69.5	50/55	90.9

Table X - continued

P_1 mating category		F_1 mating category		CT incidence[1]		Hatchability		Liveability	
Sire	Dams	Sire	Dams	No. CT/ total	%	No. chicks/ total embryos	%	No. birds/ total chicks	%
SCWL X CT		ST X ST		33/114	29.0	79/128	61.7	65/79	82.3
		ST X CT		19/84	22.6	69/88	78.4	64/69	92.8
		CT X ST		55/98	56.1	79/103	76.7	62/76	81.6
		CT X CT		45/97	46.4	81/103	78.6	74/79	93.7
CT X NH		ST X ST		22/121	18.2	117/129	90.7	106/111	95.5
		ST X CT		21/86	24.4	81/95	85.3	76/78	97.4
		CT X ST		40/159	25.2	115/175	65.7	100/114	87.7
		CT X CT		11/89	12.4	74/101	73.3	67/72	93.1
NH X CT		ST X ST		53/161	32.9	140/167	83.8	133/138	96.4
		ST X CT		4/37	10.8	36/38	94.7	33/35	94.3
		CT X ST		57/147	38.8	145/157	92.4	137/139	98.6
		CT X CT		7/27	25.9	29/31	93.6	26/26	100.0
Combined F_1									
CT X SCWL		F_1 X F_1		299/713	41.9	561/762	73.6	501/552	90.8
CT X NH		F_1 X F_1		215/827	26.0	737/893	82.5	678/713	95.1

1. Includes embryonic dead and hatched chicks.

Table XI

Hatchability and liveability (10 weeks) to show the association of CT gene complex with fitness. Backcross matings. Combined data.

P_1 mating category		Backcross mating category		CT incidence		Hatchability		Liveability	
Sire	Dams	Sires	Dams	No. CT/ total	%	No. chicks/ total embryos	%	No. birds/ total chicks	%
CT X SCWL		F_1	X P_1 SCWL	18/193	9.3	177/232	76.3	159/173	91.9
SCWL X CT		F_1	X P_1 CT	mating not made					
SCWL X CT		P_1 SCWL	X F_1	39/182	21.4**	146/215	67.9**	109/134	81.3
CT X SCWL		P_1 CT	X F_1	129/153	84.3**	135/163	82.8**	117/134	87.3
CT X NH		F_1	X P_1 NH	20/223	9.0**	207/254	81.5**	190/203	93.6
NH X CT		F_1	X P_1 CT	30/31	96.8**	21/39	53.8**	20/21	95.2
NH X CT		P_1 NH	X F_1	13/155	8.4**	140/173	80.9*	132/139	95.0
CT X NH		P_1 CT	X F_1	93/103	90.3**	78/112	69.6*	---	---

* Difference between values to CT and ST parents significant at 5% level.
** Difference between values to CT and ST parents significant at 1% level.

statistically significant increases in CT incidence were accompanied by significant decreases in hatchability.

A very different relationship is present in the backcross matings to both parental strains in the CT X SCWL lines. The backcross to the P_1 CT sire resulted in progeny with a significantly higher incidence of CT than that in the reciprocal backcross to the SCWL line, and also a significantly higher hatchability in the backcross of the P_1 CT sire to F_1 dams than in the backcross of the P_1 SCWL sire to similar dams. It should be noted that the P_1 CT sire that contributed to the high hatchability in the backcross to F_1 dams from the CT X SCWL lines is the same sire which contributed to the opposite relationship when mated to F_1 dams from the CT X NH lines.

In the reciprocal backcrosses to the SCWL line the mating with the higher incidence of CT also has the lowest hatchability. This would indicate that there is nothing within the SCWL line that is contributing to the higher hatchability with high CT incidence in the backcross to the P_1 CT line.

Liveability

The relationship between hatchability to 10 weeks of age and CT incidence are probably similar to that between hatchability and incidence (Table X). They are particularly evident in the F_1 generation. Inspection of the data from the F_2 generation does not show the same definite relation between liveability and CT incidence. This may be due in part to less uniform environmental conditions prevailing after hatching and in part to less variation occurring in the liveability data compared with the hatchability data.

A regression analysis at the dam family level of liveability to 10 weeks on CT incidence showed a significant negative regression was present in the combined total of all F_2 data (regression coefficient = -0.336, "t" = 2.18, P = 0.01-0.05 with 62 d.f.). The most significant aspect of the analysis is the fact that the regression indicates an inverse relationship between

liveability and CT incidence. The liveability of birds with F = .194 was the same as those with F = .388. Therefore, the above values for the negative regression are not biased by inbreeding effects.

Liveability to 10 weeks among the backcross progenies (Table XI) in the CT X NH lines was not associated with CT incidence and remained high (93.6 - 95.2%) in the three classes from which data are available. In the CT X SCWL lines, a comparison between the backcross progenies of the P_1 CT sire and P_1 SCWL sire mated to F_1 dams indicates that the liveability, like CT incidence and hatchability, was also higher in the progeny of the P_1 CT sire.

Discussion

A hypothesis has been presented which postulates a system of modifiers for fitness that is associated with the CT gene complex. In normal poultry flocks the modifier system is negatively associated with fitness and evidence has been presented to substantiate this view. The fixation of the CT trait in the California CT line has been accompanied by a reorganisation of the modifier system for fitness so that it has become positively associated with CT expression.

The three components of fitness that have been evaluated regarding their association with fitness have demonstrated that in most of the data there is a negative association between them and the CT trait. This is true in the two UBC parental lines and throughout the F_1 generation. The F_2 generation indicates that generally at the sire family level there is a negative association of CT with fitness. Of the sixteen F_2 sire families, three indicated that the CT trait had become co-adapted with fitness. The hatchability and liveability data generally indicate a positive association between CT and fitness in these families. Chance mating of F_1 birds carrying many different homologous chromosomes between them from the CT line parents could lead to favorable combinations of the desired modifiers for fitness in the F_2 generation.

The evidence from the backcross matings demonstrate that the CT trait exhibits the same co-adaptive properties with fitness that is present in the parental line entering the backcross. The evidence from the hatchability data is not definitive. In the CT X SCWL lines, the backcross matings to the SCWL line indicate a negative association between hatchability and fitness. The liveability data tend to support this interpretation. On the other hand, the backcross mating to the CT line indicates a positive association of hatchability and liveability with fitness. The hypothesis tends to support these relationships at least in part. The better hatchability and liveability in the backcross to the CT line may be a case of heterosis caused by the parental crosses. Why it should occur in the backcross to the CT line and not to the SCWL line may be the result of chance combining ability between the birds used in the matings. Whether this explanation is sufficient to account for the magnitude of these differences is questionable.

The backcross matings within the CT X NH lines show some very different relationships. The co-adaptive evidence agrees with the assumption that fitness is associated with the CT complex by means of a number of modifiers. The result regarding co-adaptation in these lines is similar to that in the strain crosses. Liveability is good in all backcross matings which should be expected. However, the hatchability data show the exact opposite relationships. It is important to note that the same CT sire was used in both the strain and breed backcrosses. The reasons for this reversal are obscure. Good hatchability in all backcrosses would be expected, but for some inexplicable reason the hatchability is poor in the backcrosses to the CT line.

The importance of modifiers of this type to the evolution of animal populations is considerable. The present hypothesis shows how the rapid changes in a morphological trait may occur while at the same time, underlying physiological properties associated with the trait may be reorganised to maintain a state of optimal adaptation with the environment.

DISCUSSION

One of the main objectives of the present experimental program was to carry out a preliminary investigation of possible linkage relations between components of the CT character and known major genes. The primary target of this phase of the investigation was the sex chromosome because it contained genes which were available for study within the UBC production flocks and also because evidence of sex-linkage was found in 1948 backcrosses during the development of the CT line in California. Unfortunately, due to the interaction of genes determining plumage color patterns in the crosses, the identification of phenotypes and genotypes was impossible and it was necessary to abandon this part of the experiment.

The behaviour of the CT complex from the evidence obtained in this experiment and elsewhere (Hicks, 1953; Hicks and Lerner, 1949) is summarized below:

1. The CT gene complex is present at a very low incidence in the majority of poultry flocks.

2. It is variable in its penetrance, so much so that the level of CT incidence in the offspring from single matings between parents of varying degrees of CT expression is unpredictable.

3. The expression of CT is affected by a physiological threshold based upon obligate levels of heterozygosity.

4. Inbreeding in the absence of selection will increase CT incidence; with selection it can lead to fixation of the trait.

5. Adverse environmental condition will increase the incidence of CT.

6. Correlated with an increase in CT incidence is an increase in the severity of the expression of the trait.

7. In birds unselected for CT there is a negative association between the CT complex and fitness. This can be overcome with selection.

8. The CT trait has a polygenic structure probably composed of a number of genes each with a minor effect.

9. In crossing experiments, the gene complex exhibits semi-dominance and a partial quantitative determination in the expression of the trait.

These characteristics of the behavior of the CT complex are similar to those found in Drosophila with regard to the detailed experiments on podoptera by Goldschmidt, et al (1951), and extra wing venation by Dubinin (1948). A number of the other experiments reported in less detail, cited earlier, also seem to suggest that this type of adaptive polymorphism is to be found in most cross-fertilizing organisms where the optimum adaptive potential is dependent on an obligate level of heterozygosity. Dubinin concluded that the maintenance and behavior of aberrant polymorphic traits could be explained only by assuming that they are related to the adaptive genotypic properties of animal populations. With this interpretation, the traits may be classed as adaptive polymorphism. The adaptive potential is not the polymorphism per se but is a property of the underlying and correlated physiological processes associated with the trait. It might be expected, then, that selection to increase the phenotypic incidence would result in a loss of fitness by changing the most desirable gene combinations determining the underlying physiological processes. The experimental data support this assumption. The liveability to 10 weeks of age in the F_2 generation of individual CT birds was lower (466/527 = 88.4%) than that of ST birds (1484/1592 = 93.2%). This difference is statistically significant (chi square = 12.383, $P = < .01$ with 1 d.f.). Also, there is the negative regressions of hatchability and liveability on CT incidence which support this assumption. It would be an error to assume that the morphological expression of the trait, at least in its slight phenotypic expression, would have a significant effect on the fitness of the birds.

The present experiment provides confirmation that the CT complex exhibits similar behavior when introduced to a different strain of SCWL in a different environment. Also, when the complex is introduced to a heavier, dual purpose breed which is very different from the light, egg production breed of the CT line, there is again a very similar behavior of the CT complex.

The rapidly growing body of evidence from cross-fertilizing organisms demonstrating the more adaptive characteristics of heterozygotes, particularly the work of Dobzhansky (1947a, 1947b, and 1948) and Dobzhansky and Levene (1951), which leaves little doubt of the fundamental importance of the genotypic state to animal populations. Conversely, animal breeders are only too aware of the dangers of inbreeding with regard to the fitness or adaptedness of their stock. It is apparently the greater metabolic plasticity associated with heterozygosity which is the most evident of the physiological properties connected with the CT complex.

Lerner (1954) describes phenodeviants, that is aberrant polymorphic traits, and their expression as being identified with inbreeding degeneration. It has been shown that CT indicence was higher in the more highly inbred F_2 zygotes without there being any evidence of inbreeding degeneration (using hatchability as the criterion). It would seem that the CT complex is affected primarily by heterozygosis of the genes governing the complex and probably secondarily by the totality of relationships between genes in the genotypes as evinced by the different results from strain versus breed crosses with the CT line. This could permit a measurable difference to be observed in CT incidence between birds differing in coefficients of inbreeding under the following conditions: if a relatively large degree of homogyzosity was present in the CT determining loci; and if, in the residual genotype, a comparatively high degree of heterozygosity prevailed so that other components of fitness remained unaffected. A genome with a heavy concentration of CT determining genes has been combined with that of a different breed, that is, the NH

breed, which exhibits the elements of fitness very well. The progeny coming from this cross would be expected to have very heterozygous genotypes. The F_1 generation consequently exhibited a very low incidence of CT due to a very high threshold for the expression of CT. In the F_2 generation the CT genes were present at essentially the same frequency as in the F_1 progeny. However, a comparison of the CT incidence between full sib matings and half sib matings showed that it was higher in the former matings. The greater homozygosity in the more inbred matings depressed the threshold for CT expression more so in the full sib matings with a consequently greater proportion of CT phenotypes. But the residual heterogeneity of the birds was sufficiently large to overcome any generally deleterious effects from closely related matings and consequently, hatchability remained high.

The hypothesis set forth here is that CT is a morphological expression of inbreeding degeneration. Most of the experimental evidence (for example, the negative regressions of hatchability and liveability on CT incidence in the F_2 generation) indicates that CT incidence rises with loss of fitness. This is particularly evident in continued consanguineous matings (Hicks, 1953).

The nature of the evidence so far accumulated indicates only a generalized physiological relationship between heterozygosity and the CT complex. To further emphasize this point, a histological study of the tissues of the lower leg during development (Hicks, 1953) failed to reveal any cellular or tissue differences between CT and normal embryos. Nevertheless, it seems probable that the CT complex can only be maintained extensively in poultry flocks if it is correlated with physiological effects that are advantageous under conditions of natural selection.

The adaptive ability of the CT complex under artificial selection as practised in California by Hicks show that with fixation of the trait, the early highmortality of CT embryos is lost and the embryonic liveability of CT zygotes is as good as

that in ST zygotes. The high average coefficient of inbreeding reached in the CT line has undoubtedly produced a general breakdown of the adaptive properties of that line (for example, in the CT X CT mating the hatchability was 50.9%). In the backcross matings to the CT parent within the CT X SCWL lines, the incidence of CT was very high (84.3%) and the hatchability (82.8%) was good and almost 10% above the progeny from the F_1 interse matings from the same lines. It would seem, therefore, that the manifestation of the CT trait can be accompanied by a readjustment of the relationships within the total genotype.

This could happen if the physiological changes occurring in conjuction with the increased expression of CT were balanced with other physiological changes associated with readjustments within the residual genotype. (Residual refers to all those loci with primary effects not directly related to growth processes of the distal portion of the posterior limbs). An alternate method would be the replacement of CT determining loci with isoalleles equally affecting CT expression but differing slightly in their physiological effects. Probably a combination of both methods occurs in nature. This aspect of the discussion has considerable importance to evolutionary theory. It describes a genetic property that could, under natural selection in cross-fertilizing animals, permit populations to adjust gene combinations to changing environmental conditions so that the animal remains optimally adapted to the environment. The evolution of self regulating properties would occur through the gradual accumulation of mutations which are stored in the genotype. Animals requiring a highly heterogeneous condition for optimal adaptation within a given environment could easily accumulate a large number of such genes which if stored within polygenic blocks could be more easily retained.

Artificial selection for the morphological deviant will increase the frequency of its phenotypic expression and cause natural selection to readjust the directly underlying as well as the associated physiological processes. If, under natural

selection the morphological trait, rather than the underlying physiological mechanisms, become selectively advantageous, then natural selection will act as before to adjust the physiological processes to the new morphological condition so that the animal maintains an adaptive relationship to its environment. In general, it would appear that the adaptive change in a single morphological trait causes only a minor alteration in the physiological processes, even under conditions of rapid change. To the extent that this could occur, it describes a mechanism by which rapid evolutionary changes , even to the reorganization of whole organs might be achieved.

SUMMARY

A series of strain and breed crosses in chicken have been carried out between the CT line from the University of California SCWL flock and the UBC SCWL and NH production flocks. Data have been obtained from the P_1, F_1, F_2, and backcross generations.

The results from the crossing experiments have demonstrated the following characteristics of the CT genotype and phenotype:

1. The gene complex is composed of a number of genes which exhibit semi-dominance and variable penetrance.
2. As CT incidence is increased, the expressivity of the defect is increased.
3. Incidence of CT is negatively correlated with fitness (criteria used: evidence of co-adaptation, hatchability, and liveability) in unselected flocks. It can, with selection, become positively correlated with fitness as indicated in the backcross matings to the CT line.
4. Phenotypically it is affected by a threshold mechanism for expression as indicated by the presence of a maternal influence on the incidence in the F_1 generation.
5. Incidence of CT is increased by inbreeding.
6. The expression of the defect in cross-fertilizing animals is connected with genetic balancing mechanisms based on heterozygosis.
7. The significance to evolutionary processes of the genetic mechanism conditioning CT expression are discussed.

REFERENCES CITED

Bateson, W., and Pellew, C. 1920. The genetics of "rogues" among culinary peas (Pisum sativum). Proc. Roy. Soc., B, 91, 186-195.

Chase, H.B. 1951. Inheritance of polydactyly in the mouse. Genetics, 36, 697-710.

Dobzhansky, T. 1947a. Adaptive changes induced by natural selection in wild populations of Drosophila. Evolution, 1, 1-16.

Dobzhansky, T. 1947b. Genetics of natural populations. XIV. A response to certain gene arrangements in the third chromosome of Drosophila pseudoobscura to natural selection. Genetics, 32, 142-160.

Dobzhansky, T. 1948. Genetics of natural populations. XVI. Altitudinal and seasonal changes produced by natural selection in certain populations of Drosophila pseudoobscura and Drosophila persimilis. Genetics, 33, 158-176.

Dobzhansky, T., and Levene, H. 1951. Development of heterosis through natural selection in experimental populations of D. pseudoobscura. Am. Nat., 85, 247-264.

Donald, H.P. 1949. The inheritance of a tail abnormality associated with urogenital disorders in pigs. J. Agric. Sci., 39, 164-173.

Dubinin, N.P. 1948. Experimental investigation of the integration of hereditary systems in processes of evolution of populations. Zhurn. Obsch. Biol., 9, 203-244. (Translated from the Russian by I.M. Lerner).

Goldschmidt, R., Hannah, A., and Piternick, L.K. 1951. The podoptera effect in Drosophila melanogaster. U. Calif. Publ. Zool., 55, 67-294.

Hicks, A.F., (Jr.) 1953. The genetics and development of the crooked-toes defect in chickens. Thesis. University of California.

Hicks, A.F., (Jr.) 1956. Personal communication.

Hicks, A.F., (Jr.), and Lerner, I.M. 1949. Hereditary crooked toes in chickens. Poultry Sci., 28, 625-626.

Holt, S.B. 1945. A polydactyl gene in mice capable of nearly regular manifestation. Ann. Eug., 12, 220-249.

Holt, S.B., and Wright, M.E. 1946. A further note on polydactyly in mice. Ann. Eug., 13, 206-207.

Lerner, I.M. 1954. Genetic homeostasis. Oliver and Boyd Ltd., Edinburgh.

Mather, K. 1941. Variation and selection of polygenic characters. J. Genet., 41, 159-193.

Mather, K. 1943. Polygenic inheritance and natural selection. Biol. Rev., 18, 32-64.

Mather, K. 1953. The genetical structure of populations. Symp. Soc. Exp. Biol., 7, 66-95.

Mather, K., and Harrison, B.J. 1949. The manifold effect of selection. Heredity, 3, 1-52, 131-162.

Murray, J.M. 1932. Polydactylism in mice. Science, 75, 312.

Renard, E.J. 1930. Origin and nature of rogues in canning peas. Wisc. A.E.S. Bull. 101. 56 pp.

Schmalhausen, I.I. 1949. Factors of evolution. Blakiston, Philadelphia.

Waddington, C.H. 1942. Canalization of development and the inheritance of acquired characters. Nature, 150, 563-565.

Wigan, L.G. 1944. Balance and potence in natural populations. J. Genet., 50, 206-214.

Wigan, L.G., and Mather, K. 1942. Correlated response to the selection of polygenic characters. Ann. Eug., 11, 354-364.

Wright, S. 1934a. On the genetics of subnormal development of the head (otocephaly) in the guinea pig. Genetics, 19, 471-505.

Wright, S. 1934b. An analysis of variability in the number of digits in an inbred strain of guinea pigs. Genetics, 19, 506-536.

Wright, S. 1934c. The results of crosses between inbred strains of guinea pigs, differing in number of digits. Genetics, 19, 537-551.