POULTRY BREEDING

BY

MORLEY A. JULL
Senior Poultry Husbandman, Bureau Animal Industry
U. S. Department of Agriculture

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CONTENTS

PREFACE

In many respects the greatest need of the poultry industry of every country is better-bred stock. Improvement in methods of rearing, feeding, and general management would accomplish much toward increasing the returns from the average flock of the country, but beyond a certain point further progress is impossible without an improvement in the breeding quality of the flocks. Since the numerous characters which the domestic fowl possesses are inherited, including color of plumage and ability to lay, and since many of the heritable characters are of economic importance, poultrymen everywhere should be as well informed as possible concerning principles and practices of poultry breeding in order that their work may be both interesting and remunerative.

The purpose of this book is to convey to its readers some conception of the manner in which various characters possessed by the domestic fowl are inherited. The discussion of fundamental principles involved should stimulate further research concerning the problems raised. The results of various lines of research work are reviewed and an extensive list of literature references is given, so that the investigator, teacher, and student each has a ready reference for review purposes.

The discussion of breeding practices to be followed should be of considerable value to extension workers, farmers, and commercial poultrymen. Moreover, since the most successful practices in breeding are based upon the fundamental principles of inheritance, it is obvious that every poultry breeder should know something of these principles in order to make his flock most successful from a practical standpoint. The value of progeny testing is made clear, for it is only by progeny testing that a breeder can expect to make the greatest progress.

A "Foreword" has been very kindly contributed by Dr. R. C. Punnett, of Cambridge University, where it was first determined that numerous characters of the domestic fowl are inherited along Mendelian lines.

The author is deeply indebted to the following authorities for reading and offering valuable suggestions in connection with the manuscript of the chapters accredited to each name: Chapter II, Dr. F. B.

Hutt, Minnesota Agricultural Experiment Station; Chapters III and VII, Dr. D. C. Warren, Kansas Agricultural Experiment Station; Chapter IV, Dr. L. C. Dunn, Columbia University; Chapter V, Dr. Walter Landauer, Storrs Agricultural Experiment Station; Chapter VI, Dr. T. C. Byerly, Bureau of Animal Industry, U. S. Department of Agriculture; Chapters IV, VIII, and X, Dr. C. W. Knox, Bureau of Animal Industry, U. S. Department of Agriculture; Chapter IX, Dr. F. A. Hays, Massachusetts Agricultural Experiment Station; the section on inbreeding and outbreeding in Chapter X, Dr. Lewis W. Taylor, California Agricultural Experiment Station. In addition, the entire manuscript was read critically by Dr. H. C. McPhee, Senior Geneticist, Bureau of Animal Industry, U. S. Department of Agriculture, to whom many thanks are due for numerous constructive suggestions.

The preparation of the book has been inspired by the hope of rendering the greatest possible service to the poultry industry.

M. A. J.

WASHINGTON, D. C.
June 1, 1932

FOREWORD

BY

R. C. PUNNETT

AGRICULTURE, most basic of industries, whereby man wrings his pittance from the soil, has of late years suffered much progress. And what is true of agriculture in general is true also of poultry in particular. To realize the nature of the change one has but to compare this book of Dr. Jull's with any of the standard works on poultry published ten or a dozen years ago. In taking advantage of his kind suggestion that I should write a foreword to the present volume, I do not think I could make better use of the pages at my disposal than to indulge in a few reminiscences and reflections on the way in which this change has come about.

Now in the industry there are three main things—rearing, feeding, and breeding; and the greatest of these is breeding. By rearing I include all those processes which start with the fertilized egg and end with the adult fowl. Industrially the most important of these has been artificial incubation; and the year in which Hearson first put on the market a really trustworthy self-regulating incubator must ever be a landmark for the rearer of poultry. Only then did it become possible for the industry to take advantage of the immense natural fecundity of the domestic hen. A minor invention, though very important, was that of the trap-nest at the end of last century, offering a simple and reliable method of isolating the best layers among a flock of hens. Among later developments, of which the ultimate outcome still hangs in the balance, must be mentioned the battery brooder and the use of electric light. All these things are contributions from the engineer. They are all appliances, enabling man to get more out of the hen, though without in any way altering her intrinsic qualities.

Feeding, again, is also a method of exploiting the hen without alteration in her intrinsic qualities. Great progress in this subject has been made in recent years, and we now know something about the rations necessary to keep the fowl in health and at the same time to get the utmost out of her in the way of production. The discovery of vitamins too has had its repercussions in the poultry-yard. Important, however, as these things are—and they may spell all the difference between commercial failure and success—they go no further than enabling us to make the most of such hens as we may have. Neither the most scientifically balanced of rations, nor the most discriminating dosages of vitamins will make a good layer out of a hen unless she possesses those natural qualities upon which productivity depends. A naturally good layer may do well even under adverse circumstances, but a naturally poor one will never do much though she be given the best of everything. And this is where breeding comes in, the knowledge of the transmissible qualities of poultry which enable us to build up and to maintain the ideal type of hen. This knowledge, as Dr. Jull explains in his third chapter, became possible only with the dramatic rediscovery of Mendel's classic paper on heredity in peas.

Now it was a fortunate thing for the poultry people, little as they probably realize it, that the moment of the rediscovery of Mendel's paper found William Bateson busy in Cambridge with a series of experiments on poultry.[1] He had started them with no idea of future commercial application. Like Mendel himself he chose his experimental material because it was convenient. He wanted to know how definite racial characters behaved on crossing, and so began the gathering of that knowledge which the industry is now turning to so good account. When he started there was all to know, and he began by working out the inheritance of such comparatively simple things as comb shape, and white plumage as opposed to colored. But simple as these things eventually turned out to be they seemed complex enough at first.

When I joined him in the work in January, 1904, it was still a puzzle why the walnut combs which came from crossing rose comb with pea comb should, when bred together, give single combs as well as the other three forms. There were those who clamored "ancestry," but Bateson's intellectual make-up was not of a kind to suffer mysticism gladly. So we went on breeding fowls for the sake of their combs, and out of it all eventually emerged the doctrine of the interaction of factors, one of the most important additions made to Mendel's original principles.

Another of the earlier experiments concerned the inheritance of white plumage. Early in his work Bateson had found both whites which were dominant to color and whites which were recessive. As the result of a long series of experiments involving White Leghorns,

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[1] Bateson's notebooks, from the beginning of his experiments in 1898, are at present in my possession.

Dorkings, Rose Comb Bantams, Wyandottes and Silkies it was found that there were certainly three distinct types of white plumage, differing in their behaviour on crossing though all seemingly alike to the eye. It was an impressive sermon on the text that the plumage does not always proclaim the bird. And out of it all came the explanation of the curious phenomenon of "reversion on crossing," which to Darwin and many less wise heads had long been such a puzzle.

From the point of view of the poultry industry, 1905 was an important year in these experiments, for in that year we introduced the Silky fowl into our pens. Our original intention had been to study the relations of the peculiar comb of this breed, and for this purpose it was reciprocally crossed with the Brown Leghorn. The result was something new and unexpected. For whereas the light skin of the Leghorn was dominant in both sexes when Silky hen was mated with Leghorn cock, the reverse cross gave also cocks with light skins but hens with *dark* ones. The point about the combs was thrust aside, and our attention was entirely given to this new phenomenon, the like of which Leonard Doncaster was also finding in his experiments with the currant moth. The clue was suggested by some experiments with sweet peas which we were making at the same time, and the outcome was the formulation of the principle of sex-linkage in 1908.[2] But although formulated so many years ago some time was to elapse before it became of practical importance to the industry.

In 1909 Bateson left Cambridge to take up the directorship of the John Innes Horticultural Institution just founded at Merton, and thenceforth his interests were mainly botanical. But during those years at Cambridge he had laid the foundations of the study of heredity in fowls. The inheritance of many characters such as comb shape, shank color, plumage color, etc., had been definitely worked out, and the knowledge made available to the breeder, did he choose to make use of it. But the main achievement was the demonstration that such various characters in poultry are all subject to the same general scheme of heredity to which Mendel first provided the clue. Far as we were from complete knowledge, the Cambridge experiments showed that such knowledge was to be had, and showed further the method to be pursued.

Moreover, the work had been done in the face of difficulties which experimenters in these days of endowed research probably do not

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[2] How Bateson hit upon this is vividly told in a letter of his dated January 9, 1908, to be found in "William Bateson, His Essays and Addresses," Cambridge University Press, 1928, p. 113.

realize. It was all a private venture in a little paddock at the back of Bateson's house, aided by such precarious and trifling sums as could be coaxed out of sundry societies from the meagre grants at their disposal. For at the time this kind of work was little in favor in scientific circles; and biologists, such as were not actively hostile, were as a whole more or less indifferent.

However, what Bateson achieved before leaving Cambridge had begun to turn the scale, and in 1911 the then Board of Agriculture set aside a small annual grant in aid of the experiments which I continued to carry on in Cambridge. I was then joined by P. G. Bailey, who was so soon to lose his life in the war, and we started experiments on certain characters showing what was then called "blended inheritance." For at that time it was held by many that such inheritance was of a different type from Mendelian heredity with its clear-cut ratios. As examples we chose body weight and egg color, and we were able to demonstrate, to our own satisfaction at any rate, that, although such cases are more complicated, they are none the less capable of interpretation in terms of relatively few definite Mendelian factors.

Our experiments on body weight, starting with Hamburghs and Sebright bantams, were also designed to test the heredity of henny plumage, and of silver and gold. We paid special attention to the down colors of our chicks, and in proving that silver and gold form a sex-linked pair we were at the same time able to correlate these colors with the down characters. We also showed that barred and black were likewise betokened in the down at hatching. Even then the matter remained for us one of purely scientific interest, and it was only by chance, when reading some correspondence at the Food Production Department during the war, that it occurred to me that the knowledge could be of commercial value. This was pointed out in a brief article in the Journal of the Board of Agriculture for February, 1919, and although it was some years before the idea was entertained seriously it eventually made its way. Today millions of chicks are reared annually from sex-linked crosses in this country,[3] and although America is rather more backward, I have little doubt that the advantages of the method will soon make an equal appeal there also.

More recently an interesting development has taken place in connection with sex-linkage. About ten years ago Mr. M. S. Pease and I

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[3] A well-known firm, which hatches annually about a million chicks, in 1929 put into their incubators about 30,000 eggs produced from sex-linked crosses. In the present year (1932) they have made arrangements to put in over 800,000.

started some experiments on the inheritance of the transverse barring on the feathers of fowls. We knew that the barring of the Plymouth Rock was dominant to self-color and sex-linked; we knew also that the barring of the Hamburgh and the Campine was recessive to self-color and not sex-linked. How were these two types of barring going to behave when present simultaneously? We thought that a knowledge of their combined effect might possibly shed some light upon the rhythm of feather growth, so we built up a strain which was pure for the two types of barring. And when we made it we found that the downs of the chicks were quite different in the two sexes, in spite of the fact that the strain bred perfectly true to plumage characters. We had made a breed that automatically sex-linked itself. At present it is being worked up for increased productivity. When this has been done, and the "Cambar" is loosed on the world in a few years' time, it should prove acceptable and profitable to those who wish to make use of the sex-linked result without the operation of crossing.

Even more recently a further development has taken place in connection with ducks. The Indian Runner duck, and its derivative the Khaki Campbell, are the finest egg machines in the world. But for table purposes the drakes are relatively worthless. Two years ago we succeeded in our quest for a sex-linked down character in ducks, and today we are engaged in building up breeds of Runners and Campbells giving a clear-cut sex-linked down character. This will enable the breeder to get rid of the worthless drakes at hatching, and should provide a definite stimulus to the increased production of these magnificent layers.

Such is a brief sketch of some of the poultry work at Cambridge since Bateson opened his first notebook in 1898. Materially it has greatly profited humanity, for when sex-linkage has entered fully into the procedure of the industry the world will be millions a year the richer for this one discovery alone. But it is not upon this aspect of the work that I wish to insist, for it is the moral to be drawn from it all that seems to me to be of by far the greater value. We have before us one of the most striking applications of scientific discovery to a great industry, and it is worth reflecting for a moment on the manner in which it has come about.

In these days we hear much of "team work" and of "organized research," but in the experiments I have written of that is all to seek. The span of time sketched out is 33 years, and during more than a third of these there was but a solitary worker in charge. Nor were the means provided ever on a lavish scale. In earlier days we had to do much of the menial labor ourselves; and though of late years the means have been sufficiently ample I should be much surprised if, over the whole period, the expenditure on upkeep and labor averaged as much as $2,000 a year. That so much was done with so little was of course due to William Bateson. He led and others followed.

It needs the big man to get the big thing done, and therein lies the lesson for the industry. Its problems are many and vital, and I doubt if they are going to be solved by any number of teams of second-raters, however numerous and well endowed. Rather would I suggest the policy of buying a few of the very best of the younger intellects, picking them from among the physiologists, the biochemists and the geneticists. It is all to the good that they should come to the job with fresh minds, innocent of fowl. To such men I would pay whatever was asked, and ungrudgingly bestow upon them all the hewers of wood and drawers of water they demanded. Discovery is a gamble and quite beyond the power of the wisest to control. But if one in ten succeeded the plan would have worked reasonably well.

As I see it today the greatest need of the poultry industry is fine intellects. They are rare, and must therefore be paid for; but in the long run it is worth it. Huxley once said that a potential Faraday would be cheap at a quarter of a million pounds sterling. He would indeed. But the finest constructive brains are reasonably modest in their requirements so long as they think they are being treated fairly. And since they have a way of relying on their intellect rather than their material equipment they are very much cheaper to run. However, I have labored the point enough, for I do not suppose that it will ever be acted upon. Special privileges in a democracy are reserved for champion boxers, film stars and multimillionaires.

There remains but one last reflection that I shall allow myself to make. No one who reads intelligently this book of Dr. Jull's can allow his thoughts to stay at the hen. He cannot but feel that what is written here is only part of some great scheme into which all of us living creatures must willy-nilly fit. It is true that we know far more of heredity in the fowl than in man. Since Mendel was rediscovered more than thirty generations of hens have passed, which for man would mean a thousand years in the sight of the geneticist. There can be little doubt that much of what is here recorded concerning the nature of the hen offers the clue to much that is puzzling in ourselves. It is not in Dr. Jull's province to write of man, interesting creature though he be; those who wish to follow up this track of thought cannot do better than read the volume of Bateson's "Essays" already referred to above. But let him not do so if he fear to discover that of him also is the story told.

POULTRY BREEDING

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CHAPTER I

BREEDS AND VARIETIES AND THEIR SIGNIFICANCE

THE numerous existing breeds and varieties of domestic fowls, with plumage colorations and structural features in great variety, have been developed by breeding methods practiced by man throughout the ages. Because of their relatively small size as compared with many other domestic animals and because of their adaptability to a wide variety of climatic conditions, fowls have entered into the interests of more human beings than any other animal. For thousands of years and in all parts of the world the domestic fowl has been bred by all classes of mankind.

From rather limited beginnings, the original wild fowls of the bamboo jungles of India have been developed into stocks noted for their fighting propensities or for their beauty of form and plumage pattern or for their excellence as table fowl or for abundant egg production. The relatively primitive wild type has been developed into different breeds and varieties with diverse characters adapted to different purposes, some purely esthetic and some largely utilitarian.

The Origin of the Chicken.—The most authentic information available regarding the origin of the chicken indicates that all the breeds existing today have descended from one or possibly four subspecies of wild fowl. The four subspecies are as follows:

(1) *Gallus gallus or Gallus bankiva*, the Red Junglefowl.
(2) *Gallus lafayette*, the Ceylon Junglefowl.
(3) *Gallus sonnerati*, the Gray Junglefowl.
(4) *Gallus varius*, the Javan Junglefowl.

The Javan Junglefowl differs from the other three species in having a single-median wattle, a smooth-edged comb, truncated neck hackles, and an extra pair of rectrices, or tail feathers.

The eminent naturalist Darwin (1868)[1] who made a close study of the origin of the domestic fowl, concluded that all our domestic

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[1] A list of the literature references cited in each chapter is given at the end of the chapter.

stocks descended from one species, the Red Junglefowl. The principal reason why Darwin regarded the Red Junglefowl as the progenitor of all our domestic breeds of poultry was that he observed that it resembled some of the early domestic breeds more closely than the other three species; its voice was more similar to the voice of the domestic fowl; and when mated with domestic stock it produced offspring more freely, and the offspring were much more apt to be fertile than hybrid offspring from any of the other species.

Houwink (1911), as the result of extensive observations, was inclined to agree with Darwin's viewpoint; but in later years, as a result of breeding experiments, he came to believe that our domestic breeds have not descended from the Red Junglefowl only.

Beebe (1918-1922) states that all four subspecies will cross with one another and that the hybrids are more or less fertile among themselves. Many references are cited where crossing has taken place among the four wild species and domestic stocks. The matings sometimes occurred naturally and sometimes the natives of India and Java encouraged crossing. This was done by trussing and pinning a domestic hen to the ground and, after exciting a cock by holding a wild hen near him, placing him on the domestic hen; another method was to have the three birds each in a separate cage and after exciting the cock by placing the cage containing the wild hen near his cage, suddenly to substitute for it the cage containing the domestic hen. In his exhaustive study of the wild fowl, Beebe states definitely, "There is no doubt that the Red Junglefowl alone is the direct ancestor of all of our domestic poultry, so this question is removed from the discussion."

On the other hand, Tegetmeier (1873), a co-worker with Darwin, finally arrived at a different conclusion from that of Darwin concerning the origin of all our domestic fowl. Tegetmeier pointed out that numerous hybrids were obtained from crossings between domestic stocks and the Ceylon and Javan Junglefowls. He further held: "I have no doubt in my own mind that the wild *Galli* have intermixed in not a few instances, and perhaps through not a few centuries, in producing our domestic breeds." Tegetmeier was especially doubtful of the Asiatic races of domestic fowl, Brahma, Cochin, and Langshan, being derived from the Red Junglefowl. Rather he believed that they descended from a readily domesticated, short-winged species that probably originated from the same ancestral stock that originally gave rise to the four wild subspecies referred to above.

Fertile offspring between the Gray Junglefowl and domestic fowls have been raised by Ghigi (1916), and he is led to believe (1922) that some of the domestic breeds are descended from a wild species now extinct. Lotsy and Kuipper (1922, 1923, 1924) conducted experiments in crossing representatives of the four wild subspecies with domestic stocks, the results of which give added evidence to the production of fertile hybrids in all the matings. The results secured by Houwink, as reported by Lotsy and Kuipper, give added evidence to the claim that our domestic breeds are not descended from *Gallus bankiva* only.

Furthermore, Punnett (1923) refers to a second-generation hybrid bird from a cross between the Red Junglefowl and the Javan Junglefowl, the hybrid being black in color. Regarding the significance of the appearance of this black hybrid, Punnett makes the interesting observation that the Javan Junglefowl may be one of the ancestors of some of our domestic breeds.

In conclusion, it must be admitted that not until representatives of the four wild species can be obtained that are known to be pure, and proper crosses are made among them and with domestic stocks, can the problem of the origin of domestic breeds be definitely established.

Early Influence of Cock-Fighting.—That the sport of cock-fighting exercised a tremendous influence not only in the domestication of wild birds but also in the subsequent distribution of the fowl is amply demonstrated by the importance attached to the pastime by many human races. The literature of various nations contains many references to the sport, and Brown (1929), who has given much thought to the question, concluded that the sport of cock-fighting had as much responsibility for the domestication of the fowl as demand for food, and that the sport was chiefly instrumental in making the species popular.

Influence of Exhibitions.—With the suppression of cock-fighting as a public institution, poultry exhibits had their inception. In 1849 the first poultry show was held in America at Boston, and at about the same time the first poultry show was held in England. These exhibitions gave impetus to the growing interest in the then known breeds and varieties of fowl, for, by that time, several countries had each developed races possessing characters differentiating them from races produced in other countries. India had produced its fighting cocks, Asia its massive breeds with feathered shanks, Italy its small-bodied birds with nervous dispositions, England its game-cocks and breeds excelling in fleshing properties, and America its numerous early breeds.

Poultry exhibitions had the effect of encouraging breeders to pay considerable attention to such characters as type, color markings and pattern, and other characters that were soon adopted as standard for the breed and variety in question. This has often been carried to extremes, to such an extent that the vigor and economic qualities have sometimes been sacrificed in the perfection of some character of minor importance.

Poultry exhibitions tended to encourage the development of new breeds and varieties. This was especially true of breeds and varieties with what are often called "fancy" characteristics. Consider, for instance, the miniature bantams, where smallness of size is one of the outstanding features. Consider also the vulture hocks on the Sultan breed, the highly developed crest on the Polish breed, the peculiar type of the Pit and many other Games, and the bewildering variety of color patterns in a large number of varieties.

What Constitutes a Breed?—As with other classes of livestock, so with the domestic fowl, the chief interests in breeding operations led to the establishment of breeds. Breeding for improvement was carried on largely from the standpoint of perpetuating desirable characteristics possessed by races or strains. In other cases new breeds were developed by crossing existing breeds and then practicing rigid selection until the desired characters were transmitted with reasonable regularity.

The distinguishing feature whereby one breed of fowls differs from another breed is the "type," although this is rather confusing since the visible body type is influenced not only by the actual shape of the body but also by the feather contour. In breeding standard-bred poultry, the type of a bird as determined by feather contour has been regarded as of greatest importance, so much so that in many cases the actual body type has received minor attention. The situation has developed so that it is now recognized that "shape makes the breed," shape here indicating very largely feather contour.

A breed represents a group of domestic fowls in which are inherited from generation to generation a distinctive shape of body as exemplified largely by plumage contour. Other characteristics such as shape of comb, color of earlobe, color of egg shell, and number of toes are possessed by all birds belonging to any one breed but are characteristics common to each of several breeds.

Varieties Within the Breed.—Within each breed of fowls there naturally was a tendency to segregate various color combinations or, where only one color existed in the original breed, to develop new color patterns. In either case, it was necessary to adhere to the original type or shape characteristic of the breed, and thus it has arisen that varieties of a breed are supposed to be identical in all characteristics except plumage color or, in some cases, shape of comb, standard weight, color of shanks, and other minor characteristics. There is a large grain of truth in the old saying of poultry breeders that "shape makes the breed and color the variety."

Breed and Variety Descriptions.—Detailed descriptions of the different breeds and varieties are contained in numerous "standards" published by specialty clubs and breeders' organizations. In many cases the ideal specimen of the breed or variety is illustrated; in the United States and Canada, for instance, the "Standard of Perfection" (1930) serves as a guide in determining the relative merits of birds shown at exhibitions and used in breeding pens. The American Standard of Perfection, however, contains descriptions and illustrations of breeds recognized by the American Poultry Association, and for descriptions of other breeds reference should be made to club books published by the specialty breeding clubs in various countries.

In order to simplify the description of the numerous breeds and varieties being bred in different countries, several characters, such as type of comb, color of earlobe, skin, and shanks, shank-feathering or its absence, color of egg, and the standard weights of the cock, hen, cockerel, and pullet, are given in tabular form in Tables 1 and 2. The inheritance of a number of these characters is discussed in subsequent chapters.

Since the particular interest in this book is a discussion of inheritance of the characters possessed by different breeds and varieties, and since those characters the inheritance of which has been investigated are discussed in subsequent chapters, it is necessary at this time only to make a few general observations regarding the outstanding differences that exist among breeds and varieties.

A description of the numerous existing breeds and varieties being bred in different parts of the world is simplified very materially by virtue of the fact that several varieties belonging to different breeds have the same color of plumage. There are white varieties, buff varieties, blue varieties, and black varieties of many breeds, and in each case the plumage color is identical.

Furthermore, a description of breeds and varieties is simplified because the parti-colored plumage pattern of some varieties belonging to different breeds is identical. The Dark Brahma, Silver-Penciled Plymouth Rock, and Silver-Penciled Wyandotte have the same plumage pattern; so also have the Partridge Cochin, Partridge Plymouth

Rock, and Partridge Wyandotte, and likewise the Light Brahma, Columbian Plymouth Rock, and Columbian Wyandotte.

Then, again, in several breeds there are two varieties in which a single difference makes the varieties appear quite distinct. The Partridge Plymouth Rock is similar to the Silver-Penciled Plymouth Rock except for the single difference that the "silver" or white of the latter variety replaces the "gold" or red or reddish bay of the former. The single difference between the Golden-Laced Wyandotte and the Silver-Laced Wyandotte is that the "silver" or white of the latter replaces the "gold" or golden bay of the former. The same is

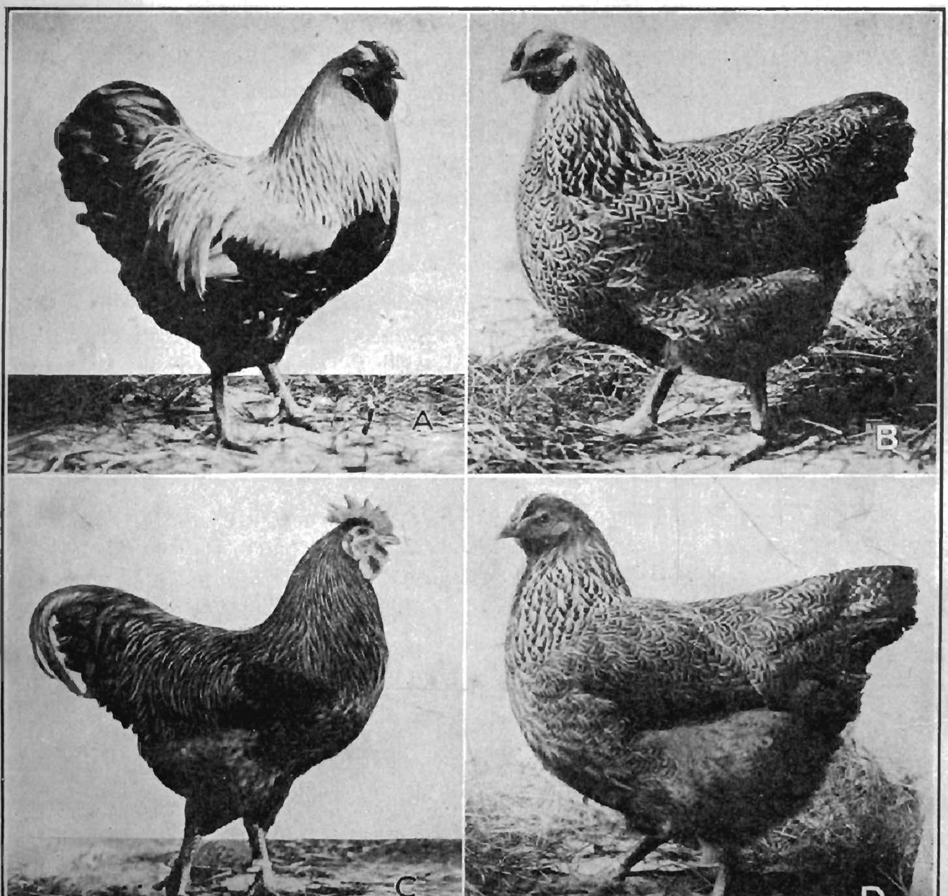

Fig. 1.—As far as plumage color is concern, the Silver-Penciled Wyandotte, shown above, differs from the Partridge Plymouth Rock, shown below, in that white replaces golden bay. The plumage pattern in the two males is identical and the same is true in the case of the two females. (U. S. D. A.)

true of the Golden Campine and the Silver Campine, and of certain varieties in other breeds.

From the standpoint of plumage color the breeds and varieties may be divided into two groups: (1) breeds and varieties that are of one color and are called solid-colored or self-colored; (2) breeds that are of two or more colors and are called parti-colored.

The self-colored group includes whites, blacks, blues, reds, and possibly buffs, although buffs frequently carry some black. The parti-colored group includes breeds and varieties that have, among others, the following kinds of plumage: barred, mottled, pied, spangled, columbian, silver-laced and golden-laced, silver-penciled and golden-penciled, black-red, and red pyle.

White Plumage.—Among the various white breeds may be mentioned the Chantecler, Rhode Island White, and White-Booted Bantam. A white variety is to be found in many of the different breeds, such as Cochin, Leghorn, Minorca, Orpington, Plymouth Rock, Wyandotte, Silkie, and Rose-Comb Bantam. White plumage free of foreign color is the one character common to all white breeds and varieties. Some of them, as the Leghorn, have yellow skin, and some, as the Orpington, have white skin, but since these and other distinguishing characteristics of each breed are given in Table 1, it is not necessary to discuss them further. It is interesting to note that from the standpoint of inheritance there are at least three different kinds of white, the differences among them being discussed in Chapter IV.

Black Plumage.—One of the most popular black breeds is the Jersey Black Giant, although there is a black variety in each of several breeds, including the Langshan, Leghorn, Minorca, Orpington, Wyandotte, and Rose-Comb Bantam. The Crevecoeur and La Fleche are two black breeds of French origin.

Buff Plumage.—A buff variety is to be found in many of the breeds, such as Brahma, Cochin, Leghorn, Orpington, Plymouth Rock, and Wyandotte.

Blue Plumage.—The Andalusian is the only blue breed, but there is a blue variety in each of the following breeds: Leghorn, Orpington, and Plymouth Rock.

Red Plumage.—The Red Leghorn is one of the very few varieties that is solid red in plumage color.

Barred Plumage.—There are three kinds of barred plumage: (1) alternating black and white bars, (2) alternating black and golden bay bars, (3) alternating white and golden bay bars.

Among the breeds having black and white barring are the Cambars, Dominiques, and Scotch Grays, and among the varieties having black

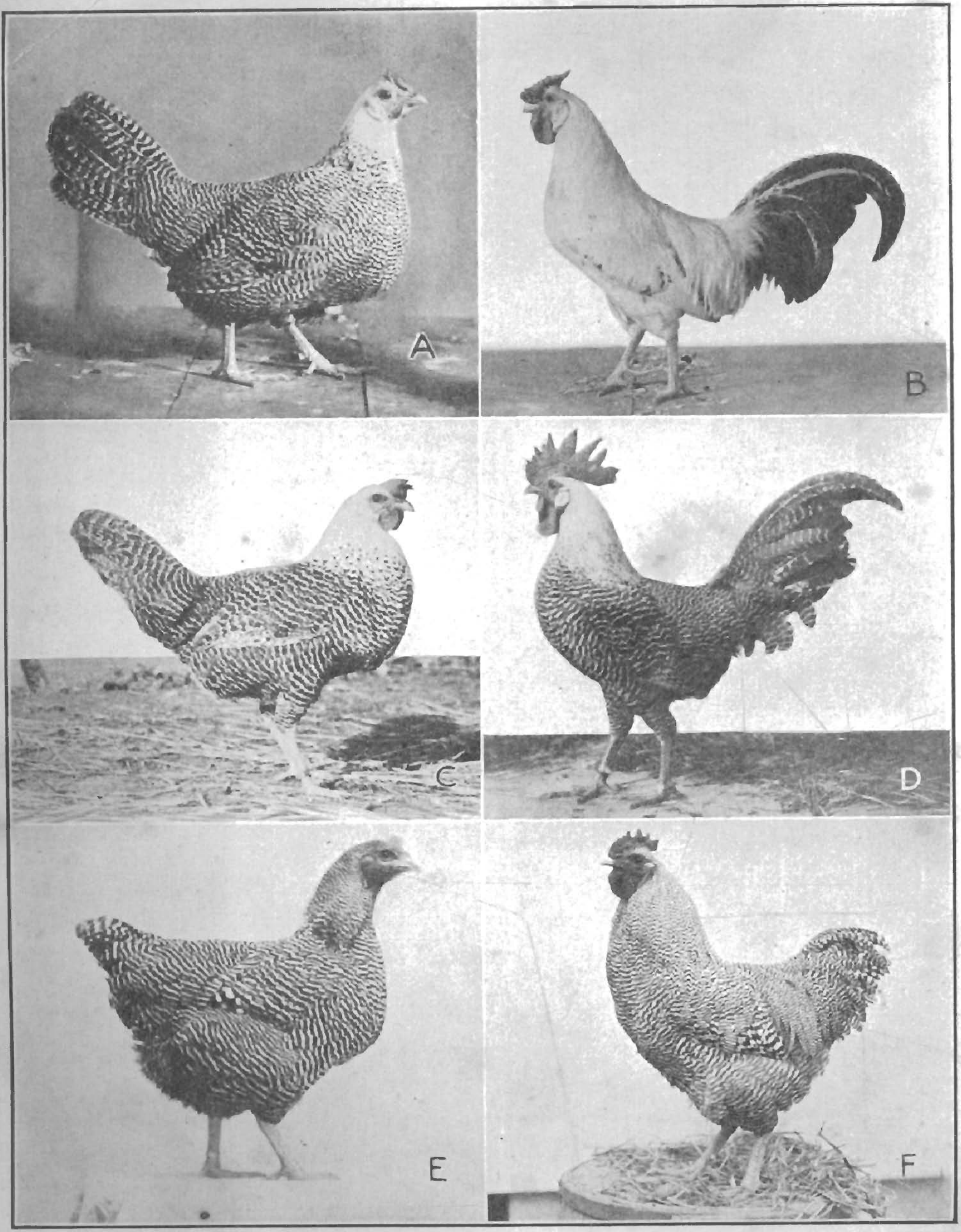

FIG. 2.—Black-and-white barring in three different varieties. The Silver-Penciled Hamburg, shown at the top, is in reality a barred variety but in the male barred feathers are restricted to the wings and the sides of the body. In the Silver Campine, shown in the middle, the black bars are much wider than the white bars. In the Barred Plymouth Rock, shown at the bottom, the black and the white bars are supposed to be of equal width. The barring character in Barred Plymouth Rocks behaves differently in inheritance from the barring character in the other two varieties. (U. S. D. A.)

and white barring are the Barred Plymouth Rocks, Cuckoo Leghorns, Silver Campines, and Silver-Penciled Hamburg females, which are in reality barred rather than penciled. It is interesting to note, as pointed out in Chapter IV, that the barring of the Barred Plymouth Rock behaves differently in inheritance from the barring in the Silver Campine and Silver-Penciled Hamburg.

The Golden Campine and Golden-Penciled Hamburg females are two varieties that have barring comprised of alternating bars of black and golden bay.

The Chamois Campine has alternating bars of white and golden bay.

Mottled Plumage.—In the Ancona breed and the Mottled Houdan and Mottled Java varieties the plumage is black but a few of the feathers are tipped with white, giving a mottled effect.

Pied Plumage.—The Exchequer Leghorn has plumage comprised of a mixture of black and white, which is called pied.

Spangled Plumage.—In the Silver-Spangled Hamburg the plumage is white except that each feather is tipped with a black spangle. In the Golden-Hamburg the plumage is golden bay except that each feather is tipped with a black spangle. In the Speckled Sussex the plumage is mahogany bay in color except that each feather is tipped with a white spangle, a crescentric black bar dividing the white spangle from the mahogany bay. The Buttercup female for the most part has golden buff plumage with black markings, called spangles, diagonally across each feather.

Columbian Plumage.—In Light Brahma, Columbian Plymouth Rock, Columbian Wyandotte, and Light Sussex the plumage is white except that the hackle and saddle feathers in the male and the neck and tail coverts in the female are black edged with white, the tail feathers in both sexes are black, and there is some black in the wings.

Laced Plumage.—A feather is said to be laced when the edge is of a different color from the rest of the feather. There are silver-laced breeds and varieties and golden-laced breeds and varieties, the only difference being that in the silver-laced breeds and varieties the neck feathers of the female and the hackle and saddle feathers of the male are black laced with white and the rest of the plumage in both sexes is white, most of the feathers being laced with black, whereas in the golden-laced breeds and varieties the neck feathers of the female and the hackle and saddle feathers of the male are black laced with golden bay and the rest of the plumage in both sexes is black, most of the feathers being laced with golden bay. If the white in Silver Sebright Bantams, Silver Polish, and Silver-Laced Wyan-

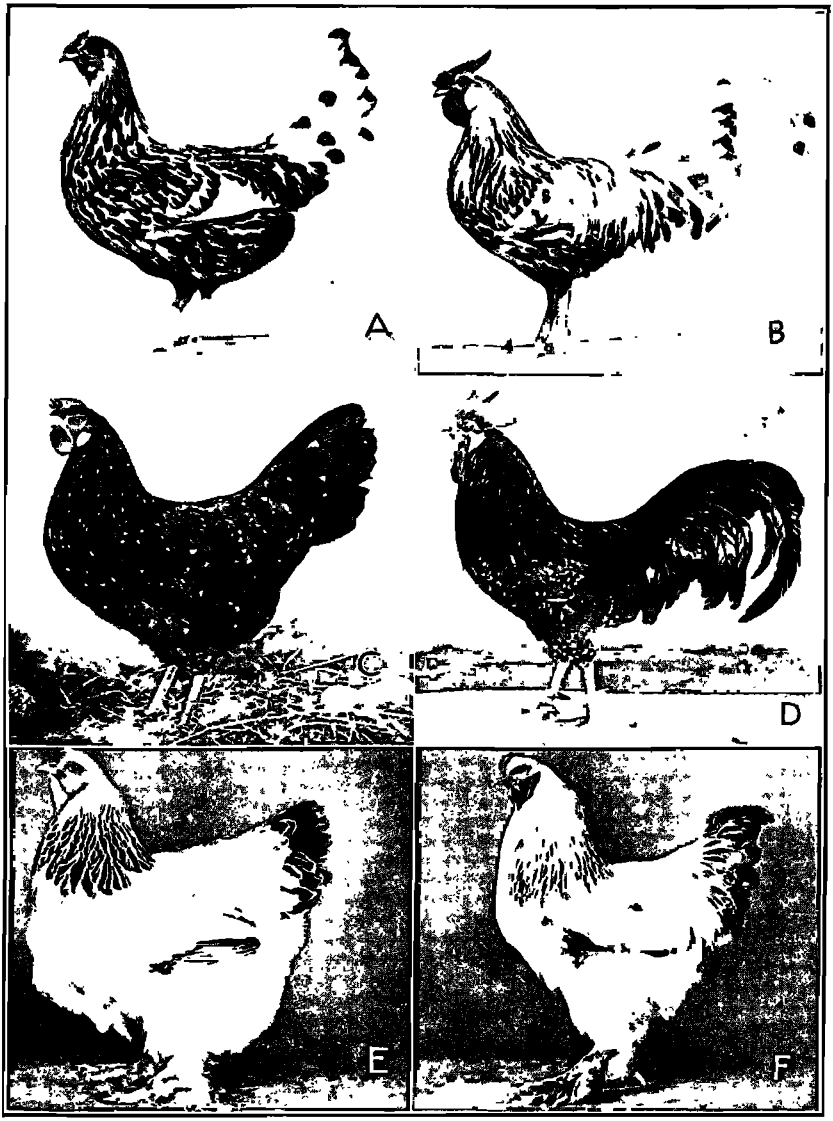

FIG. 3.—Spangled plumage in the Silver-Spangled Hamburg, shown at the top; mottled plumage in the Ancoma, shown in the middle; columbian plumage pattern in the Light Brahma, shown at the bottom. (U. S. D. A.)

dottes were replaced with golden bay they would become Golden Sebright Bantams, Golden Polish, and Golden-Laced Wyandottes, respectively.

White lacing on red feathers is found in White-Laced Red Cornish, and white lacing is also encountered in Buff-Laced Polish, the creamy white lacing being on golden buff feathers.

Blue lacing is encountered in Blue Andalusians and blue varieties of other breeds; in this case, however, the lacing is due to a difference in shade of blue.

Penciled Plumage.—A feather is said to be penciled when there are crescentric markings of a different color from the rest of the feather, these crescentric markings being one, two, or three in number depending upon the breed or variety. Moreover, penciling is confined to the female of the breed or variety. In the Dark Cornish female the feathers over most parts of the body are bay in color and have a lacing of black together with one crescentric black penciling mark, whereas in the Dark Brahma female two or three black penciling marks appear on a white feather.

The white ground color in the Dark Brahma, Silver-Penciled Plymouth Rock, and Silver-Penciled Wyandotte female is replaced with reddish bay in the Partridge Cochin, Partridge, Plymouth Rock, and Partridge Wyandotte female; otherwise their plumage pattern is identical.

Stippled Plumage.—In the Light Brown Leghorn female the feathers over the back and sides are dark brown stippled with lighter brown, the stippling constituting numerous clearly defined specks in each feather. In the Dark Brown Leghorn female there is coarse reddish brown stippling in the black portion of each feather over the back and breast. In the Silver-Gray Dorking female all the plumage, except the neck feathers and the primaries and secondaries, is gray, each feather being finely stippled with silvery white. Stippling is also found in Silver Leghorn females and in females of some of the Game varieties, including the Black-Breasted Red, the Golden Duckwing, and the Silver Duckwing.

Red and Black Plumage.—There are several breeds and varieties in which the plumage colors are confined to a combination of red and black. The Rhode Island Reds are one of the most common varieties belonging to this group; the plumage is for the most part red, black being confined to portions of the wing and the tail. Black-Breasted Red Games, Black-Tailed Red Leghorns, and Red Sussex also belong to this group.

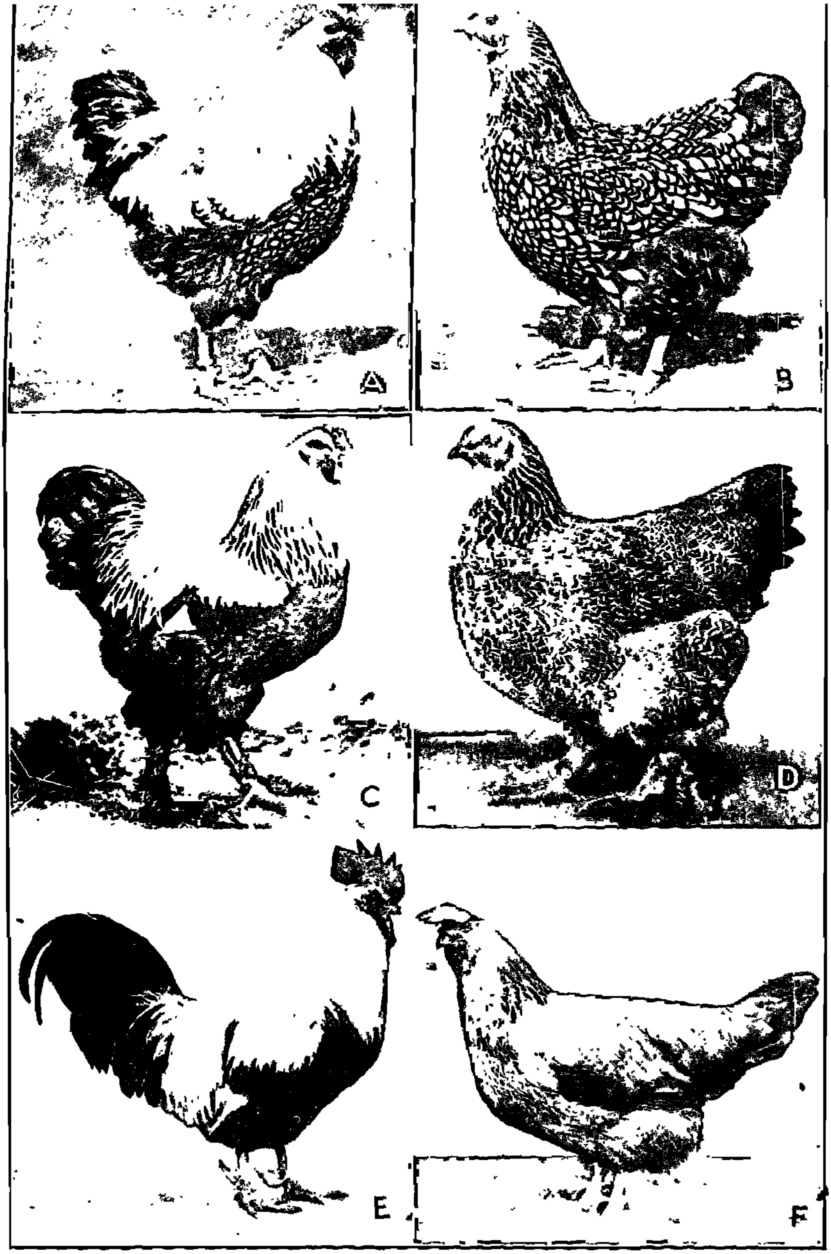

FIG. 4.—Sexual dimorphism in plumage pattern in a laced, a penciled, and a stippled variety. Silver-Laced Wyandottes at the top, Dark Brahmas in the middle, and Silver-Gray Dorkings at the bottom. Except for the lacing on the breast and body feathers of the Silver-Laced Wyandotte male and absence of lacing in the hackle of the Silver-Gray Dorking male, the three males resemble each other in appearance. The three females differ considerably, however, among themselves and from the males. (U. S. D. A.)

Majority of Breeds and Varieties Accounted For.—The various colors of plumage that have been mentioned previously embrace the great majority of the more popular breeds and varieties. The breeds whose general plumage color has been mentioned include the Ancona, Andalusian, Australorp, Jersey Black Giant, Buttercup, Dominique, Rhode Island Red, Rhode Island White, Black Sumatra, White-Faced Black Spanish, and Sultan. To be added to this list are practically all the varieties of the following breeds: Brahmas, Campines, Cochins, Cornish, Dorkings, Hamburgs, Houdans, Javas, Langshans, Leghorns, Minorcas, Orpingtons, Plymouth Rocks, Polish, Sussex, Wyandottes, and several breeds of Bantams.

Other Plumage Patterns.—Plumage colors that have not been mentioned are confined for the most part to the Games, Game Bantams, certain other breeds of Bantams, and other breeds such as the Cantonese, Faverolles, Barnevelders, Lakenfelder, and Welsummer. Since practically no investigational work has been undertaken to determine the nature of the inheritance of the color patterns of these breeds and varieties further reference to them is unnecessary at this time.

Similar Color in Both Sexes.—In all of the solid-colored breeds and varieties, including the whites, blacks, buffs, blues, and reds, the male and female in each case are of the same color. The same is true in several of the parti-colored breeds and varieties, including those with the following kinds of plumage: barred (except the Silver-Penciled and Golden-Penciled Hamburg), mottled, pied, spangled, and columbian. In some of the breeds and varieties with laced plumage, such as Silver Sebright Bantams, Golden Sebright Bantams, Silver Polish and Golden Polish, Buff-Laced Polish, Blue Andalusians and Blue Leghorns, Orpingtons, and Plymouth Rocks, the sexes have the same color scheme.

Sex Dimorphism in Color Pattern.—In numerous breeds and varieties the sexes differ in color scheme, in many cases to a marked extent, giving rise to the expression "sex dimorphism in color pattern." In the Silver-Laced Wyandotte the male is somewhat different from the female, for although practically all of the female's plumage is laced the male has silvery white wing-bows and back. A greater difference exists between the male and female color scheme in those breeds in which the females are penciled, for in this case practically all of the female's plumage is penciled whereas in the male there is no penciling in any part of the plumage. Varieties in which the females are stippled, as in the Brown Leghorn and Silver-Gray Dorking, show an entirely different color scheme in the males.

In many of the varieties of the Game breed, the sexes are distinctly different in color scheme, as, for instance, in the Red Pyle, Silver Duckwing, Golden Duckwing, Birchen, and Black-Breasted Red.

The reason why in certain breeds and varieties the plumage color differs so markedly in the two sexes but in other breeds and varieties is the same in both sexes has apparently never been determined, although the suggestion has been made that where sex dimorphism in plumage color or pattern occurs the plumage color or pattern of one sex is conditioned by secretions of some of the internal glands, some of which are mentioned in Chapter II.

TABLE 1. THE MORE IMPORTANT CHARACTERISTICS OF VARIOUS BREEDS OF CHICKENS

Breed	Type of Comb	Color of Earlobe	Color of Skin	Color of Shanks	Shanks Feathered or Unfeathered	Color of Egg
Ancona	Single and rose	White	Yellow	Yellow	Unfeathered	White
Araucana	—	—	—	—	Unfeathered	Pale blue
Aseel	Pea	Red	Yellow	Various	Unfeathered	Brown
Australorp	Single	Red	White	Dark slate	Unfeathered	Brown
Barnevelder	Single	Red	Yellow	Yellow	Unfeathered	Dark brown
Blue Andalusian	Single	White	White	Slate blue	Unfeathered	White
Brahma	Pea	Red	Yellow	Yellow	Feathered	Brown
Buckeye	Pea	Red	Yellow	Yellow	Unfeathered	Brown
Campine	Single	White	White	Leaden blue	Unfeathered	White
Cantonese	Single	Red	Yellow	Yellow	Unfeathered	Brown
Chantecler	Cushion	Red	Yellow	Yellow	Unfeathered	Brown
Cochin	Single	Red	Yellow	Yellow	Feathered	Brown
Cornish	Pea	Red	Yellow	Yellow	Unfeathered	Brown
Creeper	Single	White	White	Slate blue	Unfeathered	White
Crevecoeur	V-shape	Red	White	Leaden blue	Unfeathered	White
Dorking (Silver-Gray, Colored)	Single	Red	White	White	Unfeathered	White
Dorking (White)	Rose	Red	White	White	Unfeathered	White
Faverolle	Single	Red	White	Pinkish white	Feathered	Brown
Frizzle	Single	—	Yellow	—	Unfeathered	Brown
Game	Single	Red	White	Various	Unfeathered	Brown
Hamburg	Rose	White	White	Leaden blue	Unfeathered	White
Houdan	V-shape	White	White	Pinkish white	Unfeathered	White
Java (Black)	Single	Red	Yellow	Black	Unfeathered	Brown
Java (Mottled)	Single	Red	Yellow	Leaden blue and yellow	Unfeathered	Brown
Jersey Black Giant	Single	Red	Yellow	Black	Unfeathered	Brown
La Fleche	V-shape	White	White	Dark slate	Unfeathered	White
Lakenfelder	Single	White	White	Slaty blue	Unfeathered	White
Langshan (Black)	Single	Red	White	Bluish black	Feathered	Brown
Langshan (White)	Single	Red	White	Slaty blue	Feathered	Brown
Leghorn	Single and rose	White	Yellow	Yellow	Unfeathered	White
Malay	Strawberry	Red	Yellow	Yellow	Unfeathered	Brown
Minorca (Black)	Single and rose	White	White	Dark slate	Unfeathered	White
Minorca (Buff and White)	Single and rose	White	White	Pinkish white	Unfeathered	White

TABLE 1 (*Continued*)

Breed	Type of Comb	Color of Earlobe	Color of Skin	Color of Shanks	Shanks Feathered or Unfeathered	Color of Egg
Nagoya	Single	Red	Yellow	Leaden blue	Unfeathered	Brown
✓Orpington (Blue)	Single	Red	White	Leaden blue	Unfeathered	Brown
✓Orpington (Buff and White)	Single	Red	White	White	Unfeathered	Brown
✓Orpington (Black)	Single	Red	White	Black	Unfeathered	Brown
✓Paradis	Single	Red	White	Pinkish white	Unfeathered	White
✓Plymouth Rock	Single	Red	Yellow	Yellow	Unfeathered	Brown
✓Polish	V-shape	White	White	Slaty blue	Unfeathered	White
Polish Greenfoot	Single	Red	White	Green	Unfeathered	Various
✓Red Cap	Rose	Red	White	Leaden blue	Unfeathered	White
✓Rhode Island Red ✓	Single and rose	Red	Yellow	Yellow	Unfeathered	Brown
✓Rhode Island White	Rose	Red	Yellow	Yellow	Unfeathered	Brown
✓Silkie	Cushion	Light blue	Blue	Leaden blue	Feathered	Brown
Sultan	V-shape	Red	White	Slaty blue	Feathered	White
✓Sussex	Single	Red	White	Horn	Unfeathered	Brown
Welsummer	Single	Red	Yellow	Yellow	Unfeathered	Brown
White-Faced Black Spanish	Single	White	White	Dark slate	Unfeathered	White
✓Wyandotte	Rose	Red	Yellow	Yellow	Unfeathered	Brown

TABLE 2. STANDARD WEIGHTS OF VARIOUS BREEDS OF DOMESTIC FOWL

Breed	Standard Weight in Pounds			
	Cock	Hen	Cockerel	Pullet
Ancona	6	4½	5	4
Australorp	8½	6½	7½	5½
Brahmas:				
Light Brahma	12	9½	10	8
Dark Brahma	11	8½	9	7
Buff Brahma	11	8½	9	7
Buckeye	9	6½	8	5½
Campine	6	4	5	3½
Chantecler	8½	6½	7½	5½
Cochin	11	8½	9	7
Cornish:				
Dark and White Cornish	10	7½	8	6
White-Laced Red Cornish	8	6	7	5
Crevecoeur	8	7	7	6
Dorking:				
White Dorking	7½	6	6½	5
Silver-Gray and Colored	9	7	8	6

TABLE 2 (*Continued*)

Breed	Standard Weight in Pounds			
	Cock	Hen	Cockerel	Pullet
Faverolles	8	6½	7	5½
Houdan	7½	6½	6½	5½
Java	9½	7½	8	6½
Jersey Black Giant	13	10	11	8
La Fleche	8½	7½	7½	6½
Langshan	9½	7½	8	6½
Leghorns	6	4½	5	4
Malay	9	7	7	5
Minorca:				
Single-Comb Black	9	7½	7½	6½
Single-Comb and Rose-Comb Whites, Rose-Black, and Single-Comb Buff	8	6½	6½	5½
Nagoya	7½	6	5½	4
Orpington	10	8	8½	7
Plymouth Rock	9½	7½	8	6
Redcap	7½	6	6	5
Rhode Island Red	8½	6½	7½	5½
Rhode Island White	8½	6½	7½	5½
Sussex	9	7	7½	6
Spanish, White-Faced Black	8	6½	6½	5½
Wyandotte	8½	6½	7½	5½

THE SIGNIFICANCE OF BREED AND VARIETY STANDARDS

The greatest significance arising from the development of breed and variety standards rests in the fact that the buying public demands uniformity in the stock it buys; there must be uniformity of type, color, and productive ability. The next greatest significance in the development of breed and variety standards is the stimulation given to the poultry-breeding industry. Another significant fact is that the numerous characters which different breeds and varieties possess have served as the basis for studies on the inheritance of those characters. The fact that various characters were found to be inherited and that certain combinations of characters could be "fixed" in strains of fowls proved to be a great stimulus to poultry breeders.

In order that poultry breeders might attain the greatest success in their breeding operations it was necessary for them to have an ideal standard in mind at all times. In the early history of the poultry industry, when the production of eggs and poultry meats was not so important from the economic standpoint as it is today, it was perfectly natural that emphasis should be placed upon details of plumage color and such other characters as type of comb, color of earlobe, and the presence or absence of feathering on the shanks or between the toes.

Poultry breeding as an industry lies at the foundation of poultry husbandry, and the many diversified standard breeds and varieties which have been produced from a very small number of ancestral forms is striking evidence of the degree to which man has developed and extended his control over the inheritance of the numerous characters which fowls possess. It is a truism that man's fancies have led to the production of many of the standard breeds and varieties at present existing in many parts of the world, and the satisfaction of having developed something new has constituted one of the best stimuli in man's efforts to understand the laws of inheritance.

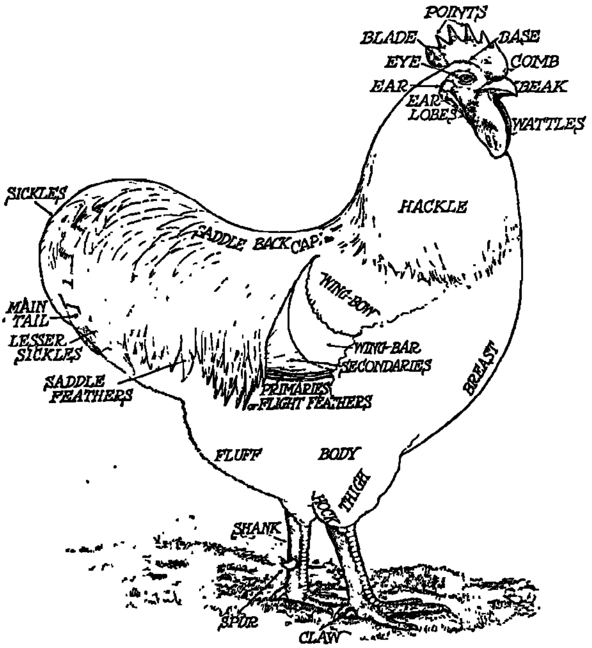

FIG. 5.—Glossary chart, giving the names of the different parts of the male fowl. (U. S. D. A.)

In a practical world, however, which we find ours to be, there has been a growing demand for the production of birds that meet man's needs as well as his fancies. The production of eggs and poultry meat has become of more importance than in former times. Therefore, more and more is the poultry breeder confronted with the question: How can one best select and breed his birds for the production of offspring possessing both standardbred and production qualities?

Although to the great majority of poultry breeders the production of eggs and meat is the main consideration, nevertheless it is true that *reasonable attention* must be given to the more important standardbred qualities. There are certain Single-Comb White Leghorn breeders who tolerate such things in their birds as side sprigs on the combs, stubs on the shanks, birds with bodies the size and shape of Plymouth Rocks, and birds with salmon-colored breasts, but they still insist that they are breeding standardbred Single-Comb White Leghorns. There are certain breeders of Rhode Island Reds who use as breeders birds with white in their earlobes, birds with straw-colored hackles, birds with white feathers, and birds the size of Leghorns, but still they insist that they are breeding standardbred Rhode Island Reds. Many breeders of other varieties also fail to give proper attention to production characters. What is needed in the poultry-breeding industry is a desirable combination of standardbred and production qualities.

The importance of breeding birds for beauty as well as utility is clearly emphasized by Dendy (1929) in the following words: "In spite of the gross materialism of the present age some of us still rejoice in the possession of an aesthetic faculty and recognize the existence of such a thing as beauty." The development of laying strains with a complete disregard for breed type and other standardbred characters would mean a great sacrifice in the interests of the art of poultry breeding. Do away with breed and variety standards, and what would happen to the poultry-breeding industry? Suppose that breed standards had never been adopted in the beef and dairy cattle, sheep and swine industries, what would be the present-day condition of these industries?

Whatever the poultry breeder's objective may be, it is a recognized fact that the basis of practically all breeding operations is the breed standard, the ideal shape or type and other characteristics by which one breed is distinguished from another. This is true whether one is breeding poultry for the novel characters they possess or for purely economic purposes. Although all breeds lay eggs and produce meat, there are some breeds that have little economic value; for instance, the author used Silkies in some crossing experiments involvin the inheritance of certain characters and found that the progeny whic inherited the blue or dark purple skin of the Silkies could not be marketed because of the natural prejudice against dressed chickens with such dark skin.

The great majority of poultry breeders of today are interested in the production of eggs or meat, for which purpose they usually breed a standard breed or variety. They are thus interested in maintaining certain breed or variety standards, particularly if they offer for sale hatching eggs, baby chicks, or breeding stock. Although it is necessary to maintain breed standards, it is true that in the early development of many breeds there was a tendency to attach too much importance to certain minor characters and too little importance to characters of economic importance. The most desirable ideal combines the essential characters of the standard for the breed and characters of the greatest economic importance.

THE IDEAL FOWL AS A BREEDING OBJECTIVE

The ideal fowl as a breeding objective is very easy to picture but very difficult to produce. The ideal fowl is one that not only possesses the most desirable characters but one that transmits those desirable characters to its progeny.

Since those who buy hatching eggs, baby chicks, laying pullets, and breeding stock demand a uniform product possessing a certain standard of excellence, and since the poultry breeder who sells hatching eggs, baby chicks, laying pullets, or breeding stock must meet the buyers' demands, it is necessary to consider the minimum requirements that breeding stock must possess in order that the poultry breeder may most readily accomplish his objective.

The great majority of poultry breeders desire to secure the greatest economic returns from their efforts; therefore, not only must their breeding stock conform to the standards of breed type and variety color, but the female breeders must be birds that are good layers of large-sized eggs, and both male and female breeders must give high fertility and hatchability of eggs and produce superior progeny. These are the minimum standards that the poultry breeder must adopt in order to make the greatest possible net income from his poultry-breeding operations.

Suppose that a farmer decides to replace his flock of mongrels with standardbred stock and has expressed a preference for birds with white plumage. As indicated below, he has the choice of several varieties, depending upon the color of skin, the color of egg laid, and whether he wants stock with rose or single combs.

Yellow skin, brown egg, single comb—White Plymouth Rock and others.
Yellow skin, brown egg, rose comb—White Wyandotte.
Yellow skin, white egg, single comb—S.C. White Leghorn and others.
Yellow skin, white egg, rose comb—R.C. White Leghorn and others.
White skin, brown egg, single comb—White Orpington.
White skin, white egg, single comb—S.C. White Minorca.
White skin, white egg, rose comb—R.C. White Minorca.

If the farmer had a preference for stock with buff or black plumage he would also have the choice of a number of varieties, depending upon the color of skin, color of egg laid, and type of comb.

As far as is known, none of the characters mentioned have any influence on factors of economic importance, such as hatchability and egg production, but the fact remains that most poultry men want their birds to conform to certain standards. The next few pages are devoted to a discussion of some of the more important requirements that birds should meet in order to conform to the standards of the breed and variety the birds represent.

Table 1 gives considerable information regarding the outstanding characters of each breed; Table 2 gives the standard weights for those breeds for which standard weights have been adopted. Among the more important characters by which a standardbred bird should be judged may be included the following: the symmetry of the bird or the degree to which its type conforms to that of the breed it represents, the relative size of the bird, the color of plumage, the kind of comb, and the absence of feathers or stubs on the shanks and toes of breeds having nonfeathered shanks. These and other characters are discussed briefly in the following pages for the purpose of giving readers some conception of the basic characters a good bird must possess.

Occasionally a bird may possess a character that is objectionable either from the standpoint of appearance or for economic reasons. A crooked keel is objectionable from the economic standpoint in marketing poultry and is considered a serious defect in breeding birds. A crooked back is also objectionable and disqualifies the bird possessing it from being considered a worthy specimen. There are other characters which birds sometimes exhibit, some of them being regarded as defects and others as disqualifications. A number of the more important defects and disqualifications which every poultry breeder should consider in the selection of his breeding stock are discussed in the following pages.

Symmetry.—By the term "symmetry" is meant the outline or contour of a bird. Is a certain bird symmetrical in all its parts? Symmetry really refers to feather contour plus the visible parts of the bird such as head and shanks and toes. Symmetry refers to the *tout ensemble* of the bird.

There are two characters that destroy a bird's symmetry and constitute disqualifications, and birds possessing either one should not be used in the breeding pen. One of the disqualifying characters is what is known as "squirrel-tail," a tail projecting forward beyond a perpendicular line drawn through the juncture of the tail and back at a right angle to the line of the back. A squirrel-tail makes a bird very unattractive. The other disqualifying character affecting the symmetry of a bird is what is known as "wry-tail," a tail turning permanently to one side from a vertical position. This character also makes a bird unsightly.

The extent to which the different breeds of chickens differ in body form without the feathers has never been determined, so that at present it is impossible to say that one breed is superior to any other *breed for egg production on the basis of body form alone.* The relationship between body form and egg and meat production is discussed in Chapter X.

Size.—The matter of size or body weight is an important one from the standpoint of maintaining breed standards. The standard weights of the different breeds have been given in Table 2, and individuals of the different breeds should be expected to attain the approximate weights given for cocks, hens, cockerels, and pullets, respectively.

In the case of Leghorns and Anconas, the standard weight of the cock is 6 pounds and that of the cockerel 5 pounds; if a cock weighs less than 4.5 pounds or a cockerel less than 3.5 pounds it is considered a disqualified bird. The standard weight of the Leghorn and Ancona hen is 4.5 pounds and that of the pullet is 4 pounds; but if either female falls more than 1 pound under the standard weight it is disqualified.

In all other breeds, except Bantams, recognized by the American Poultry Association and admitted to the Standard of Perfection, there are no weight disqualifications, but care should be exercised against breeding birds that are much below or above the standard weights given for each breed.

The Head and Its Adjuncts.—The head is usually the first part of a fowl that catches the eye, so that frequently the appearance of the head creates an impression that is applied to the rest of the bird. A male with a poorly developed or ill-proportioned head creates an unfavorable impression even though the rest of his body may be nigh perfect.

The head and its adjuncts include the beak, skull, eyes, comb, wattles, earlobes, crest, muffs, and beard. The first six characters are common to all breeds and varieties, whereas the last three are found in certain Continental and other breeds.

Beak.—The beak should be stout and of good shape, a deformed beak being a disqualification. The Standard of Perfection or the club standard for a breed should be consulted for the description of the ideal shape and color of beak, because, although most breeds have beaks that should be short or medium in length and well curved, there are marked differences between the beaks of such breeds as the Cornish, with its short, very stout, well-curved beak, and the Exhibition Game, with its long, tapering, slightly curved beak. The problem of the color of the beak in relation to egg production in breeds with yellow skin is discussed in Chapter X.

Eyes.—The eyes should be full and bright and of proper color for the breed or variety. Occasionally a bird is found in which one eye is lighter in color than the other eye; such a defect is considered quite serious.

Comb.—The types of comb common to each breed or variety have been given in Table 1. The most common type is the single comb, and the next most common is the rose comb. Other types, such as pea, walnut, V-shaped, and strawberry comb, are each common to a few breeds only.

Single combs vary a great deal in size depending upon the breed; for instance, the Cochin has a single comb of small size, the Plymouth Rock and Rhode Island Red each has a single comb of medium size, the Leghorn has a large single comb, and the Minorca has a very large single comb. All single combs should have five points, except the Minorca, which has six. The points in all single combs should be smooth; the third point is the longest and the second and fourth points are longer than the first and fifth. In Mediterranean females the single comb should begin to turn over just back of the second point. The most common defects in single combs include coarseness in texture, too many or too few points, and thumb marks or depressions on the side of the comb. Side-sprigs are a disqualification. A single comb that falls over to one side so that it becomes a lopped comb is a disqualification except in females of the Mediterranean breeds.

Rose combs are found in Wyandottes, Leghorns, Rhode Island Reds, Minorcas, Hamburgs, and other breeds. The size of rose combs varies greatly according to the breed. The points should be smooth and even. In the Leghorns and many other breeds the projection,

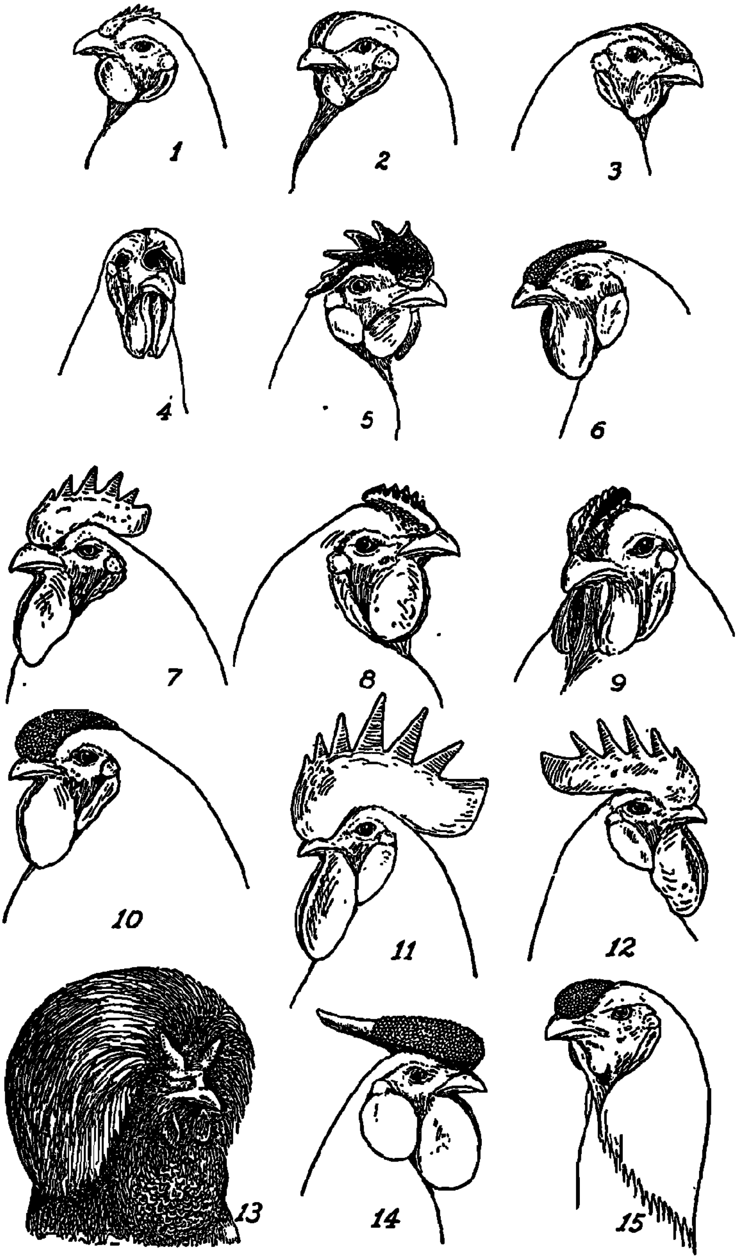

FIG. 6.—Ideal types of combs in different breeds. 1 and 7, single (Barred Plymouth Rock and Rhode Island Red); 2, 8, and 9, pea (Brahma); 3 and 10, rose (Wyandotte); 4 and 11, single (Minorca); 5 and 12, single (Leghorn); 6, rose (Rhode Island White); 13, V-shape (Houdan); 14, rose (Hamburg); 15, strawberry (Malay). (U. S. D. A.)

called spike, at the rear of the comb should extend horizontally, whereas in Hamburgs the spike should incline upward very slightly. The most serious defects in rose combs include coarseness in texture, unevenness in outline, unevenness in the points, a hollow center, and more than one spike on the rear of the comb. A rose comb lopping over to one side of the head sufficient to obstruct the sight constitutes a disqualification. A rose comb so large as to obstruct the sight is also a disqualification.

The other types of comb, such as pea and V-shaped, should be of relatively small size and well proportioned so that the bird's head has a good appearance.

Comb Quality.—The quality of the comb in all breeds is a very important matter because a comb of coarse texture is often associated with a bird having a coarse skin. The comb should be firmly attached to the head and in the case of the single comb not too thin, because a thin comb in males is inclined to lop and crack. A comb of soft, velvety texture is an indication of a soft, pliable skin which is desirable in layers.

Wattles.—The size of the wattles varies somewhat according to the breed with the exception that the Chantecler is supposed to be without wattles. The wattles of the Plymouth Rock and similar breeds should be of medium size, those of the Leghorn somewhat larger, and those of the Minorca still larger. The wattles should be smooth and of fine texture.

Earlobes.—The color of the earlobes is an important matter because, if neglected entirely, breeds with normally white earlobes may have many specimens with a great deal of red in the lobe and breeds with normally red earlobes may have many specimens with much white in the lobe. Positive enamel white in the earlobes of red-lobed breeds, except the Dorkings and Redcaps, constitutes a disqualification. The change in the pigmentation of the earlobe in relation to egg production in breeds with white earlobes is discussed in Chapter X.

Shanks and Toes.—The shanks and toes of a fowl are of importance from the standpoint of the support they give the body. The shanks should be straight and set well apart, avoiding any appearance of being "knock-kneed" or "bow-legged." The toes should be well formed. The shanks and toes should be of the proper length and color for the breed or variety which the bird represents. Dark spots on the shanks or toes of all breeds and varieties having yellow, white, or pinkish-white shanks or toes, except in the case of Anconas and Houdans, constitute a defect. On the other hand, if the shank or foot of a bird is of a color foreign to the breed or variety it represents, the bird is disqualified.

In all breeds in which nonfeathering of the shanks and toes is normal, the presence of a feather, stub, or feather-like growth on the shank or toe of a bird is a disqualification; in fact, a bird is disqualified if there is unmistakable evidence that such a character has been removed.

Plumage Color and Quality.—The color and the quality of the plumage of a bird are of importance in the maintenance of breed and variety standards. Maintaining proper color, so far as possible, is necessary; otherwise the members of a flock may soon lose all semblance of the color pattern of the variety they are supposed to represent. Good quality of feathering is important because it is apparently indicative of good health.

Some breeds differ considerably in the development of feathering: Cochins are noted for loose feathering; Leghorns have closer feathering; the Game breeds have extreme closeness of feathering.

Uniformity in Color Markings Desirable.—Some of the more important defects in plumage color and development are mentioned here because the poultry breeder should do everything possible to prevent them from becoming established in his flock. One of the greatest defects in all solid-colored varieties, such as Buff Orpingtons, Black Minorcas, and White Plymouth Rocks, is unevenness of surface color. Among parti-colored varieties, such as Barred Plymouth Rocks, Partridge Cochins, and Silver-Penciled Wyandottes, there is often lack of uniformity in feather markings and in the manner in which the colors of the different sections of the body blend with each other. Among other parti-colored varieties, such as Brown Leghorns, there is frequently a lack of distinctness in feather markings, so that certain sections, such as the hackle in the male and the wing-bows in both sexes, may be considerably "off-color" as far as the standard for the variety is concerned.

In white varieties, brassiness, a yellow cast on the surface of the plumage, is objectionable and constitutes a defect. When present, it is most noticeable in the hackle of the male and over the back and shoulders of both sexes. Certain strains of White Leghorns are inclined to show salmon color on the breast of the females. Gray specks and black ticking, sometimes present in white varieties, are defects; brown or black in the quills of the primaries or secondaries of white varieties are disqualifications.

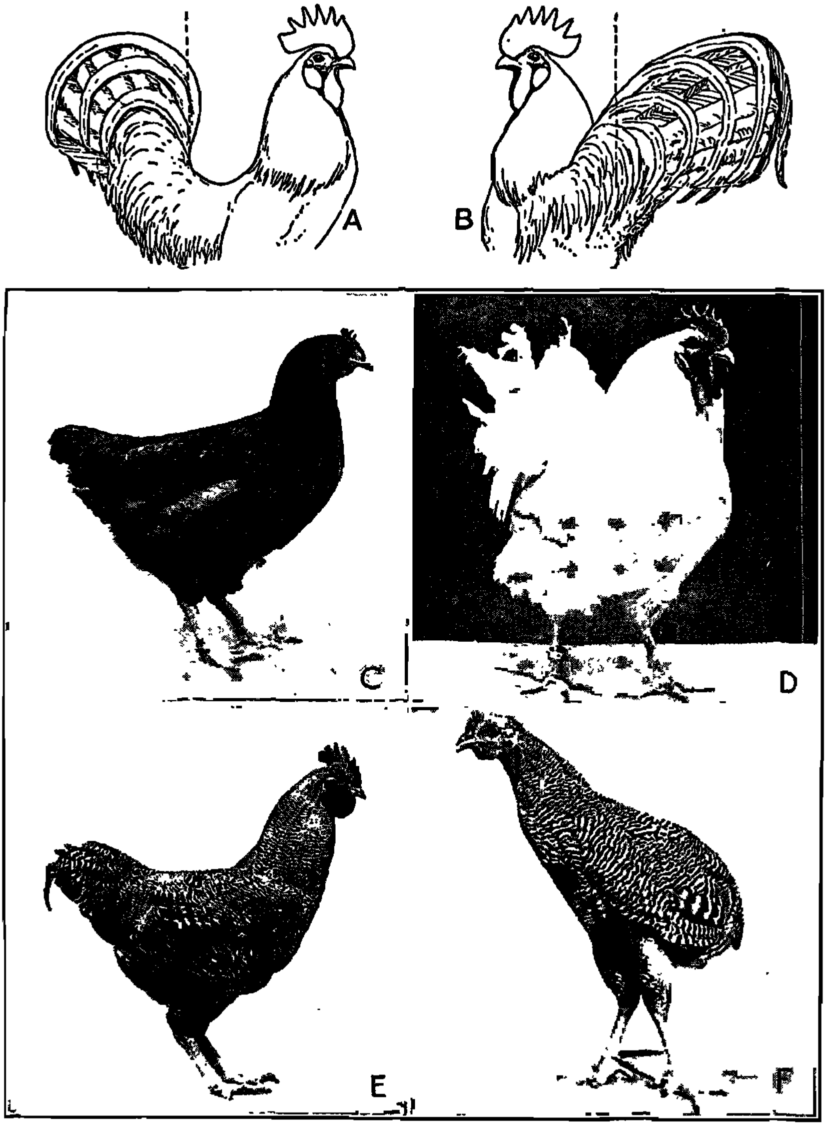

FIG. 7.—Common defects and disqualifications. A, squirrel-tail, a disqualification. B, wry-tail, a disqualification. C, split-wing, a disqualification. D, split-tail, a serious defect. E, slipped-wing, a disqualification. F, split-wing, poor body type, and weak constitution. (U. S. D. A.)

In buff varieties the appearance of black or white in any section of the plumage is a defect, as are also mealiness, light-colored shafting, and slate undercolor.

In black varieties perhaps one of the most common defects is purple barring. The primaries and secondaries of various black varieties sometimes have gray or white tips, both being defects. The presence of red or yellow in any part of the plumage of a black variety is a disqualification.

In red varieties, brassiness, mealiness, and light-colored shafting are defects. In Rhode Island Reds slate undercolor is a defect.

In barred varieties, including Barred Plymouth Rocks, Campines, and Gold and Silver-Penciled Hamburgs, unevenness of barring is a common defect. In Barred Plymouth Rocks, both brassiness and the presence of a black feather are defects.

A defect of a decidedly serious nature is a split tail, giving the tail an unfinished appearance. The defect is usually due to the faulty development of the main tail feathers, causing a gap to appear between them. A twisted feather in the wing or tail of a bird constitutes a disqualification. A wing that has a decided gap permanently developed between the primaries and secondaries is called a split wing, this being a disqualification. A wing in which the primaries are not held in proper position when the wing is folded, thus giving a drooping appearance, is said to be a "slipped wing" and is a disqualification.

For a discussion of the other defects and disqualifications of the various breeds and varieties the reader should consult the American Standard of Perfection, various breed club standards for breeds not recognized by the American Poultry Association, and a valuable discussion on judging by Lamon and Kinghorne (1929).

PROBLEMS

1. Why is it desirable for a poultry breeder to have a definite objective in mind in conducting his breeding work?

2. What is the significance of "breed" in the poultry industry, and how did the numerous existing breeds become established?

3. (*a*) What is the economic significance of the standard weights of various breeds?

(*b*) Mention five of the heaviest breeds.

4. (*a*) What two breeds have red ear-lobes and lay white-shelled eggs?

(*b*) Is there a breed with white ear-lobes that lays brown-shelled eggs?

5. (*a*) What is the chief difference in the nature of the penciling in the Partridge Cochin female and the Dark Cornish female?

(*b*) What is the difference in plumage color between partridge and silver-penciled varieties?

(*c*) What is the difference in plumage color between the Silver-Laced Wyandotte male and Silver-Penciled Wyandotte male?

6. (*a*) What are the defects and disqualifications most commonly encountered in White Leghorns?

(*b*) What are the defects and disqualifications most commonly encountered in Barred Plymouth Rocks?

7. Are the following characters of any economic importance to a poultry breeder who offers breeding stock for sale: comb conforming to the standard, color of ear-lobe, color of plumage, color of skin, color of egg, and size of bird?

8. Mention five of the most commonly occurring disqualifications.

9. Should a bird with a disqualification be used in the breeding pen?

10. Mention at least 10 varieties having white plumage, 10 having black, 5 having barred, 3 having blue, 3 having silver-penciled, 3 having partridge, and 3 having columbian.

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CHAPTER II

SEX AND REPRODUCTION

In comparison with some of the other domestic animals, the chicken is relatively a short-lived creature, its beauty and utility being spent, for the most part, in a year or two, after which replacement becomes necessary. Because it is a relatively small economic unit as compared with the larger classes of domestic livestock, the chicken can be reproduced in numbers quite readily. The reproduction of the flock involves the mating of males and females for the production of fertile eggs, the incubation of the fertile eggs produced, and the rearing to maturity of the chicks hatched. From the standpoint of poultry breeding, which is the theme of this book, the discussion on reproduction is confined to problems pertaining to sex and to the significance of mating.

PRIMARY SEXUAL CHARACTERS

Both the male and female fowl possess what are called primary and secondary sexual characters. The primary sexual characters are the organs involved in the production and elaboration of the reproductive cells; they include the primary sexual organs, such as the testes in the male and the ovary in the female, and the accessory sexual organs, which serve to carry the reproductive cells from the primary sexual organs to the exterior for purposes of fertilization. The primary sexual organs are called gonads.

The Male Gonads.—In the male the gonads consist of a pair of testes, or testicles, from each of which there is a tube called the *vas deferens,* leading to the cloaca, as shown in Fig. 8. The testes are called the primary sexual organs and the vas deferens the accessory sexual organ. The testes are situated at the anterior ends of the kidneys and are small yellowish-colored bodies frequently pigmented with melanotic pigment, according to Bittner (1925). That the left testis is usually larger than the right one has been observed by Thomsen (1911), Firket (1914), Swift (1915, 1916), Mimura (1928), and others. Domm and Juhn (1927), however, found that although this is true in very young birds, the right testis tends to become larger in older birds.

Each testis consists of a large number of slender tubes, called seminiferous ducts, from the linings of which the reproductive cells are given off, whence they are conducted to the vas deferens.

The vas deferens open into a pair of rudimentary copulatory organs or penes, which have been described by Dove (1928) and Yamaguch (1928).

The Female Gonad.—In the female the gonad consists of the ovary on the left side of the body, as shown in Fig. 8, which also shows the accessory reproductive organ, the left oviduct. In the embryo a right ovary and oviduct also develop, but they degenerate as the development of the embryo proceeds, so that at hatching time only rudiments remain. A few cases have been reported, however, showing both a right and left ovary and oviduct present in the adult fowl. As early as 1889 Brandt described an instance of the development of a right ovary in the fowl. The observations of Gadow (1891) and Chapellier (1913) demonstrate that a persistent right ovary occurs in various orders of birds. Kirkpatrick and Card (1916) describe a White Wyandotte with two functional ovaries and oviducts. Kaupp (1922). shows a photograph of the gonads of a hen having two functional ovaries and oviducts, and Atwood and Snyder (1922-23) describe a White Leghorn which laid eggs of two distinct shapes, indicating apparently the presence of a right as well as a left ovary and oviduct. Hertwig (1930) describes a chick with two well-developed ovaries.

Crew (1931) describes a Brown Leghorn with a large and completely developed right oviduct as well as a normal left oviduct and ovary. The bird carried a testis graft which had been implanted in infancy, though Crew points out that the graft could not be claimed to be responsible for the development of the right oviduct. A Wyandotte hen is also described in which were found a right and a left non-convoluted oviduct and a degenerate left ovary; no gonad was discernible on the right side. Crew explains the presence of the right oviduct on the assumption that its development took place in the absence of an internal stimulus, which causes the atrophy of the right oviduct in normal birds.

Location of Gonad.—The left gonad is situated to the left of the median line of the body just posterior to the lungs and at the anterior end of the kidney, and is attached to the dorsal wall of the body cavity. In an inactive condition, as in the case of an immature pullet, the gonad appears as a small, whitish mass of irregular contour, whereas in an active condition it appears as a yellowish cluster of cells of varying size. Each cell, with its vitelline membrane as a

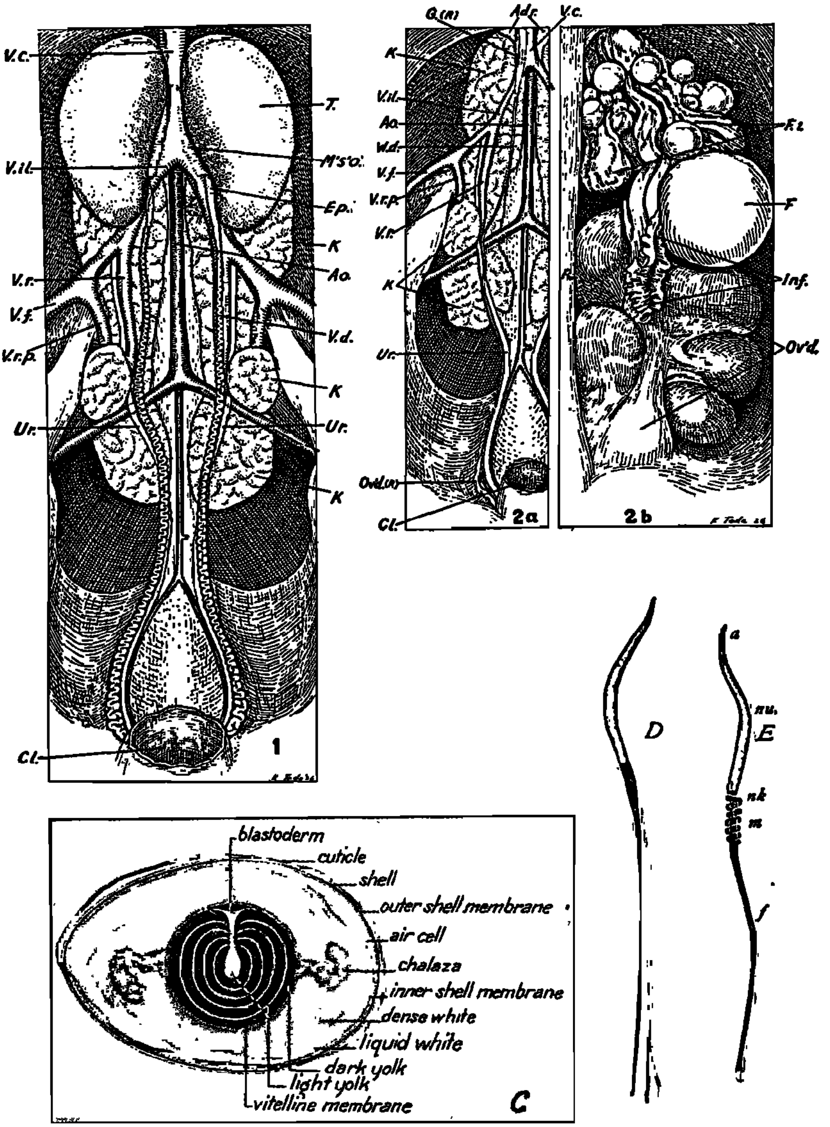


Fig. 8.—The reproductive organs and cells of the domestic fowl. 1. The reproductive organs of the male: T, testis; V. d., vas deferens; Cl., cloaca. 2a. Right side of female: G(R), rudimentary gonad; Ov'd(R), rudimentary oviduct. 2b. Left side of female: F.1, ovulated follicles; F, mature follicle; Inf. Infundibulum or mouth of the oviduct; Ov'd., oviduct. (After Domm.) C. The egg or reproductive cell of the female. The blastoderm is popularly called the germ-spot. (After Lippincott.) D and E. The reproductive cells of the male, popularly called sperm; in this illustration they are much enlarged, relatively.

lining, is an ovum and is contained in a very thin envelope called the "follicle" which is attached to the ovary by a very slender stalk. Embedded in the ovum is the nucleus, or germinal vesicle, or germ spot.

Development of the Ova.—It is in the nucleus or germ spot of the ovum that the chick originates, but all the yolk and the albumen or white of the egg contribute to the nourishment of the chick. Each ovum commences as a tiny cell in the ovary, but the accumulation of yolk granules in concentric layers of light and dark yolk soon leads to an increase in size until the ovum is ready to be discharged from the ovary.

During the growth of the ovum the follicle enlarges and, when the ovum is ready to be discharged from the ovary, bursts along a streak called the "stigma." The ovum is grasped by the mouth of the oviduct and passes down that organ by peristaltic movement.

Secretions of the Oviduct.—As the ovum, usually referred to as the yolk, passes down the oviduct, there are secreted around it the albumen, shell membranes, and shell. The albumen consists of the two chalazae, a thin fluid layer, an inner layer of dense albumen, and an outer layer of thinner albumen. The chalazae are dense portions of albumen twisted in opposite directions and are attached on opposite sides of the yolk to a layer of albumen surrounding the yolk. The shell membranes consist of the inner and outer shell membranes, surrounding the albumen and lying next to the shell. The shell is composed of two layers and a cuticle. The formation of the eggs is discussed in greater detail in Chapter VIII.

Most eggs are oval with one end larger and more blunt than the other. The egg is laid either end foremost, according to observations made recently at the U. S. Animal Husbandry Experiment Farm, at Beltsville, Maryland.

SECONDARY SEXUAL CHARACTERS

The sexes differ not only in reproductive organs but also in many other respects. Such differences are generally referred to as secondary sexual characters because they are not directly concerned in the production and liberation of reproductive cells.

Structural and Other Sex Differences.—The voice of the male differs from that of the female, and the behavior of the sexes differs, particularly in courtship. The male usually has a larger comb and wattles; the lower neck, saddle, sickle, and tail feathers are long and the first three kinds of feathers mentioned are more point than in the female. Spurs are nearly always present on the sha of mature males and rarely so on the shanks of females. These differences exist between the sexes of practically all breeds, the principal exception being in respect to the shape and length of the lower neck, saddle, and sickle feathers in henny-feathered males, which are discussed later.

Sex Dimorphism in Plumage Color.—There are a number of breeds in which the sexes differ not only in respect to the characters already mentioned but also in the color of the plumage. In many males the *tout ensemble* is more gaudy than in females. Partridge-colored, silver-laced and silver-penciled varieties, illustrated in the first chapter, are examples of sex dimorphism in plumage color. The reader is advised to refer to the illustrations in Chapter I to see clearly the differences in plumage color that exist between the sexes of several varieties.

Sex Differences in Skeleton.—Schneider and Dunn (1925) and Hutt (1929*a*) have shown that there are significant differences between the length of the wing and leg bones in males and females, males having longer bones than females. Nevertheless, Hutt was unable to find any bone measurement in the appendicular skeleton which would permit diagnosis of doubtful individuals.

Sex Differences in Body Weight.—The male is nearly always larger in size or heavier in body weight than the female of the same breed. For the extent to which the sexes differ in so-called "standard" weights of the different breeds reference should be made to Table 2. Although the results of Schneider and Dunn (1925) and Kopeć (1927) show that body weight is much more variable than bone measurements, Latimer (1927) observed a sex difference in the weights of the humerus, tibia, and tarsus, when their weights were plotted against body weight, and a sex difference was also observed in the weight of bone per unit of length in the humerus and tarsus, when plotted against body weight.

Sexes Differ in Number of Red Blood Corpuscles.—The fact that the mature male and female domestic fowl differ in the number of red blood corpuscles, or erythrocytes, they contain has been demonstrated by Blacher (1926), Chaudhuri (1926), and Juhn and Domm (1930). Chaudhuri found an average of 4,560,000 red blood corpuscles per cubic millimeter of blood in mature males and an average of 3,127,000 in mature females. Mature females contain approximately the same numbers as immature birds of both sexes. In addition, Juhn and Domm observed that in mature males the number of corpuscles fluctuates somewhat, apparently according to season or breeding activity, the highest numbers being exhibited during the breeding season.

A Chemical Test for Sex.—Manoiloff (1922-23) devised a chemical test for sex which may be made on the blood of fowls and other animals. The test is based upon oxidative reactions, a color difference being found to exist between males and females. Steele and Zeimet (1925) devised a simpler test than Manoiloff's and found that it could be applied not only to the blood but also to pulp of growing feathers. In the feather test the color change is the reverse of that given by the blood. Steele and Zeimet observe that their results indicate that quantitative rather than qualitative differences are concerned in the sex reaction.

ALTERING THE APPEARANCES OF THE SEXES

Although the sexes differ in respect to their primary sexual characters and associated organs and secondary sexual characters, research work during recent years has demonstrated that under certain circumstances a male may look like a female in external appearances and a female may resemble a male. Knowledge concerning fundamental differences between the sexes has been increased considerably, and much more is known now than even ten years ago concerning the influence of the primary sexual characters on the secondary sexual characters.

Transplanting Combs, Wattles, and Spurs.—Before discussing the influence of the gonads on the development of such characters as combs, spurs, hackle, saddle, and sickle feathers, it is well to call attention to some interesting experiments performed by Kozelka (1929, 1930), the results of which give a better understanding concerning factors that are responsible for the differences between male and female combs, wattles, and spurs. These structures were transplanted from one individual to another of the opposite sex, the operations being performed on chicks within three days after hatching It was found that when either male or female combs or wattles were grafted on the male chick they grew larger than when they were grafted on the female chick. Apparently the ultimate size of either the comb or the wattles is determined by the host rather than by the donor.

Male spurs grafted on both male and female chicks developed into characteristically male spurs, whereas female spurs grafted on the male chick developed, for the most part, into female spurs, and female spurs grafted on other female chicks retained their feminine

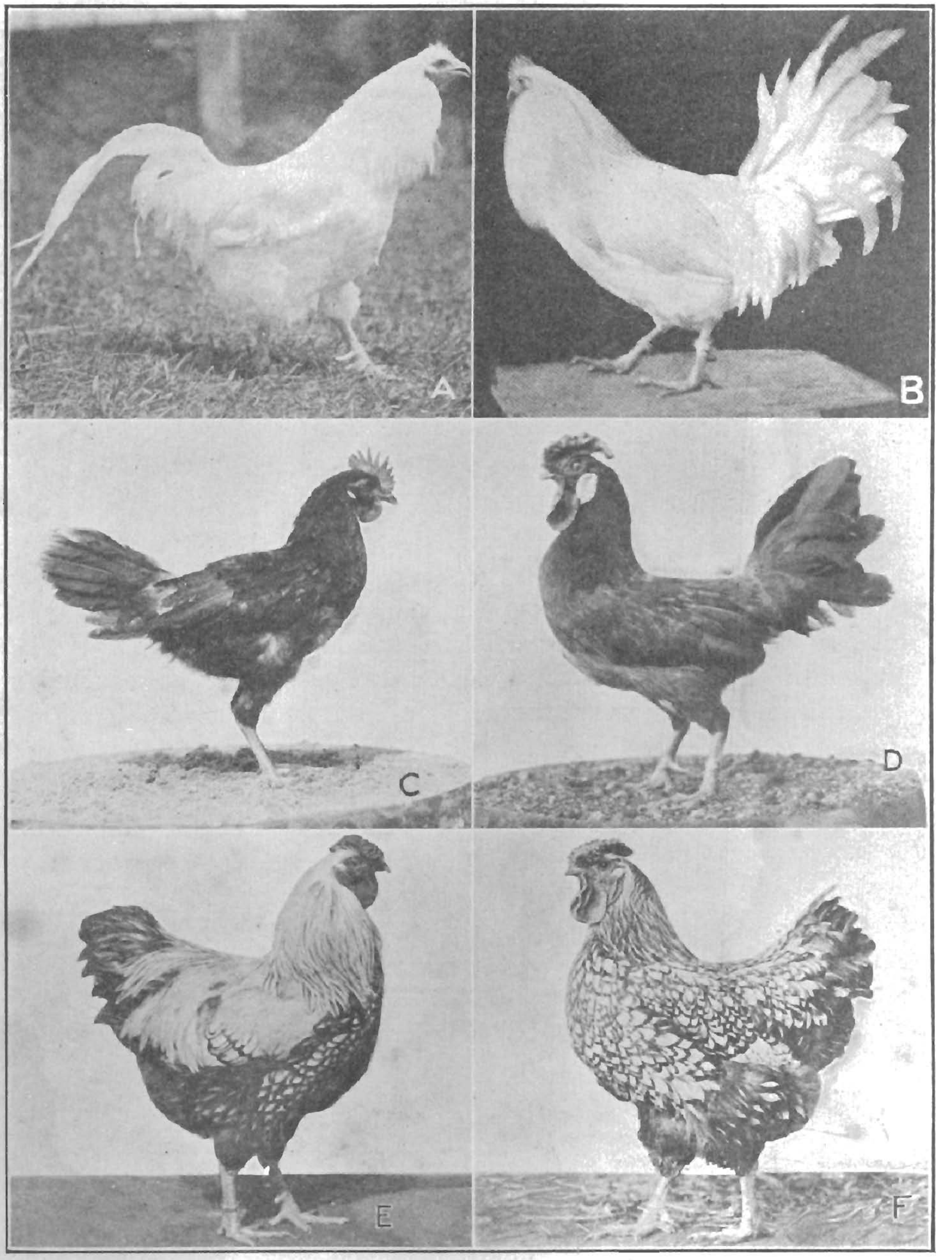


FIG. 9.—Males acquire different plumage under different circumstances. A, a capon, resulting from the removal of the testes. (U. S. D. A.) B, a developmental capon, no operation having been performed. (After Greenwood and Crew.) C, a Brown Leghorn cockerel that acquired plumage resembling that of a female as a result of being fed desiccated thyroid. D, a hen-feathered Brown Leghorn male, the result of breeding. E, a cock-feathered Silver-Laced Wyandotte, male. F, a hen-feathered Silver-Laced Wyandotte male. (U. S. D. A.)

character. The size of spur is apparently determined by the donor rather than the host.

Male Gonads and Comb Development.—It is a well-known fact that during the growth of the cockerel his gonads, or testes, increase in size as does his comb, and when he reaches maturity his other secondary sexual characters have become fully developed. Souba (1923) has shown that there is a quantitative relationship between the development of the gonads and the comb in single-comb White Leghorn cockerels. A similar finding has been reported by Finlay (1925), who in addition observed that such differences between the sexes as size, conformation, spurs, and voice are modified by gonadic activity but are not entirely dependent on the gonads since the fundamental differences between the sexes cannot be obliterated by masculinization or feminization experiments.

Greenwood and Crew (1927*a*), in a critical examination of the law of "all-or-nothing" in respect to the degree of the development of the gonad in its effect on comb size enunciated by Pezard (1922), came to the conclusion that the size of comb attained by a male is determined by the degree of cell activity in the gonad. Blyth (1928) investigated the matter still further and found that increased comb growth manifested in the "springing" of the comb is coincident with the development of certain cells in the gonad.

Domm (1930) observed that males when kept out of the sunlight usually develop combs larger than when allowed in the sunlight, thus showing that sunlight is an additional factor to gonad activity in governing comb development.

Effect of Removing Male Gonads.—When a normal male is castrated, by removing both the right and left gonads, the bird is called a capon, for an illustration of which see Fig. 9. The effects of the operation are several, including a considerable reduction in the size of the comb and wattles, longer hackle and saddle feathers, and a larger size of body than in uncastrated males. The spurs usually grow longer and are more slender than in normal males. The capon is more docile than the normal male and, according to Goodale (1916*b*), may manifest the brooding instinct in caring for chicks.

Greenwood and Crew (1927*b*) have shown that occasionally a male may become in all appearance like a capon without the removal of the testes by operation. A bird of this kind is shown in Fig. 9. Post-mortem examination of such birds, called developmental capons, revealed either complete absence or reduction in the size of the gonads.

If the operation for removing the testes is not entirely successful so that a portion of one or both gonads is left in the bird, that bird is called a "slip" and usually shows the development of comb and wattles characteristic of the normal male.

According to the observations of Benoit (1925) and Domm and Juhn (1927), when only one testis was removed by operation, the other testis increased in size until it was frequently as large as both testes in a normal male of the same age, except in the case of the right testis in birds having the left testis removed when they were young chicks. When growing cockerels were operated upon, the remaining left testis increased in size more than the remaining right testis. On the other hand, Hutt (1929*b*) observed that compensatory hypertrophy to a degree approximating to the normal weight of both testes occurred in the retained right testis of cocks castrated unilaterally on the left side at one week of age.

Feminized Male Birds.—If the gonads are removed from a cockerel and ovarian tissue from a female is grafted on the site of one of the removed gonads, the bird comes to resemble a female in almost every outward respect except size, particularly in respect to the shape of the feathers and plumage color. The change occurs when the bird molts after being operated upon. Goodale (1916*a*, 1916*b*) and others have produced feminine-appearing males in Brown Leghorns, a variety in which the adult plumage color pattern of the sexes differs markedly. Goodale (1918), Zavadowsky (1926), and Finlay (1925) demonstrated that the removal of only one male gonad and implantation of ovarian tissue resulted in the development of normal female feathering. The results of these experiments show that the influence of the female gonad is quite different from the influence of the male gonad on certain aspects of feather development.

Hen-Feathered Males.—Among the standard breeds of poultry described in the American Standard of Perfection (1930), Sebright Bantams and Campines are shown to be "hen-feathered" breeds. In these two breeds the male hackle, saddle, and sickle feathers, commonly referred to as secondary sexual characters, are of the same shape and color and relatively the same length as in the females. In other respects the color of the males is identical with that of the females. Most of the other standard breeds may be divided into two groups: (1) those in which the males differ from the females in respect to the shape and length of the hackle and saddle feathers, and (2) those in which, in addition to differences in shape and length of the hackle and saddle feathers, there are also differences in the color of the hackle and saddle feathers in the two sexes and the males frequently have breast and body feathers different in color from the females. The first group includes such varieties as White Leghorns, Light Brahmas, Barred Plymouth Rocks, Buff Orpingtons, and Jersey Black Giants. The second group includes such varieties as Brown Leghorns, Silver-Penciled Plymouth Rocks, Silver-Penciled Wyandottes, Silver Gray Dorkings, Partridge Cochins, Partridge Plymouth Rocks, and Partridge Wyandottes.

The existence of normal hen-feathered males, such as Sebright Bantams and Campines, demonstrates that the female type plumage is not always dependent upon the presence of the female gonad, or ovary. It has been demonstrated by Roxas (1926) and Greenwood (1928) that when gonad grafts from hen-feathered males are implanted in castrated cock-feathered males the plumage is cock-feathered, whereas when gonad grafts from cock-feathered males are implanted in castrated hen-feathered males the plumage is hen-feathered.

In a series of experiments over a period of years, Morgan (1913, 1915, 1917, 1919, 1920*a*, 1920*b*) has shown that the castrating of the Sebright Bantam male results in his becoming completely cock-feathered.

Thyroid and Plumage Development.—The fowl possesses a number of ductless or endocrine glands which produce internal secretions, called hormones, some of which have been shown to produce pronounced effects on the development of the plumage, in respect to both the color and the shape of feathers in males. The hormones secreted by the thyroids have a particular bearing on the development of hen-feathering.

That a tendency toward hen-feathering may be induced in cock-feathered males by feeding them desiccated and raw thyroid has been demonstrated by Torrey and Horning (1922, 1925), Cole and Reid (1924), Crew (1925), and Cole and Hutt (1928), who found, however, that feeding thyroid induced no change in the hen-feathered condition of Sebright males.

Greenwood and Blyth (1929) advance the hypothesis that the female gonad stimulates the thyroid to a higher level of activity than the male gonad and that the female gonad acts directly on the feathers, modifying the effects of thyroid activity, so that in such varieties as Brown Leghorns the deposition of melanic pigment is restricted. According to Danforth (1928, 1929*a*, 1929*b*), differences in feathers are due to genetic differences in the feather follicles.

Females That Change Color.—Several cases have been reported in which colored females developed into white-plumaged birds. Lippincott (1920) observed such a phenomenon in the case of a Blue

Andalusian, and Crew (1922) described a Black Leghorn which turned to white. Such changes have been reported to be due to the development of a tumor on the ovary or to other pathological conditions affecting the ovary, though it has apparently never been established definitely that such is the cause.

Females That Look Like Males.—Goodale (1913, 1916c) has shown that the removal of the ovary in the case of Brown Leghorn and other dimorphically colored varieties results in the development of cock-feathering. This is true also in the case of Sebright Bantam females. On the other hand, testicular tissue added to ovarian tissue in females does not produce any change in the female plumage. Boring and Pearl (1918), Cole and Lippincott (1919), Parkes and Brambell (1926), Cole (1927), and others have shown that when the ovary of a female is affected by a tumor or in some other abnormal way the female develops cock-feathering. Gates (1918) and others have reported cases of females developing head furnishings and spurs as in males, such changes being nearly always due to some abnormal condition in the ovary. Gatenby and Brambell (1924) describe a White Leghorn completely henny except for its head, which resembled that of a cock bird. It courted other hens up to a certain point and then attacked them savagely, and it crowed often and loudly. On the left side there was an ovary full of scar tissue and it contained testicular tubules.

A case of double change in sex appearance has been reported by McCance and Walton (1930), the bird being a Light Sussex pullet which laid up to the time she was about one year old, then in her second year she gradually assumed male plumage, developed spurs, and grew two inches taller than other pullets of the same age kept with her all the while. She behaved as a male and was observed mating with one of the other hens. In the spring of the third year she was seen going to the nests, and when she became broody a dozen eggs were placed under her, eleven of which hatched and the chicks were brooded successfully. In the late spring of her fourth year she began laying again, and in the fall she molted and reassumed hen plumage.

The results of extensive experiments in removing the ovary in Brown Leghorn females have been reported by Domm (1924, 1927), who confirmed the results of Goodale concerning the development of cock-feathering following the removal of the ovary. Domm carried the work much further, however, and observed that the cock-feathered females subsequently became hen-feathered. He found that when the ovary was completely removed there was compensatory growth of

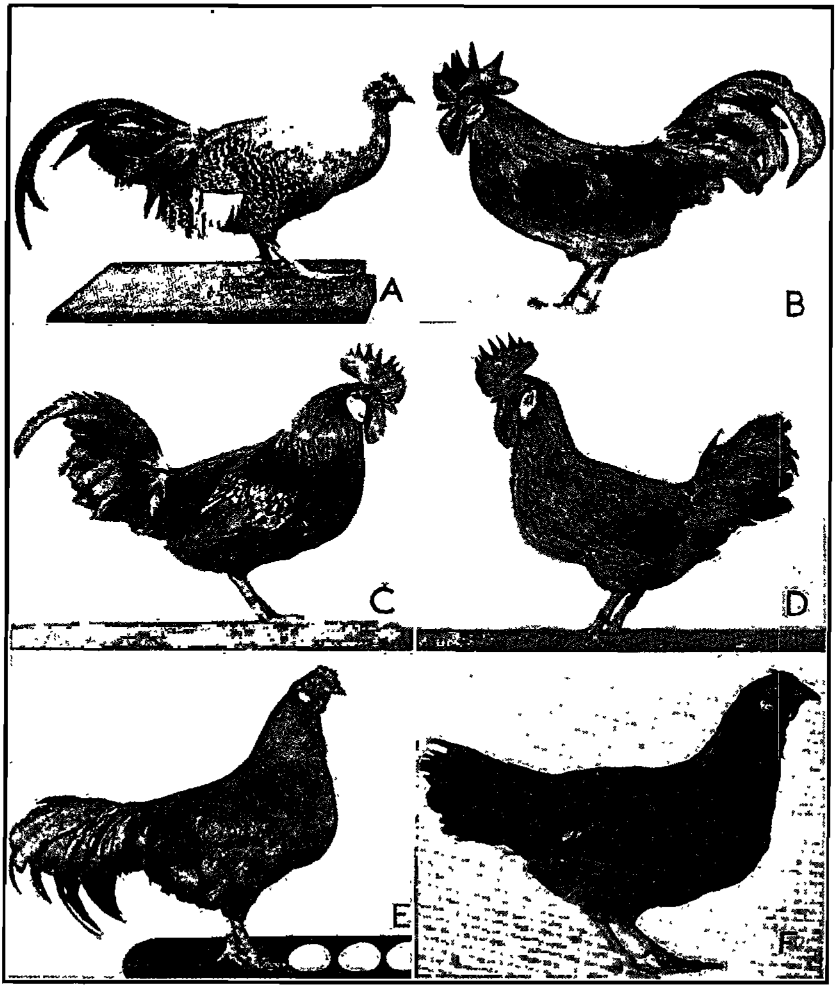


FIG. 10.—Females sometimes look very much like males. A, a female that assumed male plumage and developed spurs, known as a developmental poularde. (After Greenwood and Crew.) B, a female Brown Leghorn from which the left ovary was removed at thirteen days of age, photographed two years later; she is known as a poularde. (After Domm.) C, a female Brown Leghorn which assumed male head furnishings and plumage and seven months later her plumage returned to that of a female, as shown in D, although she retained male head furnishings. (After Greenwood and Crew.) E, a female that looked like a male but laid eggs and later acquired female plumage, as shown in F. (After Cole.)

the right gonad, which had the appearance of a testis. The growth of a similar structure was occasionally observed on the site of the removed ovary. He further found (1929*a*) that when the compensatory gonads were destroyed by cauterization the females became capon-feathered. That is, a Brown Leghorn female, hen-feathered originally, became cock-feathered when the ovary was removed and then became hen-feathered owing to the influence of the compensatory gonads, and when these were removed the final plumage development was capon-feathered.

Besides the changes in plumage following the removal of the ovary there is further development of the comb and wattles and spurs so that the female resembles a male very closely. Such a female, called *poularde*, behaves much like males, sometimes to such an extent as to tread other hens. When the compensatory gonad is destroyed by cauterization the head furnishings remain small and spurs develop so that these birds resemble capons.

Hermaphrodites and Gynandromorphs.—By the term hermaphrodite is understood an animal, such as the earthworm, containing male and female gonads that function in the production of male and female reproductive cells. So far as is known, no case has ever been reported of a fowl having functioning male and female gonads at the same time although several instances have been reported of birds possessing both a male and a female gonad, and such specimens have been called hermaphrodites. Some of the more outstanding of such cases are those described by Shattock and Seligmann (1906, 1907), Pearl and Curtis (1909), Parhon and Parhon (1922), and Hartman and Hamilton (1922), the one reported by Hartman and Hamilton being the nearest approach to a truly hermaphrodite bird in nature. Boring and Pearl (1918) describe two abnormal birds which exhibited normal male sexual desire but laid eggs.

In view of the results secured during recent years in the removal and transplantation of male and female gonads, it is apparent that the so-called hermaphrodites have developed as such as a result of an abnormal development of the gonads.

A gynandromorph is an animal in which part of the body is male and the other part female. Macklin (1923) has described a bird which in general appearance resembled a female except that the neck feathers were like hackle feathers of a male and the tail feathers were slightly longer than those of a normal hen. The comb and right wattle were typically male in appearance, and the bird exhibited male sexual behavior, mating with hens. Upon examination, a testis was found on the right side and an ovary and oviduct on the left side. The bones of the right side were longer and larger than the bones of the left side of the body. Lillie (1931) has offered the suggestion that the gynandromorphic condition in plumage is dependent upon a subnormal amount of female hormone.

IS SEX REVERSAL POSSIBLE?

Greenwood (1925*a*) secured results which indicate that in the fowl the processes of sexual differentiation are not capable of modification solely through the action of gonadic implants on embryos at seven days of incubation. Subsequent experiments by Willier (1927) and Willier and Yuh (1928) also seem to show that gonad grafts on the chorio-allantoic membrane of the developing embryo do not exert a specific effect on the reproductive system of the host embryo.

As a result of further investigations, Greenwood (1925*b*) developed the hypothesis that the right gonad is fundamentally female in constitution, and that if it be differentiated under a specific stimulus an ovary would be formed.

Sex Reversal in Nature.—A case of sex reversal in the domestic fowl has been reported by Crew (1923). A Buff Orpington hen maintained a normal condition for over three years, during which time she laid many eggs and raised many of her own offspring for her original owner. At the age of about three and one-half years her head furnishings increased in size, and after molting the feathers of the neck, saddle, and tail resembled those of a male. The following spring the bird behaved like a male and was placed by Crew with a virgin Buff Orpington hen, from which mating two chicks were hatched. The gonads of the fowl whose sex had become reversed were examined by Fell (1923), who observed that the bird had been suffering from abdominal tuberculosis. Fell found present two functional testes, a thin oviduct, and paired vasa deferentia. Here, then, is a case of complete sex reversal in the domestic fowl, assuming that there is no question of the bird having been originally a normal female.

Sex Reversal Induced Experimentally.—During recent years experimental evidence has been secured which shows that sex reversal in the domestic fowl may apparently take place, but it should be noted that it is only females that can be induced to change their sex. It has never been demonstrated that males can be induced to become females, nor has a case ever been reported where a functional male ever became a functional female, although, as related in previous sections of this chapter, there are many cases where males have come to resemble females very closely. The important point to bear in mind, therefore, is that females may became males but males apparently cannot become females.

According to the work of Swift (1914, 1915), Firket (1914, 1920), and Brode (1928), primordial germ cells are present in the medulla of both right and left gonads of the female chick in its early stages of development, although Brode has shown that these primordial germ cells decrease in number until about three weeks after hatching when practically all have disappeared from the right gonad, which itself becomes a mere rudiment. Domm (1929*a*) removed the ovary from females as early as the seventh and eighth day after hatching and observed in some cases that the right gonad contained active spermatozoa. In this respect his results confirmed the observations of Benoit (1923*a*, 1923*b*, 1923*c*) and Zavadowsky (1926).

According to Lillie (1927) the female fowl is a hermaphrodite with respect to its endocrine organization, the male component being quiescent but never extinguished. Domm (1929*b*) believes that the primordial germ cells, in the female at least, may lead to the development of a male under certain conditions; the gonad of the female produces male as well as female sex hormones, whereas the gonad of the male produces male sex hormones only. According to Domm, the female fowl is in reality bisexual, and whether she remains a female or finally becomes a male seems to be dependent upon whether the secretions of the female sex hormones are maintained or inhibited, the latter condition allowing the male sex hormones to come into play.

From the results of his examination of a number of right gonads and associated organs which had developed in females after removal of the left ovary, Gray (1930) makes the observation: "The female fowl thus has the potentiality for forming a complete male genital system from gonad to cloaca."

THE SEX RATIO

Studies on the sex ratio of the domestic fowl are of interest from the standpoint of ascertaining the normal sex ratio and the extent and causes of deviations therefrom which may occur under varying circumstances. A determination of the cause or causes of any deviation from the normal sex ratio might lead to the possibility of modifying it as a result of breeding practice. First, however, it is necessary to determine the normal sex ratio, meaning the percentage of males of the total population.

The Normal Sex Ratio.—The most extensive data on the normal sex ratio in the domestic fowl have been contributed by Pearl (1917), who observed a sex ratio of 48.57 ± 0.28 among various breeds. This sex ratio was determined on the basis of 10 or more chicks per family and was regarded by Pearl as being much nearer the true biological norm for the sex ratio of his flock than that determined on families of all sizes. On the other hand, Jull (1931*a*) has shown that size of family does not affect the sex ratio of the total population when the sex ratios of a large number of families are taken into consideration.

Sex ratios of various strains of domestic fowl reported by various workers are given in Table 3.

TABLE 3. SEX RATIOS IN DIFFERENT STRAINS OF DOMESTIC FOWL OBTAINED BY VARIOUS INVESTIGATORS

Investigator	Year	Number of Observations	Sex Ratio
Darwin	1874	1,001	48.65 ± 1.06
Field	1901	2,105	44.63 ± 0.73
Thomsen	1911	805	47.82 ± 1.19
Pearl[1]	1917	20,037	48.57 ± 0.28
Pearl[2]	1917	22,791	49.45 ± 0.22
Crew and Huxley	1923	763	48.62 ± 1.21
Jull[3]	1924	936	48.82 ± 0.80
Jull[4]	1924	2,396	48.41 ± 0.47
Musschl	1924	1,514	52.25 ± 0.87
Lambert and Knox	1926	2,910	51.13 ± 0.62
Horn	1927	2,131	51.62 ± 0.73
Lambert and Curtis	1929	2,501	46.82 ± 0.67
Callenbach	1929	7,850	49.41 ± 0.45
Christie and Wriedt	1930	3,680	49.60 ± 0.82[5]

[1] Families of 10 or more chicks per family.
[2] Families of all sizes.
[3] Families of 10 or more chicks per family, produced in the normal hatching season.
[4] Families of 10 or more chicks per family, produced during the first year of egg production of the dams.
[5] Standard error.

Factors That Do Not Affect the Sex Ratio.—A number of observations have been made concerning factors which do not affect the sex ratio. That prenatal mortality does not affect the sex ratio has been determined by Thomsen (1911), Pearl (1917*a*), Crew and Huxley (1923), Jull (1924), Lambert and Knox (1926), Horn (1927), and Lambert and Curtis (1929).

That large eggs tend to produce male chicks and small eggs female chicks was the observation of Lienhart (1919), but the observations of Jull (1924) and Jull and Quinn (1924, 1925) show quite definitely that egg weight bears no relation to sex ratio. Jull and Quinn (1925) found no significant difference between the weights of male and female chicks at hatching time, and Jull and Heywang (1930) found that the ratio of chick weight to initial egg weight is independent of the sex of the chick. Jull and Quinn (1924) also found that there is no relationship between the sex of the chick and the absolute length or the relative length or the shape of the egg from which it is hatched.

Jull (1924) showed that there is no relationship between yolk weight of egg and sex nor between yolk water content of egg and sex, and Jull and Heywang (1930) found that the ratio of yolk weight to chick weight at hatching time is independent of the sex of the chick.

Lambert and Curtis (1929) and Christie and Wriedt (1930) observed no significant differences among sex ratios of families of hens of different ages.

Antecedent Egg Production and the Sex Ratio.—The results secured in a cross between Brown Leghorn males and Barred Plymouth Rock females made by Jull (1924) indicated that the greater the egg production prior to the hatching season the lower the sex ratio, the sex of the chicks having been determined at hatching time. The results secured by Musselil (1924), Lambert and Curtis (1929), Callenbach (1929), and Christie and Wriedt (1930) show no relationship between antecedent egg production and sex ratio, in all these cases the sex ratio having been determined when the progeny approached maturity. Moreover, as the result of more recent investigations, Jull (1931*b*) found that in the case of Barred Plymouth Rocks, Rhode Island Reds, and White Leghorns antecedent egg production did not affect the sex ratio, which was determined when the progeny reached maturity.

Breeding and the Sex Ratio.—Callenbach (1929) secured results indicating that different strains of domestic fowl produce differing sex ratios. Musschl (1924) secured results that show sex ratios from different males differing materially, and Jull (1924) secured sex ratios of 91.67 and 66.67, respectively, from two hens based on their total annual egg production. Christie and Wriedt (1930) observed that some of their females gave aberrant sex ratios, six each giving a low sex ratio and three each giving a high sex ratio.

Evidence bearing on the problem of the sex ratio in the domestic fowl in relation to inbreeding has been presented by Jull (1931*b*) in the case of the inbred Barred Plymouth Rocks and White Leghorns. It was found that such close inbreeding as mating full-brothers-and-sisters and half-brothers-and-sisters for three years in succession has no significant effect on the sex ratio.

Postnatal Mortality and the Sex Ratio.—Since it has already been observed that prenatal mortality does not affect the sex ratio, it would naturally be expected that postnatal mortality between the sexes would not differ significantly. Landauer and Landauer (1931) found, however, that among 5,683 crossbred and Leghorn chicks that died between hatching time and the end of the second month there were more males than females.

Since the sex ratios of the chicks that died differed significantly from a sex ratio of 50.00, Landauer and Landauer have suggested that more males than females died because of the existence of a higher metabolic rate in the male than in the female, the metabolic rate of the latter being regarded as approaching optimal conditions. Just why such a condition should affect postnatal but not prenatal mortality is not clear, and further evidence is awaited with interest.

Jull (1932) has shown that the tendency to produce a preponderance of either sex is apparently not inherited.

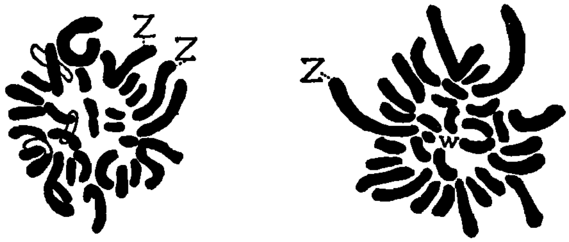
THE SIGNIFICANCE OF MATING

The problem of paramount importance in poultry breeding is to determine how the characters which domestic fowls possess, as described in the previous chapter, are inherited from generation to generation. This is accomplished for each character by mating a bird possessing that character to another bird that does not possess the same character and studying the offspring as well as their offspring when they are mated among themselves. Jennings (1920) has stated the problem simply and clearly: "The really fundamental thing that mating does is to produce new combinations of hereditary characters."

How Fertilization Takes Place.—The mating of a male and a female serves the purpose of allowing the male and female reproductive cells to unite, for only in this way can a chicken be produced. The reproductive cells of the male are called spermatozoa; those of the female are called ova. The fertilization of an ovum or egg of the female is accomplished by its union with a spermatozoon. According to Lillie (1919), only one spermatozoon fertilizes the ovum, although several spermatozoa may be present in the semen surrounding the ovum. At the time of copulation the copulatory organs of the male eject semen containing spermatozoa into the cloaca of the female, and the spermatozoa then traverse the length of the oviduct and apparently each ovum is fertilized shortly after it enters the oviduct.

Gametes and Zygotes.—From the standpoint of reproduction and the inheritance of characters, the reproductive cells are spoken of as "gametes," the term "gamete" meaning a spouse. The ovum is the female gamete and the spermatozoon is the male gamete. The fertilization of the female gamete by the male gamete produces the fertilized egg, which is spoken of as the "zygote," a term meaning yoked together. It is the zygote that develops into the chick.

Chromosomes.—Each gamete contains little thread-like bodies called "chromosomes," which are transmitted from parent to offspring. A fact of fundamental importance is that the number of chromosomes in any given species of animal is constant, as suggested by Agar (1920). The number of chromosomes in the chicken has been studied by Guyer (1916), Stevens (reported by Boring, 1923), Shiwago (1924), and Hance (1924 and 1926), all of whom observed a relatively large number, a few being large and several very small. Hance (1926) suggests that the number is approximately 35 or 36, and if this proves to be the correct number it is probable that in the female there are 35 and in the male 36 chromosomes, although it has been suggested that the female may also contain 36 chromosomes.



Male Female

FIG. 11.—The male and female chromosome groups of the domestic fowl. (After Shiwago.) The chromosomes are contained in the nucleus of the reproductive cell and are always in pairs, except for the single sex chromosome in the female. Each chromosome is made up of a large number of tiny bodies, called genes, which are the units that give rise to the numerous hereditary characters of the fowl.

Sex Chromosomes and Autosomes.—The difference between the number of chromosomes in the male and the female is due to the fact that the male has one more sex chromosome than the female. The sex chromosomes in any species are apparently always associated with sex and may be a factor in its determination, hence their name; the rest of the chromosomes are called "autosomes" or ordinary chromosomes, and they are always in pairs. The male chicken probably has

17 pairs of autosomes and 2 sex chromosomes, whereas the female chicken also has 17 pairs of autosomes but only 1 sex chromosome.

Sex Inheritance.—It has been pointed out previously that the zygote is the result of the union of the male and female gamete, and

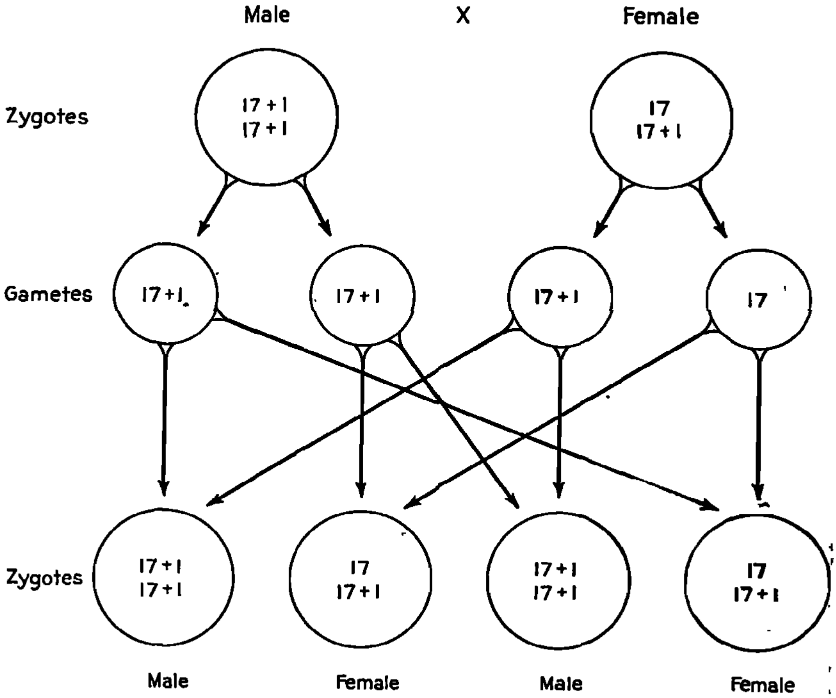


FIG. 12.—The male fowl has 17 pairs of autosomes plus 1 pair of sex chromosomes, whereas the female fowl has 17 pairs of autosomes but only 1 sex chromosome. The male produces but one kind of gametes, each of which contains 17 autosomes plus 1 sex chromosome. The female produces two kinds of gametes, one kind containing 17 autosomes plus 1 sex chromosome and the other containing 17 autosomes but no sex chromosome. A male gamete uniting with a female gamete containing 17 autosomes plus 1 sex chromosome produces a zygote containing 17 pairs of autosomes plus 1 pair of sex chromosomes; such a zygote develops into a male. A male gamete upon uniting with a female gamete containing 17 autosomes but no sex chromosome produces a zygote containing 17 pairs of autosomes but only 1 sex chromosome; such a zygote develops into a female.

it has also been stated that it is the zygote that develops into the mature chicken.

If the male chicken has 17 pairs of autosomes and 2 sex chromosomes, it is obvious that the two gametes which united to produce the zygote that developed into a male must each have contained 17 autosomes and 1 sex chromosome. Perhaps an equation would make the matter clear: Male gamete with 17 autosomes and 1 sex chromosome + female gamete with 17 autosomes and 1 sex chromosome = a zygote with 17 pairs of autosomes and 2 sex chromosomes.

Since the female chicken has 17 pairs of autosomes and 1 sex chromosome, it is obvious that of the two gametes uniting to form the zygote, one must have had 17 autosomes and 1 sex chromosome and the other must have had 17 autosomes only. In the form of an equation the situation is thus: A gamete with 17 autosomes and 1 sex chromosome + a gamete with 17 autosomes = a zygote with 17 pairs of autosomes and 1 sex chromosome.

So far, only one phase of the reproductive cycle has been discussed, namely, that of a male gamete uniting with a female gamete to produce a zygote. The other phase of the reproductive cycle consists in the zygotes producing the gametes. Each zygote produces gametes. The complete reproductive cycle, therefore, consists of gametes uniting to form zygotes and zygotes dividing to produce gametes. The reproductive cycle is illustrated in Fig. 12.

The zygote of the male, containing 17 pairs of autosomes and 2 sex chromosomes, divides to form gametes, each containing 17 autosomes and 1 sex chromosome. The zygote of the female, containing 17 pairs of autosomes and 1 sex chromosome, divides to form two different kinds of gametes because one gamete contains 17 autosomes and 1 sex chromosome whereas the other gamete contains 17 autosomes only.

Genes Give Rise to Characters.—The chromosomes are the bearers of the hereditary characters, but, since there are hundreds of characters and only 17 pairs of autosomes and 1 or 2 sex chromosomes according to the sex, it is obvious that each chromosome must be responsible for the development of many characters. Each chromosome is made up of smaller units called "factors" or "genes." It is the genes that give rise in development to such characters as plumage color, lacing, penciling, spangling, barring, single comb, rose comb, feathered shanks, yellow shanks, and others.

THE INHERITANCE OF SEX-LINKED CHARACTERS

Many characters which fowls possess are inherited equally from sire and dam. The genes giving rise to such characters are borne on the 17 pairs of autosomes common to both sexes, half of the chromosomes being of maternal and half of paternal origin in the case of any individual fowl.

There are certain characters, however, that are transmitted from dam to son but not from dam to daughter, although they are transmitted from sire to both son and daughter. Characters transmitted from dam to son only are called "sex-linked" characters because it is reasonably certain that the genes that give rise to such characters are borne on the sex chromosomes.

***WZ* Type of Sex Inheritance.**—The fact that certain characters are inherited on a sex-linked basis is easy to understand when one keeps in mind the difference between the male and female chicken in respect to the number of sex chromosomes each possess.

It will be recalled that the male chicken has 2 sex chromosomes whereas the female has only 1. In the case of the chicken the inheritance of sex is commonly referred to as the *WZ* type because the symbol *Z* is used to denote the presence and *W* the absence of one of the pair of the sex chromosomes. Every male zygote has 2 sex chromosomes (*ZZ*), so that among all male gametes produced each contains one *Z* chromosome. Every female zygote has only 1 sex chromosome (*Z*), and it produces gametes in approximate equality with and without the *Z* chromosome, a gamete with the *Z* chromosome being called a *Z* gamete and one without the *Z* chromosome being called a *W* gamete. Sex-linked genes, being borne on the sex chromosome only, are contained in the *Z* gametes only, the *W* gamete having no sex chromosome and, therefore, containing no sex-linked gene.

The *WZ* type of sex inheritance is common to birds and certain moths, but in many other animals another type of sex inheritance occurs. It is called the *XY* type of sex inheritance, in which the male is heterozygous for sex because he has only 1 sex chromosome (*X*) and the female is homozygous for sex because she has 2 similar sex chromosomes known as *X* and *X*. As far as sex is concerned, the female zygote contains *X* and *X* chromosomes and produces gametes each having an *X* chromosome, whereas the male zygote, which contains but 1 *X* chromosome, produces two kinds of gametes in approximate equality, one gamete containing an *X* chromosome for every one without it, the latter being known as the *Y* gamete. The difference between the *WZ* and *XY* types of sex inheritance is that in the *WZ* type the male is homozygous for sex chromosomes and consequently for sex-linked genes, whereas in the *XY* type the female is homozygous for sex chromosomes and consequently for sex-linked genes.

A Typical Example of Sex Linkage.—The results of a mating between a Rhode Island Red male and a Barred Plymouth Rock female are illustrated in Fig. 13. The male progeny are barred and the female progeny are black or largely so. Some of the female progeny may have red on the neck and breast feathers, but black is the predominant plumage color.

The results of a mating between a Barred Plymouth Rock male and a Rhode Island Red female are illustrated in Fig. 14. The male and female progeny are all barred.

It is observed that different results are produced in these two matings, depending upon whether the female used was barred or not. The results secured in the reciprocal matings between Rhode Island Reds and Barred Plymouth Rocks demonstrate that the gene that produces barring is sex-linked, inasmuch as the Barred Plymouth Rock female transmits barring to her sons but not to her daughters. A true test of the sex-linkage of the gene for barring is a mating of a Rhode Island Red male and the black females produced from a cross between a Rhode Island Red male and Barred Plymouth Rock females. The progeny of the Rhode Island Red male mated to the black females are nonbarred, showing that the black females did not possess the gene for barring. However, since the Rhode Island Red male when mated to Barred Plymouth Rock females produces barred sons and black daughters, it is obvious that the gene for barring is sex-linked and is transmitted from the barred female parent to her sons only.

The female fowl is heterozygous (from *heteros*, meaning different, and *zugon*, referring to the condition of the zygote, WZ) for sex because she has only 1 sex chromosome, whereas the male is homozygous (from *homo* meaning alike, and *zugon*, referring to the condition of the zygote, ZZ) because he has 2 sex chromosomes. The gene for barring, being sex-linked, is borne in the sex chromosome Z.

Barring Dominant to Nonbarring.—The results of the mating between the Barred Plymouth Rock male and Rhode Island Red female demonstrate that the gene for barring is dominant to the gene for nonbarring as in the Rhode Island Red. The term "dominant" simply means that one character dominates or suppresses the other. Although in the WZ type of sex inheritance W represents the absence of one of the pair of sex chromosomes, the customary way of indicating the absence of a sex chromosome is by the use of a dash, so that the female sex chromosome condition is expressed as Z— whereas the male sex chromosome condition is ZZ.

If the symbol B be used to denote the sex-linked gene that produces barring, then the genetic constitution of the Barred Plymouth Rock female becomes ZB— and the genetic constitution of the Barred Plymouth Rock male becomes $ZB\ ZB$, as far as the inheritance of barring alone is concerned. Since barring is dominant to nonbarring, as in the Rhode Island Red, the symbol *b* represents the gene for nonbarring. The genetic constitution of the Rhode Island Red female, therefore, is represented by *Zb*— and that of the Rhode Island Red male by *Zb Zb*.

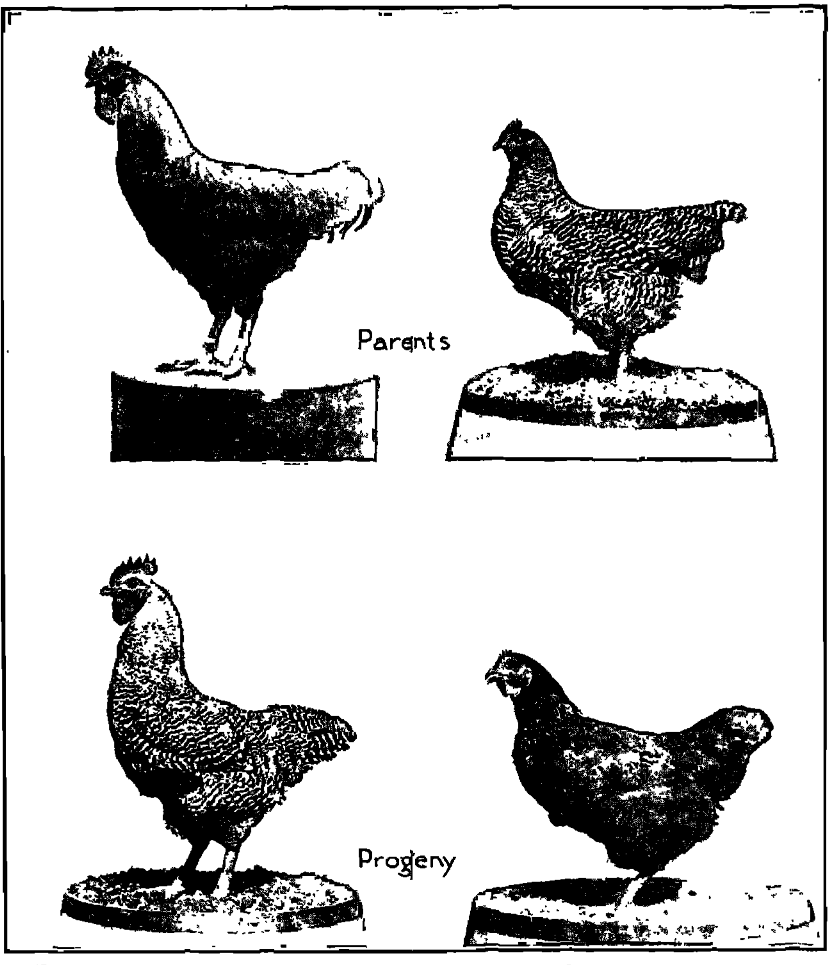


FIG. 13.—Illustrating the inheritance of a sex-linked dominant character. The gene for barring in Barred Plymouth Rocks is contained in the sex chromosome and when a Barred Plymouth Rock female is mated to a nonbarred colored male, such as Rhode Island Red, the gene for barring is transmitted to the sons only. The manner in which this is accomplished is shown in Fig. 15. The daughters are black, sometimes with a reddish tinge on the head, neck or breast. The daughters are nonbarred because each one received its sex chromosome from the nonbarred sire, as shown in Fig. 15. (U. S. D. A.)

The results, concerning the inheritance of barring, of the mating between a Rhode Island Red male (17 + *Zb* and 17 + *Zb*) and a Barred Plymouth Rock female (17— and 17 + *ZB*) are illustrated

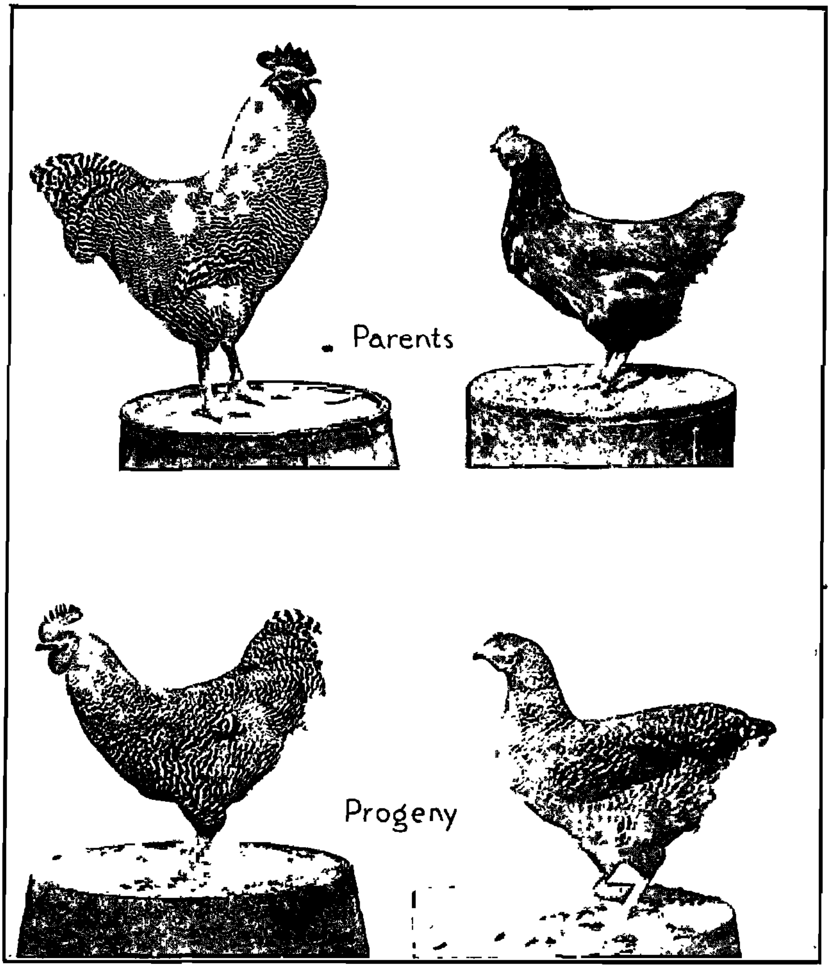


Fig. 14.—When a Barred Plymouth Rock male is mated to a nonbarred colored female, such as Rhode Island Red, the daughters as well as the sons are barred. The dominant sex-linked gene, B, for barring is transmitted from the sire to the daughters and to the sons, as shown in Fig. 16. (U. S. D. A.)

in Fig. 15. The Rhode Island Red male produces but one kind of gamete, 17 + *Zb*, whereas the Barred Plymouth Rock female produces two kinds of gametes, 17 + *ZB* and 17—, the 17 autosomes being included merely for the purpose of representing each gamete with its full complement of chromosomes. The scheme in Fig. 15 illustrates a point that should always be kept in mind in similar matings, namely, that either male gamete may fertilize either female gamete.

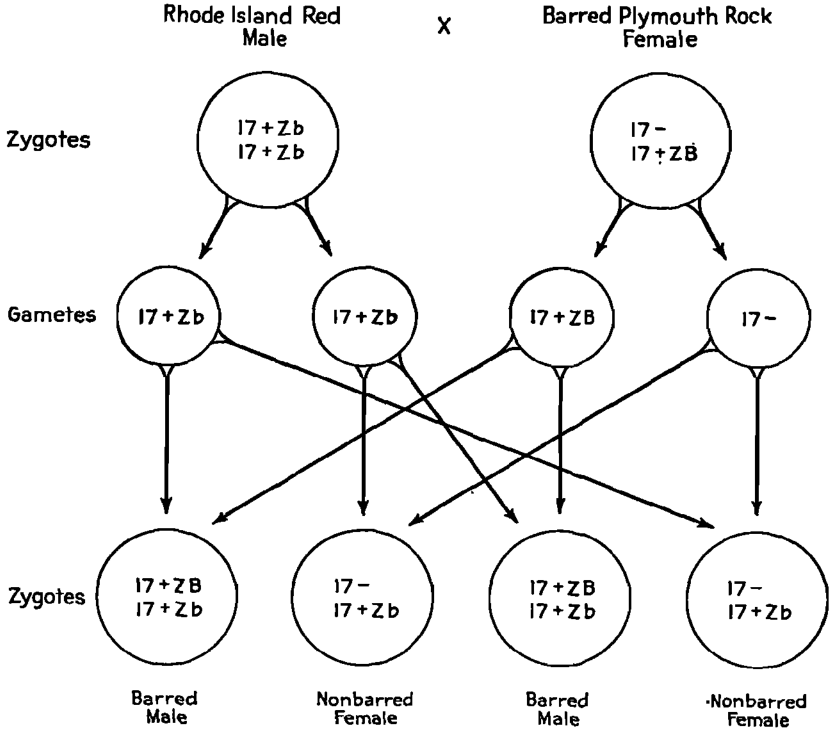


Fig. 15.—Showing the manner in which the gene for barring in a Barred Plymouth Rock female is transmitted to her sons only. The gene for barring is indicated by B and the gene for nonbarring by b, each being contained in the sex chromosome, indicated by Z.

The mating of the 17 + *Zb* male gametes with each of the two female gametes produces the two kinds of zygotes (17 + *ZB* and 17 + *Zb*) and (17— and 17 + *Zb*), respectively. The zygotes (17 + *ZB* and 17 + *Zb*) are in the first place males, because 2 sex chromosomes are present in each zygote, and in the second place barred because the gene for barring (*B*) is present. The zygotes (17— and 17 + *Zb*) are in the first place females because only 1 sex chromosome is present in each zygote, and in the second place non-barred because the gene for barring (*B*) is absent. The scheme in Fig. 15

shows clearly how the Barred Plymouth Rock female transmits barring to her sons only.

The results of the mating between a Barred Plymouth Rock male (17 + *ZB* and 17 + *ZB*) and a Rhode Island Red female (17— and 17 + *Zb*) are illustrated in Fig. 16. The Barred Plymouth Rock male produces but one kind of gamete, 17 + *ZB*, whereas the Rhode Island Red female produces two kinds of gametes, 17 + *Zb* and 17—. The mating of the 17 + *ZB* male gametes with each of the two female gametes produces two kinds of zygotes (17 + *ZB* and 17 + *Zb*) and (17— and 17 + *ZB*). The zygotes containing 2 sex chromosomes are males whereas those containing 1 sex chromosome are females but both males and females are barred because the gene for barring (*B*) is present in each zygote. The scheme in Fig. 16 shows clearly

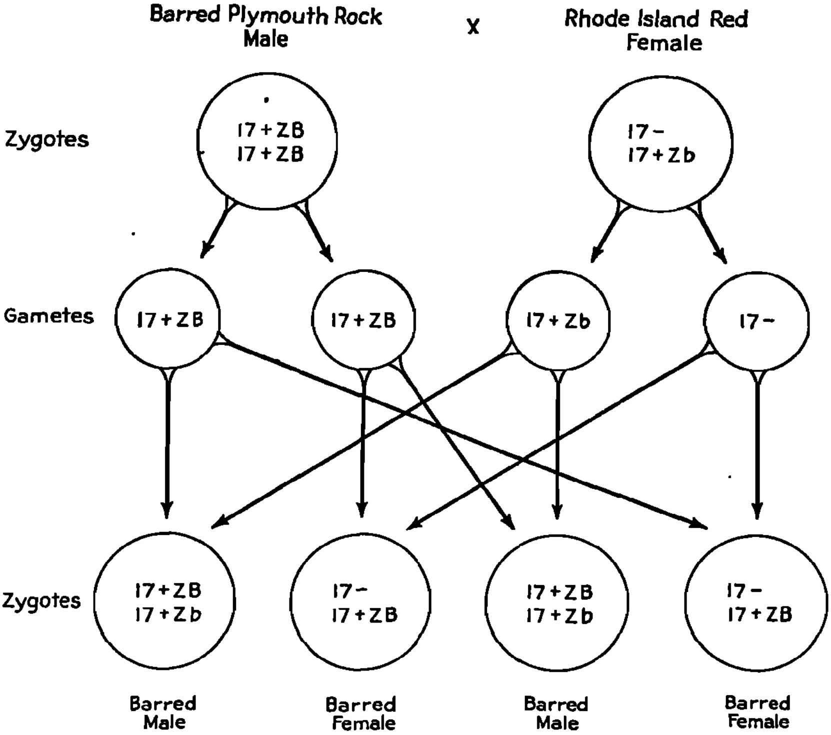


FIG. 16.—Showing the manner in which the dominant sex-linked gene, B, for barring is transmitted to the daughters as well as the sons in a mating of Barred Plymouth Rock male x Rhode Island Red female.

how the Barred Plymouth Rock male transmits barring to his daughters as well as his sons.

Distinguishing the Sexes at Hatching Time.—An interesting feature about the inheritance of several sex-linked characters is that the sexes of the chicks can be distinguished at hatching time, thus allowing for the separation of males and females for any particular purpose.

In the case of the mating between a Rhode Island Red male and a Barred Plymouth Rock female the male chicks at hatching time resemble purebred Barred Plymouth Rock male chicks very closely. There is the characteristic white or light spot on the back of the head, the under part of the body is grayish but all the rest of the down is black in color, and the beak and shanks and toes are yellow. The female chicks from the cross are quite different from the males inasmuch as the down color is all black, including the top of the head, and the beak, shanks, and toes are black or very dark in color. The chicks can be separated according to sex with a high degree of accuracy. The male chicks develop into barred birds, whereas the female chicks develop into black ones, some perhaps having some red on the neck or breast or both.

Other crosses can be made involving the inheritance of sex-linked characters which make it possible to distinguish the sex of chicks at hatching time. Such cases as well as other sex-linked crosses that do not permit the separation of the chicks according to sex at hatching time are discussed in later sections of the book.

PROBLEMS

1. What are the primary sexual characters and how do they function?

2. What are the chief differences between the sexes in respect to secondary sexual characters?

3. What is the relationship between the gonads and the development of the comb, wattles, and spurs?

4. (*a*) What are the more important changes that take place when a male is castrated?

(*b*) What are the more important changes that take place when the ovary of a female is removed?

(*c*) What are hen-feathered males, and what factors are responsible for the kind of feathering they have?

5. How is it that females may become males but males apparently never change into females?

6. What is the normal sex ratio of the domestic fowl, and what factor or set of factors may lead to a modification of the normal sex ratio?

7. What does mating accomplish?

8. What is the relationship between gametes and zygotes?

9. What part do chromosomes play in inheritance?

10. Of what significance are genes?
11. What is meant by the *WZ* type of sex inheritance?
12. What practical use can be made of sex-linked inheritance?

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CHAPTER III

MENDELIAN INHERITANCE

ALTHOUGH the science of breeding has enabled mankind to develop races of fowl more and more perfectly adapted to modern requirements, much remains to be accomplished. That which has been accomplished is largely a matter of history, but the manner in which many of the new characters have become fixed in the different breeds and varieties is largely a mystery.

Who is there who can tell why the barring found in Barred Plymouth Rocks behaves differently in inheritance from the barring found in Silver Campines? Who can tell how it is that a mating of a White Dorking and a white Silkie produces nothing but colored offspring? Who can tell how it is that when a White Leghorn is mated to a Black Leghorn all the offspring have white or almost entirely white plumage whereas when a White Minorca is mated to a Black Leghorn all the offspring have black plumage? Who knows the proper steps to follow in developing most efficiently a strain of excellent egg producers that lay eggs of good size and good quality?

An answer to each of these questions and many others of interest to poultry breeders is given in the discussion in the following chapters. In the meantime, in order to understand the significance of the observations made concerning the inheritance of various characters, poultry breeders should have a general knowledge of the fundamental principles of inheritance, which is the theme of this chapter.

THE PHENOMENON OF INHERITANCE

The inheritance of many of the characters possessed by the domestic fowl is a phenomenon of such universal occurrence that it is accepted by most poultrymen as a matter of course, something so evident that it requires no explanation. The possession of feathers is a character confined exclusively to birds, but the fact that some birds have laced feathers while other birds have penciled feathers, and the fact that some birds lay well whereas others do not, are matters that do require explanation if one is to gain a clear understanding of the manner in which the different characters which birds possess are reproduced from one generation to the next. From the standpoint of inheritance, the term character means any one of the many details of form, substance, structure, or function which make up a fowl.

Inheritance is transmission from parent to offspring. The characters are not transmitted bodily, however; for instance, there are no feathers in the egg or on the chick when hatched but the chick possesses the ability to grow feathers. It is the ability, power, or potentiality to develop such characters as white or yellow skin color, barred or spangled feathers, crests, feathered shanks, brown or white color of egg shell, that is inherited. It is the ability to produce an abundant amount of flesh of excellent quality or the ability to lay well that is inherited.

Although it is true that the characters which a fowl possesses are not transmitted bodily, it seems justifiable to speak of the inheritance of characters, as for instance, the inheritance of white and black, of barring, and of egg production. Such a method of discussing the subject of inheritance simplifies the problem of presenting the matter to the layman.

The Significance of Variation.—Reference has already been made to numerous characters possessed by domestic fowls, but the fact should be emphasized here that each and every individual fowl possesses a large number of characters. A Barred Plymouth Rock possesses a single comb; barred feathers; red earlobes; yellow skin, beak, and shanks; nonfeathered shanks; four toes, as well as many other characters. A Light Brahma possesses a pea comb, a columbian colored plumage pattern, and feathered shanks, and has a different build from that of the Barred Plymouth Rock. A White Plymouth Rock, however, has the same build as the Barred variety but differs from it in having white plumage. Moreover, not all White Plymouth Rocks are exactly alike. There is always some difference, however minute, that distinguishes two individuals that are otherwise much alike, and this is as true among men as among domestic fowls.

Since it is true that there are no duplicates among domestic fowls, it is obvious that the old saying "like begets like" cannot be wholly true, for the simple reason that there is no exact likeness between parent and offspring or among brothers and sisters. It is true, of course, that all Leghorns do resemble each other to a marked degree when compared with all Rhode Island Reds, but it is also true that a particular Leghorn may resemble a particular Rhode Island Red much more closely regarding ability to transmit egg production than either of these two birds is resembled by all other members of its breed.

The fact that there is great variation among fowls is of particular significance in inheritance. Without variation, progress in breeding work would be impossible. Without variation, the selection of superior individuals would be impossible. Without selection, improvement is impossible. Variation makes selection possible, and selection makes improvement possible.

MENDELIAN INHERITANCE

The fact that there is great variation among fowls has made possible the development of the science of breeding upon a very definite basis. Although it is true that there are no two Barred Plymouth Rocks that are exactly alike it is also true that as long as Barred Plymouth Rocks are mated among themselves nothing but barred birds are produced, except white "sports" very occasionally. Barring is regarded as a stable character that is transmitted regularly from generation to generation, although the quality of barring in any two individuals always differs somewhat.

The character black plumage in Black Langshans, Jersey Black Giants, Black Rose-Comb Bantams, and other black varieties is regarded as a stable character transmitted regularly, except for occasional white "sports" which appear from time to time, when birds of the same variety are mated among themselves.

White Rose-Comb Bantams and other white varieties breed true when bred among themselves so that the character white plumage is regarded as stable.

But when fowls possessing unlike characters are mated together some very interesting and sometimes very surprising results are secured. The manner in which black and white are inherited in a cross between Black Rose-Comb and White Rose-Comb Bantams serves to illustrate the kind of results secured in the inheritance of most pairs of characters. In this case black is one character and white the other; in presenting the results secured in the form of tables it is a matter of convenience to denote the different generation of families by symbols. The parental generation, meaning the parents used in the first cross, is designated by the symbol P_1. The family or progeny secured from the original cross or mating is known as the first filial generation and is designated by the symbol F_1. When members of the first filial generation are mated among themselves they produce the second filial generation, which is designated by the symbol F_2. Briefly then, P_1 produces F_1, and F_1 produces F_2.

The manner in which the characters black and white are inherited in a cross between Black Rose-Comb and White Rose-Comb Bantams will serve to illustrate the mechanism involved in the inheritance of most pairs of characters. The first, and, so far as can be deter-

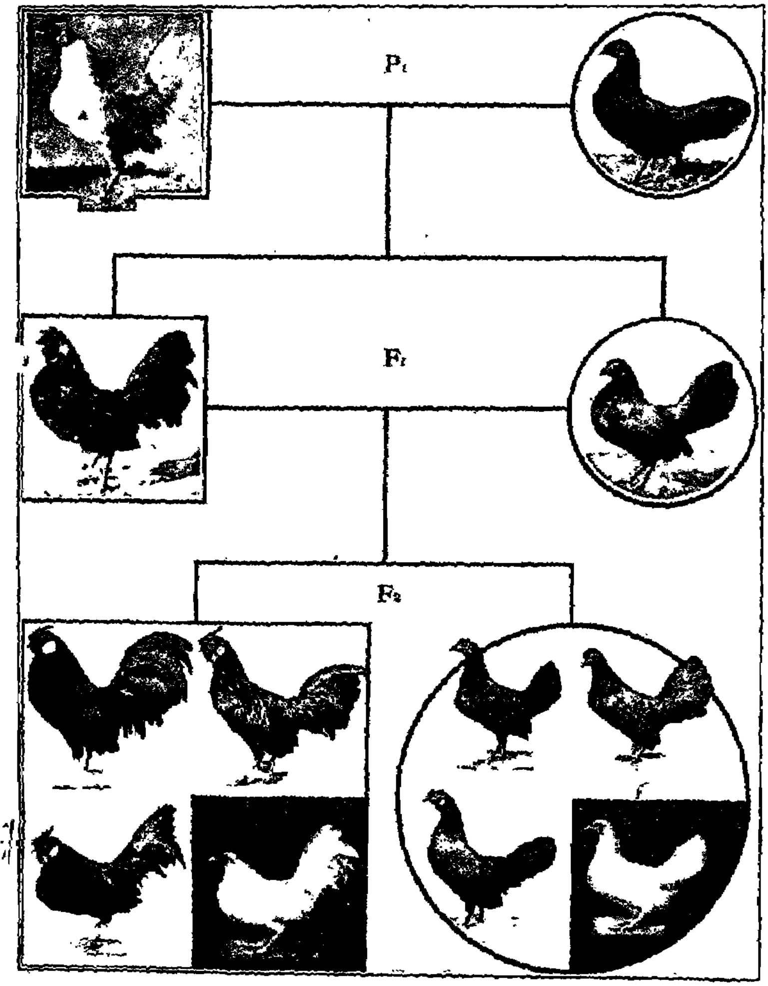

FIG. 17.—A White Rose-Comb Bantam male mated to a Black Rose-Comb Bantam female (the P_1 generation) produces offspring (the F_1 generation), all of which are black. In this mating the gene for black plumage is dominant and the gene for white plumage is recessive so that all of the F_1 birds are black although each has received a dominant gene for black from the female parent, and a recessive gene for white from the male parent, the genes for black and for white being contained in the autosomes. When an F_1 male is mated to an F_1 female an F_2 generation is produced consisting of 3 blacks to 1 white, in both sexes. In each sex 1 black out of every 3 is pure for black whereas the other two blacks each carry the gene for white as well as black. The F_2 white birds are pure for white, so that when they are bred among themselves they produce nothing but white offspring. The appearance of white birds in the F_2 generation illustrates the principle of the segregation of the genes. In the F_1 generation the genes for black and for white were combined whereas in the F_2 generation they segregated to give a proportion of 3 to 1. (Photo by Jour. Hered.)

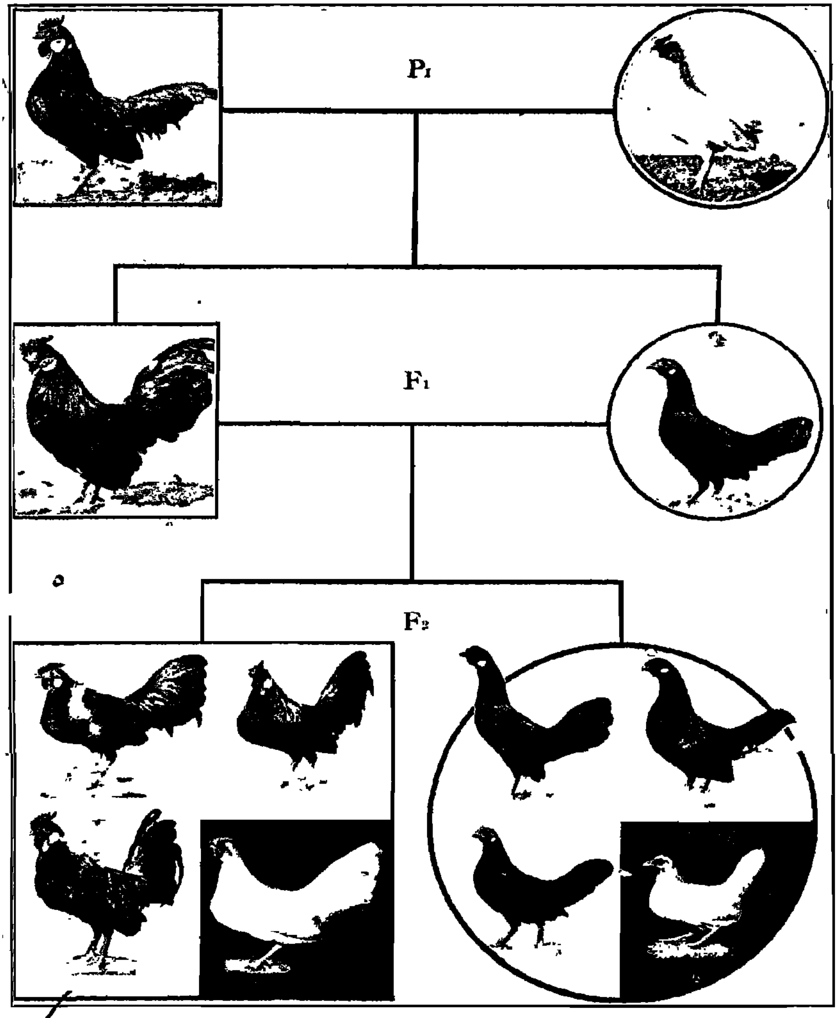

FIG. 18.—A Black Rose-Comb Bantam male mated to a White Rose-Comb Bantam female (the P_1 generation) produces offspring (the F_1 generation) all of which are black, as in the reciprocal cross illustrated in Fig. 17. Similar results are secured in the F_2 generation, 3 blacks to 1 white, due to the well established mendelian principle of the segregation of the genes. The results secured in this cross and in the cross illustrated in Fig. 17 demonstrate that the genes for black and for white are contained in the autosomes and not in the sex chromosomes. See Figures 19 and 20 which show clearly how the proportion of 3 blacks to 1 white is secured in the F_2 generation of the crosses illustrated. (Photo by Jour. Hered.)

mined, the only, reference to such a cross having been made, is reported by Bateson and Punnett (1908). They mated Black Rose-Comb Bantams to White Rose-Comb Bantams and secured black progeny only. They mated 3 of the F_1 black females to 1 of the F_1 black males and secured 70 black and 24 white progeny. This approximates very closely a ratio of 3 blacks to 1 white.

The results of crosses between White Rose-Comb and Black Rose-Comb Bantams secured at the U. S. Animal Husbandry Experiment Farm, Beltsville, Maryland, are given, together with photographs of birds used in the various matings. In the spring of 1927 one pen of 5 White Rose-Comb Bantam males mated to 17 Black Rose-Comb Bantam females produced 107 progeny, all of which were black. During the same breeding season another pen of 2 Black Rose-Comb Bantam males mated to 5 White Rose-Comb Bantam females produced 39 progeny, all of which were black. It is observed that both crosses produced black progeny.

During the breeding season of 1928 two matings were made. The first mating consisted of black brothers and black sisters from the first mating of 1927, White Rose-Comb males and Black Rose-Comb females. Observations were made on the color of the chicks that died in the shell at hatching time as well as those which hatched and matured. Among the chicks that died there were 81 black and 24 white chicks. Among the chicks which hatched and matured there were 189 black and 65 white chicks. Among the total progeny, therefore, there were 270 black and 89 white chicks, a ratio approximating closely 3 to 1.

The second mating made in 1928 consisted of the black brothers and black sisters from the second mating of 1927, Black Rose-Comb males and White Rose-Comb females. Among the chicks that died in the shell at hatching time there were 21 black and 9 white chicks. Among the chicks that hatched and matured there were 29 black and 9 white chicks. The total progeny, therefore, gave 50 black and 18 white chicks, again a fairly close approximation of a 3-to-1 ratio.

Both matings made in 1928 gave 320 black and 107 white chicks, almost exactly a 3-to-1 ratio. The results are shown in Table 4.

The results secured in this simple experiment involving one pair of characters demonstrate two important features. The first important feature is the demonstration of the fact that in this particular cross the first filial generation are all black in spite of the fact that one of the parents is white. The second important feature is the fact that in the second filial generation the two characters black and

In one cross both dominant characters were brought in by one parent, *RRNN*, and both recessive characters by the other parent, *rrnn;* whereas in the other cross one dominant and one recessive character were brought in by each parent, *RRnn* and *rrNN*. Both crosses produce the same results in the F_2 generation, showing clearly that the genes responsible for the two pairs of characters assort themselves independently of each other and recombine in definite proportions. The principle of the independent assortment of the genes is fundamentally important to a proper understanding of the general problem of inheritance.

The F_2 Ratio in Relation to Pairs of Genes in Original Cross.—In crosses in which more than two pairs of independent characters are involved the segregation and independent assortment of the genes occur in precisely the same way as in the inheritance of one pair or two pairs of independent characters. It will be recalled that in the case of one pair of characters two kinds of F_1 gametes are formed, and in the case of two pairs of characters four kinds of F_1 gametes are formed. The number of different kinds of gametes formed by the F_1 birds is doubled with each increase in the number of different genes involved.

In the inheritance of three pairs of characters eight kinds of F_1 gametes are formed, and in the inheritance of four pairs of characters sixteen kinds of F_1 gametes are formed. Each time the different genes involved are increased by one the number of F_1 gametes formed is increased by two. On the other hand, for each increase in the number of different genes involved, the average number of F_2 individuals required to be produced to secure the appearance of the various combinations of characters resulting from the chance combination of the different kinds of F_1 gametes is increased by four, as shown in Table 5.

It becomes clear, therefore, that, regardless of the number of independent characters involved in the original cross, the mode of inheritance is the same, and the different types produced in the F_2 generation always bear a certain mathematical proportion, depending upon the number of independent pairs of genes involved.

Three Fundamental Principles of Mendelian Inheritance.—The discussion in this chapter brings out clearly the three fundamental principles of inheritance established by the work of Mendel. The first is the principle of the dominance of one character over another of a given pair so that when a bird is heterozygous for both characters only the dominant one is visible. The second is the principle of the segregation of the genes, whereby a gene for a dominant character from one parent and a gene for a recessive character from another

Table 5. Showing, for Each Increase in the Number of Different Pairs of Genes, the Number of Different Kinds of F_1 Gametes Formed, the F_2 Ratio, and the Average Number of F_2 Individuals Necessary to Secure the Appearance of All Possible Combinations of Characters

Number of Different Pairs of Genes in the Cross	Number of Different Kinds of F_1 Gametes Produced	The F_2 Ratio	Average Number of F_2 Individuals Necessary to Secure the Appearance of All Possible Combinations of Characters
1	2	3:1	4
2	4	9:3:3:1	16
3	8	27:9:9:9:3:3:3:1	64
4	16	81:27:27:27:27:9:9:9:9:9:9:3:3:3:3:1	256
n	2^n	$(3:1)^n$	4^n

parent coming together in the F_1 generation segregate in the F_2 generation as demonstrated by the appearance of true-breeding dominant and recessive types in F_2. The third is the principle of the independent assortment of the genes in inheritance, as ~~demonstrated in the~~ appearance in the F_2 generation of new types possessing characters in different combinations from those of either of the parents in the original cross.

Such are the fundamental principles of Mendelian inheritance. They have constituted a notable contribution to the science of breeding, for they have enabled man to produce results with increasing rapidity and precision. In view of the great variety of plumage color patterns and structural features among domestic fowls that have been developed out of the original wild types, it is true that "it is hardly too much to say that we are beginning to look upon the whole organic world as a storehouse of potentialities which may be realized in whatsoever permutations and combinations we may desire." (Dendy, 1919.)

A knowledge of the fundamental principles of Mendelian inheritance enables one to predict the results to be secured from many matings. Dendy (1919) further observes: "By appropriate mating of carefully selected individuals we may introduce good features and eliminate bad ones, and so literally build up races of plants or animals to suit our special needs." But that is not all; in fact, it is not the most important service which Mendel's work has done for the science of breeding. Mendel's greatest achievement was, as Darbishire (1913) points out, "The establishment of the principle that the contents of the germ-cells, and not the outward characteristics of the animals and plants dealt with, must be our guide in breeding."

With many poultry breeders the practice has been to select breeding stock based upon its appearance or its pedigree. Mendelism shows that this is not good enough; the progressive poultry breeder must consider the kind of offspring produced to determine the worth of any bird as a breeder. Instead of looking to the ancestry only, one should also consider the offspring; in fact, in many cases the kind of offspring produced is the only reliable criterion in determining the breeding value of any individual. The progeny test is of paramount importance in successful breeding operations.

PRESENT-DAY KNOWLEDGE OF INHERITANCE IS BASED ON MENDELISM

Since the rediscovery in 1900 of the illuminating results which Mendel secured, which gave rise to the three fundamental principles of inheritance—dominance, the segregation of genes, and the independent assortment of the genes—results have been secured which show that in certain cases there are modifications of the original concepts on which Mendelism is based. These modifications do not detract from the validity of the Mendelian theory of inheritance but merely show that the inheritance of certain characters is more complex than that of the characters with which Mendel dealt.

Lack of Dominance.—In certain cases there is a lack of dominance of one character over the other. For instance, when two breeds that differ widely in body weight are crossed, the F_1 birds are usually intermediate in weight, as pointed out in Chapter V. Lack of dominance is apparently due to the fact that several genes are responsible for the size that a given bird attains.

"Linked" Characters.—In certain cases it has been found that two given characters introduced into a cross together tend to stay together in their passage from generation to generation, showing that the segregation and independent assortment of the genes do not take place. These cases were regarded as exceptions to Mendelism, but the fact that these "linked" characters are inherited in Mendelian manner is shown in Chapter VII.

Different Kinds of Genes According to the Effects They Produce.—In the cross between Black Rose-Comb Bantams and white single-comb bantams, discussed previously in this chapter, the genes involved each produced a specific effect, but there are instances where two different genes have a complementary effect and give rise to an F_2 ratio of 9:7 instead of 9:3:3:1. The manner in which such a ratio results is given in a subsequent chapter. The genes in question are called **complementary genes.**

There are cases in which genes belonging to different pairs, although inherited independently, affect one another as they express themselves in the characteristics of the individual, so that a given character depends upon the **interaction of two or more genes.** In poultry one of the most notable examples of such a situation is found in comb inheritance. Rose comb breeds true and pea comb breeds true, but when rose-comb and pea-comb fowls are crossed the F_1 generation has walnut combs. As explained in Chapter V, an interaction takes place between the genes for rose comb and the genes for pea comb so that an entirely new type of comb is produced.

A number of cases have been discovered in which two or more genes not only affect the same character but affect it in the same way, such genes being shown as **duplicate genes.** Then again, several genes may interact to produce a given effect, one of the genes determining the presence of a certain character while the other genes affect the degree of the development of the same character or otherwise modify the expression of the principal gene. Such genes are called **modifying genes.** Still other instances have been found where **a single gene affects several characters,** and occasionally a gene is found which produces such an extreme modification in the development of the embryo as to cause its death, such a gene being known as a **lethal gene.** Illustrations of these various types are given in subsequent chapters.

Modern Terminology.—During recent years remarkable advances have been made by investigators in their studies on the inheritance of many characters, some of which have been found to be rather complex. In the literature dealing with inheritance problems certain terms have acquired common usage; since in subsequent chapters a number of these terms are used, they are explained at this time as a matter of convenience to the reader.

When a cross is made between one pair of contrasting characters, such as black and white, the cross is called a **monohybrid** cross and the F_2 ratio of 3:1 is called a monohybrid ratio. A cross involving two pairs of contrasting characters, such as black and white and single comb and rose comb, is called a **dihybrid** cross and the F_2 ratio of 9:3:3:1 is called a dihybrid ratio. A **trihybrid** cross involves three pairs of contrasting characters.

Two terms that occur frequently in the literature dealing with inheritance studies in plants and animals are **genotype** and **phenotype**. The difference in the meaning of these terms is made clear by referring to the results secured in the F_2 generation from the original cross between Black Rose-Comb Bantams and white single-comb bantams. It has already been observed that the following results were secured:

1 *RRNN*	9 rose-comb black
2 *RRNn*	
2 *RrNN*	
4 *RrNn*	
1 *RRnn*	3 rose-comb white
2 *Rrnn*	
1 *rrNN*	3 single-comb black
2 *rrNn*	
1 *rrnn*	1 single-comb white.

There are 9 groups of birds differing in genetic constitution, including: *RRNN, RRNn, RrNN, RrNn, RRnn, Rrnn, rrNN, rrNn,* and *rrnn.* Each of these groups is called a **genotype**.

There are 4 groups of birds differing in type of comb and plumage color, including: 9 rose-comb blacks, 3 rose-comb whites, 3 single-comb blacks, and 1 single-comb white. Each of these groups is called a **phenotype**, meaning that all the birds in each group look alike.

A group of birds belonging to one phenotype may include several genotypes, as for instance, the phenotype of 9 rose-comb blacks comprises the 4 following genotypes: *RRNN, RRNn, RrNN,* and *RrNn.*

Another term that is used frequently in the literature on inheritance is **allelomorph**, which has a very simple meaning. It has already been pointed out in Chapter II and it has been demonstrated in this chapter that for each character there is always a contrasting character, such as black plumage and plumage that is not black. Another pair of contrasting characters noted in this chapter is rose comb and a comb that is not rose. Such pairs of characters are termed **allelomorphic** pairs, each of the two characters being the allelomorph of the other. The same term is applied to the contrasting pairs of genes which give rise to the contrasting pairs of characters. Genes that are allelomorphs occupy the same **locus** in a chromosome.

Multiple allelomorphs are those that occupy the same loci in pair of chromosomes, each allelomorph producing a visibly effect, and although multiple allelomorphs behave as though pletely linked only one of them is ever present in any

A condition known as **epistasis** occurs in the White Leghorn. As pointed out in the next chapter, the White Leghorn carries genes for color and for barring but they have no effect on the appearance of the bird because there is also present a gene which inhibits or prevents color from being expressed. A gene which thus prevents the expression of another gene is said to be **epistatic** to it. The gene which is prevented from expressing itself is said to be **hypostatic** to the other gene.

It is important to distinguish clearly between dominance and epistasis and between recessiveness and hypostasis. The terms dominance and recessiveness are applied to the behavior of alternative characters based upon genes occupying the same locus in a chromosome, such genes being allelomorphs. The gene *I*, which inhibits the development of color in the White Leghorn, is the allelomorph of *i*, which allows color to be expressed, as in many different varieties. *I* and *i* occupy the same locus in a chromosome. But the White Leghorn also carries the gene *B* for barring and genes for color, as explained in the next chapter, but these genes have no effect because the white of the White Leghorn is epistatic to barring and to color. The genes *I* and *B* and the genes for color do not occupy the same locus in a chromosome; therefore, they are not allelomorphs.

Another example will help to distinguish between dominance and epistasis and between recessiveness and hypostasis. The Barred Plymouth Rock carries the gene *B* for barring and the gene *E* for the extension of black pigment to all parts of the plumage. *B*, barring, is dominant to *b*, nonbarring, as explained in the previous chapter; *B* and *b*, therefore, are genes that occupy the same locus in the chromosome. But *B* is epistatic to *E*, otherwise the bird would have solid black plumage; the gene *E* is prevented from expressing its effects in the presence of *B*. The gene *E*, therefore, is hypostatic to *B*, whereas *e* is recessive to *E*.

The White Plymouth Rock, as pointed out in the next chapter, carries the gene for barring but it is not able to express itself because the genes for the production of pigment or coloring matter are absent. The gene for barring in the White Plymouth Rock is known, therefore, as a **cryptomere**.

Sometimes a new character appears unexpectedly in one genera-
and is transmitted through inheritance to succeeding generations.
t w character is called a "**sport**" or a "**mutation**".
comb **deas Discarded.**—Just as the most recent investigations of
9:3:? itance of various haracters have resulted in the devel-
pai

ment of new ideas concerning inheritance in general, so the newer knowledge has supplanted some of the old ideas once held concerning inheritance. Since some of these old ideas are still held by certain poultry breeders, a brief explanation is necessary to show why they are untenable.

Reversion, or the appearance of offspring resembling remote ancestors, has long been regarded by some poultry breeders to denote so-called impurity of breeding, but, as a matter of fact, it has a simple Mendelian explanation. In the next chapter it is observed that when a white variety, such as the White Dorking, is crossed with the White Silkie, the F_1 birds are colored, the males resembling males of the wild type, *Gallus bankiva.* Instead of there being impurity in either the White Dorking or White Silkie to account for the results, it is pointed out that the White Dorking lacks a gene for the production of color which the White Silkie provides, and the White Silkie lacks the gene for the production of color which the White Dorking supplies. The term **reversion** has no standing in present-day discussions on inheritance.

Atavism has long been known as the phenomenon of resemblance of progeny to one or more of their grandparents but not to their parents. That this phenomenon is due to the segregation and recombination of genes has already been demonstrated, and numerous other illustrations are given in subsequent chapters.

Telegony is a term used with reference to the supposed influence of a previous mating on later offspring. A case is known of a poultry breeder who believed that if a Brown Leghorn male mated with a White Leghorn female, never again would the White Leghorn female produce purebred White Leghorn chicks when mated to a White Leghorn male. The origin of such a peculiar belief is probably due to the fact that in cases where a "foreign" male has mated with a female, eggs have been saved for hatching prior to the time that all the spermatozoa of the "foreign" male had perished, even though the female had later been mated with one of her own kind. At any rate, there is no such thing as telegony, as shown by the results secured in hundreds of cases.

The **inheritance of acquired characters** has been a subject of great controversy among plant and animal breeders for many years. A few breeders have claimed that a character acquired during the lifetime of the organism may be inherited, but the great majority have claimed that such is not possible. A good illustration of an acquired character in the case of the domestic fowl is the dubbed comb, that is, a comb that has been cut off. If dubbing were to be practiced on many successive generations of birds there is no reason to believe that the dubbed comb would be transmitted in inheritance, judging from the results secured with various animals in tests designed for the purpose of testing the validity of the theory of the inheritance of acquired characters.

Prepotency has long been regarded by practical poultry breeders as the ability of an individual to impress its characteristics upon its offspring to a much more marked degree than do other individuals. In some cases prepotency has been confused with dominance, as in the case of a White Leghorn being mated to a Barred Plymouth Rock or any other kind of colored bird. The progeny are not white because the White Leghorn had the stronger or more vigorous constitution but because the gene responsible for the white of the White Leghorn is dominant to the gene for color. A black bird that is homozygous for black will produce nothing but black offspring when mated to a homozygous recessive white, like the White Minorca, whereas a black bird that is heterozygous for black will produce progeny consisting of one-half black and one-half white when mated to the same homozygous recessive white. The homozygous black bird is not more prepotent, in the sense in which it is usually used, than the heterozygous black bird but produces relatively twice as many black progeny because it has two genes for black instead of only one.

Present-day knowledge of inheritance teaches poultry breeders that they must look to the contents of the germ cells, the gametes, and not to the outward appearance, in order to ascertain the breeding value of a given bird.

PROBLEMS

1. What is implied by the term "inheritance"?
2. Explain how variations that exist among domestic fowls are of value in studying the inheritance of characters.
3. State the derivation of each of the following terms and give an illustration of the proper use of each term: gene, gamete, genotype, phenotype, homozygous, heterozygous, monohybrid, F_1, F_2, allelomorph, lethal.
4. Of what value in studies on the inheritance of characters is the fact that certain characters show dominance over others?
5. What are the three major principles of inheritance established by the work of Mendel?
6. Make out a checkboard scheme showing the zygotes produced in a cross between Black Single-Comb Bantams and White Rose-Comb Bantams, the symbol *R* being used for rose comb and *r* for single comb, and *N* for the black plumage and *n* for white plumage.
7. The zygote of the Rose-Comb White Leghorn is represented by *RRII* and the zygote of the Single-Comb Black Leghorn is represented by *rrii*, rose comb being dominant to single comb and white being dominant to black, the white of the White Leghorn being due to a dominant gene *I*, which inhibits the devel-

opment of color. What is the zygote of the F_1 generation and what are the genotypes and phenotypes produced in the F_2 generation?

8. What is the significance of the segregation and independent assortment of the genes in inheritance?

9. In what way may a knowledge of Mendelian inheritance be of value in practical poultry breeding work?

10. Write a brief essay on Mendel's contribution to the science of breeding.

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CHAPTER IV

THE INHERITANCE OF COLOR CHARACTERS

COLOR characters in domestic fowls are among the most conspicuous of all the characters they possess and constitute the basis for differentiating the varieties of a breed. Color characters include the down color of chicks, adult plumage color, skin color, earlobe color, shank color, and egg shell color, a discussion of the last character being reserved for the chapter devoted to the inheritance of egg characters. A review of the numerous investigations undertaken to determine the nature of the inheritance of these various color characters must of necessity be brief in a book of this kind.

In order that the poultry breeder may secure the most satisfactory results from his poultry-breeding operations he should know as much as possible concerning the genetics of the breed or variety in which he may be interested. A knowledge of the manner in which a certain undesirable character is inherited may enable him to eliminate it from his flock with comparative ease. Moreover, when one knows how various characters are inherited breeding work becomes much more interesting and may be made much more profitable.

THE INHERITANCE OF WHITE PLUMAGE

In Chapter I mention is made of certain white breeds, such as the Silkie and White-Booted Bantam, and white varieties of a large number of breeds, such as White Cochin, White Dorking, White Hamburg, White Leghorn, White Minorca, White Plymouth Rock, White Wyandotte, and White Rose-Comb Bantam. That at least three different kinds of white have been amply demonstrated and definitely established by investigational work is generally recognized. The white of the White Leghorn is of the dominant type, whereas among the other white breeds and varieties mentioned there are at least two kinds of recessive whites. The Silkie and the White Rose-Comb Bantam belong to one recessive white group, and such varieties as White Dorking, White Minorca, White Plymouth Rock, and White Wyandotte belong to the other.

Down Color.—Although the down color of the great majority of the chicks of all white breeds and varieties is pale yellowish cream, occasionally some chicks appear that are chalk white, some that are smoky white, and some that are reddish white.

Regarding the down color of the chicks of one of the recessive white groups, Punnett (1923) points out that the chicks of the Silkie and White Rose-Comb Bantam differ somewhat in that in the Silkie the down color is yellowish cream with generally more or less buffish orange tinge on the dorsal surface whereas in the White Rose-Comb Bantam the down color is creamy on the ventral and pale bluish on the dorsal surface.

The down color of the chicks of the other recessive white group is usually yellowish cream, some of the chicks being chalk white and sometimes, as Punnett (1923) points out, homozygous recessive whites may show an occasional black tick in the plumage.

Dominant White Plumage.—Bateson (1902) demonstrated that the White Leghorn is white because of the presence of a gene which prevents the production of melanic pigment (black). Bateson's observation regarding the color-inhibiting nature of the gene in White Leghorns has been confirmed by Bateson and Punnett (1905, 1906), Hurst (1905), Davenport (1906), and Hadley (1913, 1914, 1915), who proved conclusively that the White Leghorn possesses a gene for the production of color, which, however, does not find expression because of the presence of the inhibiting gene, the symbol for which is *I*. Gortner (1910) found that the dominance of white in the White Leghorn is due to the presence of an enzyme, which prevents the development of color.

When a White Leghorn, either male or female, is mated with a colored bird, such as Black Minorca, the F_1 chicks are white, except that many of the chicks may have black spots in the down. These chicks with black ticking usually develop into adults having some black in their plumage, the partially black feathers exhibiting barring except in the case of F_1 females secured from a cross of a colored male and a White Leghorn female. The dominant inhibiting gene, *I*, has also been reported to be present in certain White Minorcas and White Plymouth Rocks, although the results of the great majority of investigations concerning the inheritance of white plumage in these two varieties have shown that white is recessive to color. The strains of White Minorcas and White Plymouth Rocks which were found to carry the dominant white may have resulted from previous crossings of these varieties with White Leghorns. Even if such crossings had been made and the progeny invariably conformed to the breed type and color standard of the White Minorca and White Plymouth Rock, the progeny in each case might well be regarded as White Minorcas and White Plymouth Rocks.

Punnett (1923) points out that in England breeders of White Wyandottes have sometimes used White Leghorns in their matings, but so long as the progeny of such matings are of the Wyandotte shape and have rose combs they are regarded by the poultry breeders as being White Wyandottes.

That the dominant inhibiting gene is not completely dominant in the case of certain crosses is shown by the appearance of partially colored F_1 birds in certain matings. Jull and Quinn (1931) have observed that, in reciprocal matings between White Leghorns and Partridge Plymouth Rocks, a number of F_1 adult males have red shoulders and some red over the back and some of the F_1 adult females have a reddish cast on the underside of the throat and over the breast. Serebrovsky (1926) states that the inhibiting gene of White Leghorns inhibits the development of all color except the red color of the shoulders, back, hackle, and saddle of the male. Warren (1930*a*) concluded that the salmon-breast condition in a strain of White Leghorn females is due to a single gene, which behaves as a recessive toward the white of the White Leghorn. Until more is known concerning the nature of the other genes affecting the color of F_1 progeny produced from crosses between White Leghorns and colored varieties, it is sufficient to consider the gene *I* as a dominant inhibitor of color.

Recessive White Plumage.—There are at least two kinds of recessive whites, a fact first demonstrated by Bateson and Punnett (1908). Reasons are given below for placing the White Silkie and White Rose-Comb Bantam in one group of recessive whites and all other white breeds and varieties that have been investigated in the other group of recessive whites.

Serebrovsky (1926) studied Faverolle Bantams and reported the appearance of two forms of recessive white chicks, with rosy and white greenish down. Unfortunately the genetic nature of the difference was not investigated.

First Group of Recessive Whites.—It has already been shown in Chapter III on "Mendelian Inheritance" that the white of the White Rose-Comb Bantam behaves as a simple recessive to color. This was first shown to be true by Bateson and Punnett (1908) in crosses between White Rose-Comb and Black Rose-Comb Bantams, and the results of similar matings made by Jull and Quinn (1929) are illustrated in Chapter III.

The recessive nature of the white plumage of the White Silkie breed was demonstrated by Darwin (1868), Bateson and Punnett (1908), Cunningham (1912), and Bonhote (1914).

Second Group of Recessive Whites.—In the following white varieties, white has been shown to be recessive to color: White Wyandotte by Bateson (1902) and Sturtevant (1912), White Cochin Bantam by Davenport (1906), White Dorking by Bateson and Punnett (1906), White Langshan by Goodale (1910), White Minorcas by Hadley (1913), and White Plymouth Rocks by Hadley (1914). When any one of the white varieties mentioned above was mated to a colored variety, the F_1 birds were colored, and if F_2 progeny were secured they consisted of 3 colored to 1 white, showing that in these varieties the white plumage is due to a single pair of recessive autosomal genes.

Other Recessive Whites.—Investigational work during recent years has disclosed the fact that there are apparently recessive whites other than those mentioned previously. Among these may be included the following: the Blue-Splashed White Andalusian, whose inheritance is discussed later; white birds derived by Dunn (1923) from birds with the columbian pattern but lacking black in the neck feathers, wings, and tail; and albinos secured by Warren (1931).

Colored Progeny from White Parents.—Since the recessive white of the White Silkie and White Rose-Comb Bantam, and the recessive white of the group represented by White Dorkings, in each case behaves as a simple Mendelian recessive to color, it would normally be expected that crossings between the two kinds of white recessives would produce nothing but white progeny. That such is not the case, however, has been demonstrated by Bateson and Punnett (1906) in a cross made between the White Silkie and the White Dorking. The F_1 progeny from such a mating was colored, and the F_2 progeny consisted of the proportion of 9 colored to 7 white birds.

These results show that, although neither of the two genes recessive for white is capable, by itself, of producing color, when they are brought together the production of a colored bird is the result. The two recessive white genes are complementary, that is, one gene supplies what the other lacks; as long as a bird possesses one only of the two kinds of genes it is a white bird.

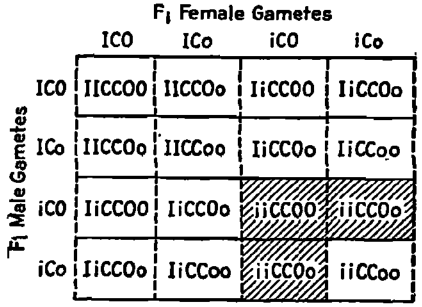
The Genes for White.—It has been suggested that the difference between the gene of the Silkie and White Rose-Comb Bantam and the gene of the other recessive white group is of a chemical nature, the gene of one group producing an oxidase which when present with chromogen makes possible the production of color. The gene of the White Silkie and White Rose-Comb Bantam group is represented as producing chromogen, the symbol used being *C*. The gene of the second recessive white group, White Dorking, etc., is represented as producing the oxidase, the symbol used being *O*. From the standpoint of the inheritance of color, the zygote of the White Silkie and White Rose-Comb Bantam is *CCoo*, and that of the second recessive white group is *ccOO*.

All the F_1 progeny of a cross between a White Silkie (*CCoo*) and a White Dorking (*ccOO*) are colored, because the presence of *O*, representing the production of oxidase, makes possible the production of color through its action on *C*, representing chromogen. An F_1 male and an F_1 female each produces four kinds of gametes, *CO, Co, cO,* and *co*.

A ratio of 9 colored to 7 white birds is obtained in the F_2 generation because whenever *C* and *O* are brought together color is produced. The 16 zygotes consist of

1 *CCOO* 2 *CCOo* 2 *CcOO* 4 *CcOo*	9 containing both *C* and *O*	9 colored birds
1 *CCoo* 2 *Ccoo*	3 containing *C* but not *O*	7 white birds
1 *ccOO* 2 *ccOo*	3 containing *O* but not *C*	
1 *ccoo*	1 containing neither *C* nor *O*	

Since a crossing of birds belonging to the two different groups of recessive white produces a 9:7 ratio, it is interesting to note that when birds belonging to either one of the first two white recessive groups mentioned previously are crossed with birds belonging to the dominant white group a 13:3 F_2 ratio is produced, as shown in Fig. 23.



F_1 Female Gametes

F_1 Male Gametes	ICO	ICo	iCO	iCo
ICO	IICCOO	IICCOo	IiCCOO	IiCCOo
ICo	IICCOo	IICCoo	IiCCOo	IiCCoo
iCO	IiCCOO	IiCCOo	▨ iiCCOO	▨ iiCCOo
iCo	IiCCOo	IiCCoo	▨ iiCCOo	iiCCoo

FIG. 23.—The F_2 generation secured from an original cross between a dominant white, the White Leghorn, and a recessive white, the White Silkie, consists of 13 white to 3 colored birds. The gene I inhibits the development of color but where it is not present both C and O must be present in order that color may be produced.

Bateson and Punnett (1908) crossed White Leghorns × White Silkies, Hadley (1914) crossed a White Leghorn male × White Plymouth Rock females, and Dunn and Jull (1927) crossed White Leghorn × White Silkies; in each case an F_2 progeny in the ratio of 13 white birds to 3 colored ones was secured.

The foregoing discussion on the inheritance of white plumage makes it clear that such a simple character has a rather complex background.

INHERITANCE OF BLACK PLUMAGE

Black breeds and varieties are very numerous; they include Jersey Black Giants, Black Sumatras, Black Hamburgs, Black Langshans, Black Leghorns, Black Minorcas, Black Orpingtons, Black Wyandottes, Black Rose-Comb Bantams, and others.

Down Color.—The down color of the chicks of all black breeds and varieties is black, except that there is usually a variable amount of white or gray on the ventral surface.

How Black Behaves in Inheritance.—Black is recessive to the white of the White Leghorns. Crosses made by Davenport (1906) and Hadley (1914) between black and recessive white varieties have shown that black is dominant.

In a cross between Black Langshans and Brown Leghorns made by Punnett and Bailey it is reported by Punnett (1923) that the F_1 chicks were black, and as adults the pullets were full black whereas the cockerels were black with some gold in the hackles and on the shoulders. "In the F_2 progeny the black and the brown striped downs segregated cleanly, giving a simple 3:1 ratio." Punnett adds that the results of this cross suggest that brown is differentiated from black by a single gene and that there are various forms of brown which can be transformed into black by the addition of this gene.

In black breeds and varieties the melanic pigment is distributed evenly to all parts of the plumage, and from crosses between Black Orpingtons and Light Brahmas, which have black restricted to the neck, wings, and tail, Dunn (1922*a*, 1923) has suggested that black breeds and varieties contain a pair of genes, designated EE, for the extension of the black or melanic pigment. Dunn used the symbol E^m, but since he refers to the same gene as other investigators who have investigated the inheritance of black plumage and since they have used the symbol E to denote the gene having the same effect as Dunn's E^m gene, the symbol E only is used in this discussion. That the Black Langshan carries EE has been demonstrated by Lippincott (1923), Serebrovsky (1926), and Knox (1927), and Serebrovsky (1926) also showed that EE is present in Black Minorcas and Black Orpingtons.

Occasionally the inheritance of black cannot be interpreted on a monohybrid basis, a case in point being a cross reported by Punnett (1923) between Black Langshans and Golden-Penciled Hamburgs. The F_1 chicks were all black, and as adults the females were solid black and the males were black with some gold in the hackles. The F_2 progeny consisted of 113 blacks and 80 nonblacks, which is very close to a 9:7 ratio (108.56:84.42). This suggests the inheritance of black in this particular cross on a dihybrid instead of a monohybrid basis. Moreover, F_1 birds backcrossed to Golden-Penciled Hamburgs produced 29 blacks and 92 nonblacks, expectation being one-fourth blacks in the total progeny or a proportion of 30.25 blacks to 90.75 nonblacks. It is quite evident, therefore, that the Golden-Penciled Hamburg lacks two genes necessary for the extension of black pigment.

THE INHERITANCE OF BUFF PLUMAGE

Buff varieties are numerous and include Buff Brahmas, Buff Cochins, Buff Leghorns, Buff Orpingtons, Buff Plymouth Rocks, Buff Wyandottes, and others. Foreign color, including black, in any part of the plumage is regarded by poultry breeders as a serious defect. At the same time, it is well known that black in varying amounts is sometimes present in the feathers of the neck, wings, and tail. Because of this condition, Dunn (1923) has suggested that buff is in reality a pattern.

Down Color.—The down color of the chicks of buff varieties is buff, often varying from a very light to a very dark shade, and frequently being of a lighter shade on the ventral than on the dorsal surface.

How Buff Behaves in Inheritance.—Comparatively few experiments have been conducted with the view of determining the nature of the inheritance of buff, but the results of crosses made in recent years suggest that the situation is more complicated than was originally supposed.

The results of a cross of Buff Cochins × Black Hamburgs made by Hurst (1905) and of a cross of Black Cochins × Buff Cochins made by Davenport (1909) indicate that buff is recessive to black.

The results secured from reciprocal crosses between Buff Orpingtons and Light Brahmas, which have what is called the "columbian color pattern" as found in Columbian Plymouth Rocks and Columbian Wyandottes, led Dunn (1922*a*, 1922*b*, 1923) to conclude that "buff and columbian colorations of fowls differ in one principal gene determining the presence or absence of buff in the plumage and probably in multiple factors (genes) determining the amount of black developed in wing, tail and hackle feathers." In connection with this discussion concerning the relationship between buff color and the columbian pattern, Warren (1928*a*) states that the Buff Leghorn carries the columbian pattern, in which black pigment is restricted to the neck feathers, tail, and portions of the wings.

Dunn (1923) concluded that buff differs from black by a gene determining the restriction of black to the hackle, tail, and wings. The dominant allelomorph of this gene is present in self-blacks, as previously observed under the discussion of the inheritance of black, where it was pointed out that *EE* effects the extension of black pigment to all parts of the plumage. According to Dunn, therefore, black fowls are genetically buffs with the extension gene superimposed, buff varieties carrying *ee*.

Knox (1927) made reciprocal crosses between Buff Orpingtons and Black Langshans and secured F_1 blacks only, except that there was a slight amount of buff across the wings and back and in the neck, thus showing that buff is in general recessive to black. Knox also crossed Buff Orpingtons and White Plymouth Rocks reciprocally, and the buff color appearing in all F_1 hybrids showed buff to be dominant to the recessive white.

Knox found that the results he secured could be interpreted only on the assumption of there being two pairs of genes responsible for the development of buff color, each pair producing the same effect, and that there is an interaction between these genes for buff and the genes *C* and *E* depending upon whether either one or both is in a homozygous condition. Knox has designated the symbols *Bu Bu* and *Bu′ Bu′* to represent the two pair of buff-producing genes, their respective allelomorphs being *bu bu* and *bu′ bu′*.

The results which Knox secured in his F_2 and backcross generations led him to make the following assumptions: Buff is epistatic to black when three or four genes for buff are in the presence of *CC* and *EE*; buff is epistatic to black when three or four genes for buff are in the presence of either *Cc* and *EE* or *CC* and *Ee*; buff is epistatic to black when two or more genes for buff are in the presence of *Cc* and *Ee*.

Although relatively few experiments have been conducted involving the inheritance of buff plumage, the results secured indicate that buff color or buff "pattern," if such there be, rests upon a complex genetic basis, and much further work seems necessary to test the validity of the hypotheses put forward.

THE INHERITANCE OF BLUE PLUMAGE

There is one blue breed, the Blue Andalusian, and a few blue varieties, including Blue Leghorns, Blue Orpingtons, and Blue Plymouth Rocks.

Down Color.—The down color of the chicks of the blue breed and varieties is an even shade of slaty blue, except that the breast and ventral surface of the body are lighter, approaching bluish white.

Blue a Heterozygous Color.—The results secured from matings of Blue Andalusians represent the classical example of the peculiar mode of inheritance in all blue varieties and are in marked contrast to the results secured from matings of all other breeds and varieties.

A mating of Blue Andalusian males to Blue Andalusian females does not produce all Blue Andalusians, for if large enough numbers of progeny are produced one-fourth are black, one-fourth are white with a few blue feathers, and one-half are typical Blue Andalusians. In other words, the Blue Andalusian does not breed true.

Bateson and Punnett (1906) made all possible types of matings between each two of the three different colors—blacks, blue-splashed whites, and blues—and found that the blacks and the blue-splashed white breed true, whereas the blues were heterozygous in that they invariably produce progeny in the ratio of 1:2:1, that is, 1 blue-splashed white to 2 blues to 1 black.

Hagedoorn and Hagedoorn (1914) crossed a Blue Andalusian with a recessive white and secured equal numbers of blue and black progeny.

Concerning the genes responsible for the development of blue plumage, Lippincott (1918, 1921, 1923) proposed the theory that two pairs of genes are involved, the dominant condition of both never being present in the same gamete. Punnett (1923) points out, however, that Blue Andalusians are fundamentally a black breed and that the blue-splashed white birds and blue birds result from the operation of a gene which partially inhibits the production of pigment, the inhibiting gene being in a homozygous dominant condition in the blue-splashed white birds and in heterozygous condition in the blue birds. The inhibiting gene would naturally be entirely lacking in the black birds. Serebrovsky (1926) mentions the same gene for blue which inhibits black and calls it "todi."

Punnett's interpretation of the situation explains in a satisfactory manner the results secured from the various matings among the three kinds of Andalusians as well as between each of the three kinds of Andalusians and recessive whites.

It should be pointed out, however, that the gene which partially inhibits the development of black pigment in blue-splashed white and Blue Andalusians is not the same gene which inhibits the development of pigment in White Leghorns.

THE INHERITANCE OF "RED" PLUMAGE

So far as is known the Red Leghorn is the only variety that is red in all parts of its plumage, although from the standpoint of inheritance "red" is also understood to mean the color found in Rhode Island Reds and Black-Tailed Red Leghorns, a variety of Leghorns developed recently. The plumage color is a rich, brilliant red with the exception that there is black in the wings and tails of both sexes and in the hackle of the males and frequently in the neck feathers of the females.

Down Color.—The down color of the chicks of these "red" breeds and varieties varies considerably in the shade of red. The lightest chicks are cream colored, with perhaps but a tinge of red, whereas the darkest chicks are a chocolate brown. Frequently the ventral surface is of a lighter shade of red than the dorsal surface and occasionally dark striping is present.

Warren (1929) made a comprehensive study of down color in Rhode Island Red chicks by selecting for a period of four years a light-colored-down strain and a dark-colored-down strain, after which the strains were crossed with a view of determining whether or not there is inheritance of down color. Warren found that selection was much more effective in the light than in the dark strain. During the last two years of the breeding of the selected strains each strain was relatively homozygous, with very few chicks of the medium shades in either the light or the dark strain. The results Warren secured when he crossed the light and dark strains led him to conclude that variations in the shade of down color are inherited, a single gene accounting for the results secured, although neither "light" nor "dark" shade is dominant.

Genes Associated with "Red" Plumage Development.—A survey of the literature reveals the fact that very little experimental work has been done with Rhode Island Reds to determine their genetic constitution.

It is interesting to note that Goodale (1911) obtained some F_2 birds resembling Rhode Island Reds from a cross between Brown Leghorns and Buff Plymouth Rocks.

Ladebeck (1922) investigated the pigment of Rhode Island Reds and observed that the red feathers contain reddish-brown to reddish-yellow pigment globules of melanic nature. The black feathers contain rod-shaped and elliptical-shaped black pigment granules of varying sizes.

Dunn (1922*b*) states that red varieties (except presumably the Red Leghorn) are of the recessive type *ee*, *e* being the recessive allelomorph of *E*, the gene for the extension of black pigment in black varieties. In crosses between Rhode Island Reds and Barred Plymouth Rocks, Agar (1924) refers to a brown pigment which he called "chestnut" and which he found to be independent of the gene for "gold" and not sex-linked.

Hays (1926) crossed Rhode Island Reds with recessive whites obtained from "a White Plymouth Rock foundation crossed on Brown Leghorns and later bred back to Brown Leghorns and finally Rhode Island Reds from which extracted whites came in later generations." The results secured by Hays led him to conclude that three pairs of genes are chiefly concerned in the development of Rhode Island Red plumage color, but the number of birds secured by Hays in many of his matings appears to be too limited to draw definite conclusions regarding the inheritance of such a complex character as Rhode Island Red plumage color.

THE INHERITANCE OF "BLACK-RED" PLUMAGE

The Modern Black-Breasted Red Game is a typical example of the so-called "black-red" breeds and varieties. As the name suggests, there is a mixture of black plumage and red or shades of red plumage. In the male the front of the neck, the breast, the shoulders, practically all of the primaries and part of the secondaries, the body, and the tail and tail coverts are black whereas the hackle and saddle are bright red. In the female the neck is light golden, each feather having a black stripe through the middle; the front of the neck and the breast are salmon colored; the primaries and main tail feathers, except the two top ones, are black, and the rest of the plumage is ashy brown, that over the shoulders and the wing-bows and the secondaries being stippled with golden brown.

The single-comb Brown Leghorn is another black-red variety, the color pattern being somewhat the same as in the Black-Breasted Red Game. *Gallus gallus bankiva* is of the same general color pattern.

Very little is known concerning the inheritance of the "black-red" plumage pattern although the results of a few experiments lead to interesting observations regarding the relationship between black-reds and blacks and between black-reds and varieties like the Silver-Gray

Dorking, the Silver Duckwing Game, and the Dark Dorking, varieties in which the females have stippled plumage.

In a cross between Brown Leghorns and Black Langshans, Punnett (1923) found that the F_1 females were completely black and the F_1 males were black with some gold in the hackles and on the shoulders. This is not a case of sex-linked inheritance, because the same results were obtained from reciprocal crosses. Apparently one or more pairs of genes are involved which are responsible for the development of gold in the hackle and on the shoulders of the males, and except for this difference it is apparent, as Punnett has suggested, that the Brown Leghorn can be transformed into a black bird by the addition of the gene *E* for the extension of black pigment.

THE INHERITANCE OF THE RED PYLE PATTERN

The color of the Red Pyle Game involves a very interesting though complex problem concerning the nature of the inheritance of certain colored sections of the plumage. Both sexes are for the most part white. The male has a considerable amount of orange and red feathers on his dorsal side as follows: the neck and hackle feathers are light orange, the wing bows are red; the outer webs of the lower primary feathers are bay colored; part of the outer web of the secondaries are red; the feathers over the back are red and the saddle feathers are light orange. In the female, except for the white neck feathers being edged with gold, the only section having colored feathers is the front of the neck, where the feathers are white tinged with salmon.

Hurst (1905) and Davenport (1906, 1909), crossed buff varieties with the White Leghorn, the F_1 birds being somewhat like pyle birds in plumage color. Punnett (1923) points out that the Red Pyle Game can produce black-reds, the white of the Red Pyle Game being dominant to the melanic ground color of the black-red. Cunningham (1919), however, has shown that the white plumage of a Red Pyle may be of the nature of a recessive white, since he was able to produce pyle-colored fowls from a cross between the Jungle Fowl and the White Silkie.

Punnett (1923) states that the orange-red pattern of the Red Pyle Game behaves as a distinct plumage character and may be associated with different ground colors, and that "it is neither inhibited by the dominant white nor prevented from making its appearance when some constituent for the development of the melanic pigment is absent, as in recessive whites of the Silky type." The fact that Davenport (1909) secured pyle-colored birds in the F_2 generation from a White Leghorn × buff cross led Punnett to suggest that the orange-red color in the dominant white bird is inhibited by the presence of a gene for "silver." The fact that the White Leghorn possesses the gene for silver has been demonstrated by various workers, as pointed out later.

Serebrovsky (1926) suggests that the gene which he calls "tule" is responsible for the development of the red in the shoulders, back, saddle, and hackle feathers in the male.

THE INHERITANCE OF MOTTLING

The Mottled Ancona and Mottled Houdan have what is known as mottled plumage, in which the ground color is black, a variable portion of the black feathers in different sections of the bird being tipped with white.

Down Color.—The down color of Mottled Ancona chicks is black on the dorsal surface and creamy yellow shading to white on the lower part of the head, the breast, and ventral surface. The down color of Mottled Houdan chicks is black on the dorsal surface and on the sides of the body, including the outer thighs, whereas the crest, throat, breast, and fluff are lemon yellow.

How Mottling Behaves in Inheritance.—Both Hurst (1905) and Davenport (1906) crossed the Mottled Houdan with the White Leghorn and each secured an F_2 generation indicating that mottling behaves as a simple Mendelian recessive to the white of the White Leghorn. Davenport (1906) also crossed the Mottled Houdan with the Black Minorca and observed that the F_1 birds were almost completely black, the black of the Minorca being dominant to mottling. Apparently no F_2 generation was raised.

Serebrovsky (1926) observed that the mottling of the Mottled Orloff is recessive to solid color but differs from the mottling of the Mottled Houdan, since the crossing of Mottled Orloffs and Houdans produced self-blacks.

Asmundson and Milne (1930) made crosses between Mottled Anconas and each of the following colored varieties: Black Minorcas, Black Orpingtons, and Buff Wyandottes. The crosses between Mottled Anconas and Black Minorcas and Black Orpingtons produced F_1 birds that were entirely black and F_2 birds consisting of 45 black and 14 mottled ones, the expected ratio on a monohybrid basis being 44.25 blacks to 14.75 mottled ones. The results of the F_1 and various backcross matings indicate that mottling is recessive to self-color on a monohybrid basis.

The results which Asmundson and Milne secured when Mottled Anconas were crossed with Buff Wyandottes led them to conclude that Mottled Anconas carry *EE*. The results they secured between Mottled Anconas and Black Minorcas and between Mottled Anconas and Black Orpingtons led them to conclude that Mottled Anconas carry a pair of genes, *e'e'*, whose presence is responsible for the appearance of the white tips on some of the feathers.

THE INHERITANCE OF PIED PLUMAGE

What is known as pied plumage is found in Exchequer Leghorns and is characterized by a mixture of black and white. In the male the neck and hackle feathers are black or mostly black, each feather having a streak of white down the center; the breast, wing bows, and thighs are white evenly mottled with black; the main sickle feathers are white, whereas the tail and saddle feathers are black with white markings. In the female the ground color is white, many of the feathers being marked with black concentric spots, the general appearance of the female being much like that of the male.

Apparently the chief differences between pied and mottled plumage are that in pied birds there are some feathers that are entirely white, and the black markings are much more irregular than in mottled birds.

Down Color.—The down color of pied chicks is practically the same as the down color of Mottled Ancona chicks.

Pied Plumage Recessive to Self-Black.—In studies on the inheritance of pied plumage, Punnett and Pease (1927) came to the conclusion that pied plumage behaves as a simple recessive to full color. They found that a pied bird looks lighter when the pied character is associated with the Plymouth Rock type of barring "than when the same grade of piedness is on a self-black basis."

Since pied plumage is characteristic of the Exchequer Leghorn, further experiments were conducted by crossing a Black Leghorn male × Exchequer Leghorn females. It was found that the pied character behaves in the same way as the mottling character toward black, each being recessive to black on a monohybrid basis, although the genetic relationship between piedness and mottling apparently has not been worked out.

THE INHERITANCE OF SPANGLING

The spangled character of plumage coloration, found in Silver-Spangled and Golden-Spangled Hamburgs, consists of a V-shaped black spangle at the tip of each feather, the rest of the feather except for the fluff at the base being white in the Silver variety and gold in the Golden variety.

Down Color.—According to Dunn and Landauer (1930), the down color of Silver-Spangled Hamburg chicks "is a light bluish black indistinctly striped on the back with black and white. The tips of the dark down are yellowish white giving the chicks a general silvered or dusty appearance. On the head and neck the base of the down is bluish black while the tips are yellowish white." According to Punnett (1923), the down color of Golden-Spangled Hamburg chicks "is chocolate-brown with much wider stripes and a more or less golden head."

Acquiring the Spangled Pattern.—Dunn and Landauer (1930) found that the pattern of the spangled fowl appears gradually during the growth of the chick through the replacement of the original non-spangled feathers by feathers showing the spangled pattern. They found that almost none of the feathers which developed before the chick was twenty-five days old showed the spangled pattern, whereas the feathers developing after that time showed it.

The Genetics of Spangling.—The results secured by Lefevre (1917) and Lefevre and Rucker (1923) in crosses between Silver-Spangled Hamburgs and Brown Leghorns led them to conclude that spangling was dominant and sex-linked. The sex-linkage of spangling was not borne out, however, in results which Punnett (1923) secured from a cross of Silver-Spangled Hamburgs × Golden-Penciled Hamburgs since of 22 F_2 birds there were 16 spangled and 6 barred birds, 3 of the latter being males and 3 being females, whereas if spangling is sex-linked all the barred birds should have been females. Punnett says that spangling is probably related to lacing and barring but that the appearance of spangling depends upon a gene not found in laced and barred breeds.

The results secured by Taylor (1932) from reciprocal crosses between Silver-Spangled Hamburgs and Black Minorcas led him to conclude that spangling is due to a pair of dominant autosomal genes, that is, spangling is not sex-linked. Taylor further observed that: "The expression of spangling is partially or completely inhibited in the presence of extended black. A greater inhibition of spangling in female offspring than in male offspring may be due to the action of the female sex hormone on the development of black pigment in birds of genetically extended black types." Taylor found that birds homozygous for spangling were more completely spangled than birds heterozygous for spangling.

Agar (1924) crossed a Golden-Laced Wyandotte male × Barred Plymouth Rock females and then mated an F_1 male to a Golden-Laced Wyandotte female and was led to conclude that lacing is nearly completely epistatic to barring but is hypostatic to extended black. It is difficult to understand how lacing can be nearly completely epistatic to barring when it is well known that barring is dominant to extended black (non-barring) and also apparently dominant to lacing, judging by the results which Punnett (1923) secured. It is quite obvious that much work remains to be done to establish the genetics of lacing upon a definite basis.

THE INHERITANCE OF PENCILING

In penciled plumage each feather has one or more stripes of the same shape as the outline of the feather but differing in color from the rest of the feather. The feathers of the female of the Dark Cornish have one stripe; those of the females of the Silver-Penciled Plymouth Rocks, Silver-Penciled Wyandottes, Dark Brahmas, Partridge Plymouth Rocks, Partridge Wyandottes, and Partridge Cochins have three stripes. The tail feathers of penciled females are black. None of the feathers of the males of any of the penciled varieties are penciled, as shown in Fig. 1. The difference between the silver-penciled and the partridge females is that in the silver-penciled varieties the black penciling is on a white background whereas in the partridge varieties the black penciling is on a reddish-bay ground color.

Up to the present, practically nothing is known concerning the genetics of penciling.

THE INHERITANCE OF BARRING

The inheritance of barring as a sex-linked character in Barred Plymouth Rocks has already been discussed in Chapter II. It was pointed out that the gene *B*, which produces the barring effect on each feather, is contained in the sex chromosome; the barred female being heterozygous for sex transmits the *B* gene to her sons only. The barred male being homozygous for sex transmits the *B* gene to his daughters as well as to his sons.

The barred breeds and varieties include the Barred Plymouth Rock, Dominique, Scotch Gray, Cuckoo Leghorn, Campine, and Golden-Penciled and Silver-Penciled Hamburg. In spite of the name, the two varieties of Penciled Hamburgs have barred feathers, although barring in the Campine and Hamburg behaves differently in inheritance from the barring in the Barred Plymouth Rock, Dominique, Scotch Gray, and Cuckoo Leghorn.

Down Color.—The down color of the Barred Plymouth Rock chicks is black over the dorsal surface and on the sides except that there is a light yellowish gray patch at the back of the head and the ventral surface is creamy white, the extent of which varies considerably. Punnett (1923) says, "In various experiments made at Cambridge it has been found that the light head patch invariably accompanies the barred plumage." In matings involving a cross between a Barred Plymouth Rock female and a male of a nonbarred variety, except the White Leghorns, the sex of the chicks can be distinguished at hatching time by the presence or absence of the light patch at the back of the head. The chicks with the light head patch are males and those without it are females.

Fig. 25.—When Rhode Island Red males are crossed with Barred Plymouth Rock females, the sex of the chicks can be distinguished at hatching time, as shown in this illustration. The females, solid black in down color, are shown on the left and the males, each with a light patch on the head, are shown on the right. As adults the females are black, sometimes with a tinge of red on the neck and breast whereas the males are barred. The females have black or very dark shanks and toes whereas the males have yellow shanks and toes. (U. S. D. A.)

Although the down color of the Silver Campine chick is grayish brown and that of the Golden Campine chick is of a medium brown shade, it is sometimes difficult to distinguish the chicks of the two varieties because the median dorsal and the two lateral stripes along each side of the back are of such a rich dark chocolate color and are sometimes so wide as to obscure the ground color.

In the Golden-Penciled Hamburg the down color is of the striped form, the ground color being golden buff with striping along the median line of the head and back.

Barring Versus Nonbarring.—The fact that barring is sex-linked was apparently first observed by Cushman (1893), although Punnett and Bateson (1903) and Spillman (1908) were the first to suggest that the inheritance of barring rested on a sex-linked basis, and Morgan (1910) was apparently the first to explain that sex-linked characters were such as a result of the genes producing the characters residing in the sex chromosomes.

The inheritance of barring as a sex-linked dominant character has been demonstrated by a number of investigators, including: Goodale (1909, 1910), Pearl and Surface (1910*a*, 1910*b*), Morgan and Goodale (1912), Holdefleisz (1911), Frateur (1914), Dunn (1923), Jull (1924), and Punnett (1929).

Punnett and Pease (1930) have developed a breed called the Cambar out of matings between Barred Plymouth Rocks and Gold Campines, the Cambar having the unique distinction of producing within the breed chicks the sex of which can be distinguished at hatching time, when the male chicks have pale "blotchy" down color whereas the females have down color characteristic of the Gold Campine chicks.

Table 6 gives the matings between nonbarred males and barred females that may be used to produce chicks the sex of which can be determined at hatching time.

The Effect of the Sex-linked Gene for Barring.—Although it has been observed that barring is dominant to color and that the gene for barring is sex-linked, at the same time, Punnett (1923) points out that the barring in Barred Plymouth Rocks, Dominiques, Scotch Grays, and Cuckoo Leghorns is genetically quite distinct from the barring in Campines and Penciled Hamburgs, concerning the inheritance of which but little is known at present.

The gene for barring as found in Barred Plymouth Rocks is regarded as restricting the black pigment to bars, for if Barred Plymouth Rocks did not have the gene *B* they would be black. Dunn (1923*a*) states that the barring effect in Barred Plymouth Rocks, consisting as it does of alternate white and black bars, is dependent upon two sex-linked genes, one of which is *B* for barring pattern and the other is a gene which prevents the development of buff in what

TABLE 6. MATINGS INVOLVING THE SEX-LINKAGE OF BARRING WHICH MAKES IT POSSIBLE TO DISTINGUISH THE SEX OF CHICKS AT HATCHING TIME

Mating No.	Nonbarred Males	Barred Females	Color of Chick	Color of Adult Progeny
1	All black breeds and varieties.[1]	Barred Plymouth Rocks. Dominiques. Scotch Grays. Cuckoo Leghorns.	Males black on top of body except white spot on top of head. Beak, shanks and toes yellow.	Males barred. Beak, shanks, and toes yellow.
			Females all black on top of body. Beak, shanks, and toes black or very dark.	Females black. Beak, shanks, and toes black or very dark.
2	Rhode Island Red, Buff Plymouth Rock and all other color varieties except blues.	Same as above.	Males and females same as in mating No. 1.	Males same as in Mating No. 1
				Females black except they may have some red or other color in the neck or over other parts of body. Beak, shanks, and toes black or very dark.
3	White Minorca and other white recessives except White Plymouth Rock.[2]	Same as above.	Males and females same as in mating No. 1.	Males and females same as in mating No. 1.
4	Cambar.	Cambar.	Males pale "blotchy."	Males much paler in color than females.
			Females like Campines.	

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[1] Punnett (1929) points out that difficulty may be encountered in distinguishing the sexes of chicks at hatching time if Black Sumatra and Black Leghorn males are used, owing to the fact that the white normally present on the ventral surface of all chicks of black breeds and varieties may in the case of Black Sumatra male × barred female and Black Leghorn × barred female matings extend to the dorsal surface over the head and neck so that the sexes cannot be distinguished accurately.

[2] A White Leghorn or a La Bresse male could not be used in mating No. 3 because in each case the white is dominant to color and all the chicks would be white with a few black spots. The White Plymouth Rock male could not be used because, although it is a recessive white, it carries the gene for barring, or at least most White Plymouth Rocks do, but all White Plymouth Rocks lack the gene for color.

would otherwise be the white bars of the barring pattern. When this second gene, known as "silver," is absent the barring pattern consists of black and "gold" bars instead of black and white bars. Punnett (1923) also observed that the Barred Plymouth Rock carries the gene for silver. As far as the inheritance of barring is concerned, however, the presence of the gene for the production of silver does not affect the situation.

Punnett and Pease (1928) have described a barred variety developed recently in England, the Gold-Barred Plymouth Rock, in which the black of the Barred Plymouth Rock is replaced by a rich buff, so that the Gold-Barred Plymouth Rock is barred with buff on a white background. The barring was found to be sex-linked as in the case of the Barred Plymouth Rock, and Punnett and Pease, in view of the results secured from various matings, have suggested that the genes for barring in the Barred variety and in the Gold-Barred variety differ in their inhibitory potency and are allelomorphic to one another. The gene *B* occurring in the Barred variety is regarded as being more potent than the gene *B'* occurring in the Gold-Barred variety. The latter variety is essentially a buff with the addition of the barring character.

Hadley (1914) found that the gene for barring is present in both White Leghorns and White Plymouth Rocks, males being homozygous for this sex-linked gene (*BB*) and females being heterozygous (*B*—). The White Leghorn is white, however, because of the presence of the inhibiting gene *I*, and the White Plymouth Rock is white because of the absence of chromogen material. When the White Leghorn is crossed with a colored variety the F_2 generation frequently contains some barred birds.

Punnett (1923) makes an interesting observation concerning the effect that the gene *B* in White Leghorns has on the color of hybrids produced from matings of White Leghorns with colored varieties. He points out that although the gene *I* exercises a more or less complete effect in inhibiting the development of pigmentation, the effect is augmented by the presence of the barring gene, *B*.

Barring in Campines Not Sex-linked.—In Barred Plymouth Rocks, Dominiques, Scotch Grays, and Cuckoo Leghorns the barring character is produced by alternating black and white bars. Among the Campines an interesting situation exists regarding three different kinds of barring. The Silver variety has black and white bars, the Golden variety black and golden bay bars, and the Chamois variety white and golden bay bars.

Since the plumage of the Silver is dominant to that of the Golden variety, Punnett (1923) points out that the white bars of the Silver variety are due to the action of a gene which inhibits the development of golden bay. This inhibiting gene is the same as the one that produces the difference between the silver and gold characters as explained a little later in this chapter. Punnett further points out that the plumage of the Chamois is dominant to the plumage of the Golden variety, the difference between white and golden bay bars and black and golden bay bars being due to a single gene, as Punnett and Pease (1921) have shown.

It is apparent, then, that the golden bay bars of the Chamois variety correspond to the golden bay bars of the Golden variety, and that the Chamois variety contains a gene which inhibits the development of the melanic pigment contained in the black bars of the Golden variety. Therefore, a cross between the Silver and Chamois varieties should produce white birds, which Punnett found to be the case.

By the use of appropriate symbols the production of white birds from a cross between the Silver and Chamois varieties is readily demonstrated. The Silver variety contains the gene S which inhibits the development of golden bay. The Golden and the Chamois varieties, therefore, carry s. The Chamois variety contains the gene I^b which inhibits the development of black. The Silver and the Golden varieties, therefore, carry i^b. The Silver variety is SSi^bi^b; the Golden variety is ssi^bi^b; the Chamois variety is ssI^bI^b. When the Silver and Chamois varieties are crossed the following result is secured:

	SILVER CAMPINE	×	CHAMOIS CAMPINE
P_1 zygotes	SSi^bi^b		ssI^bI^b
P_1 gametes	Si^b		sI^b
F_1 zygotes		SsI^bi^b	

The F_1 zygotes SsI^bi^b develop into white birds because the gene S inhibits the development of golden bay and the gene I^b inhibits the development of black.

THE INHERITANCE OF "SILVER" VERSUS "GOLD" PLUMAGE

The terms "silver" and "gold" are used with reference to two well-known ground colors of the down of chicks of several different breeds and varieties.

To the "silver" class belong the Silver-Laced and Silver-Penciled Wyandottes, Silver Campines, Silver-Penciled Plymouth Rocks, Silver-Spangled Hamburgs, Silver-Gray Dorkings, and other varieties, including those in which the ground color of the down is creamy silver, such as Salmon Faverolles, Light Brahmas, Light Sussex, Columbian Plymouth Rocks, and Columbian Wyandottes.

Davenport (1912) observed that in a cross between the Dark Brahma and the Brown Leghorn the "silver" character in the Dark Brahma was transmitted as a sex-linked character. That the Barred Plymouth Rock carries silver as well as barring has been demonstrated by Dunn (1923*a*, 1924) and Punnett (1923). Asmundson and Milne (1930) demonstrated that the Mottled Ancona carries silver. In a cross between White Leghorns and Brown Leghorns Punnett (1923) obtained some silver-grays in the F_2 generation, demonstrating that the White Leghorn carries the gene for silver.

The White Wyandotte, although it is a recessive white, has usually been found to possess the gene for silver, the White variety apparently having originated from the Silver-Laced variety as a sport. Warren (1930*b*) points out that difficulty arises, however, from the fact that the white plumage makes it impossible to detect individuals that do not possess the gene for silver and that some White Wyandottes also carry black and produce black chicks when crossed with gold varieties, it being impossible to determine the sex of the black chicks from their appearance.

To the "gold" class belong all breeds in which the ground color of the down is some shade of buff or golden brown, such as Buff Cochins, Buff Leghorns, Buff Orpingtons, Buff Plymouth Rocks, Buff Wyandottes, Rhode Island Reds, and Red Sussex. Also belonging to the gold class are those breeds or varieties in which the male is some form of black-red in plumage color, such as Barnevelders, Brown Leghorns, Cornish, Partridge Cochins, Plymouth Rocks and Wyandottes, and Golden-Laced Wyandottes.

The gene for silver is sex-linked, as demonstrated in the cross between Silver-Penciled and Partridge Plymouth Rocks made by Jull and Quinn (1931). In this cross both varieties have the triple-penciled pattern character, so that the only difference is that one variety has white and the other gold.

The results of the crosses are illustrated in Figs. 26 and 27, and show that silver is sex-linked, being transmitted from dam to sons only but from sire to both sons and daughters. The Silver-Penciled Plymouth Rock male, therefore, is *SS* and the female is *S*—, the dash (—) representing the absence of a sex chromosome.

Distinguishing the Sex at Hatching Time.—It has been found that when females belonging to the silver class are mated to males of the gold class the sex of the chicks can be distinguished at hatching time, with the exception of a few particular crosses.

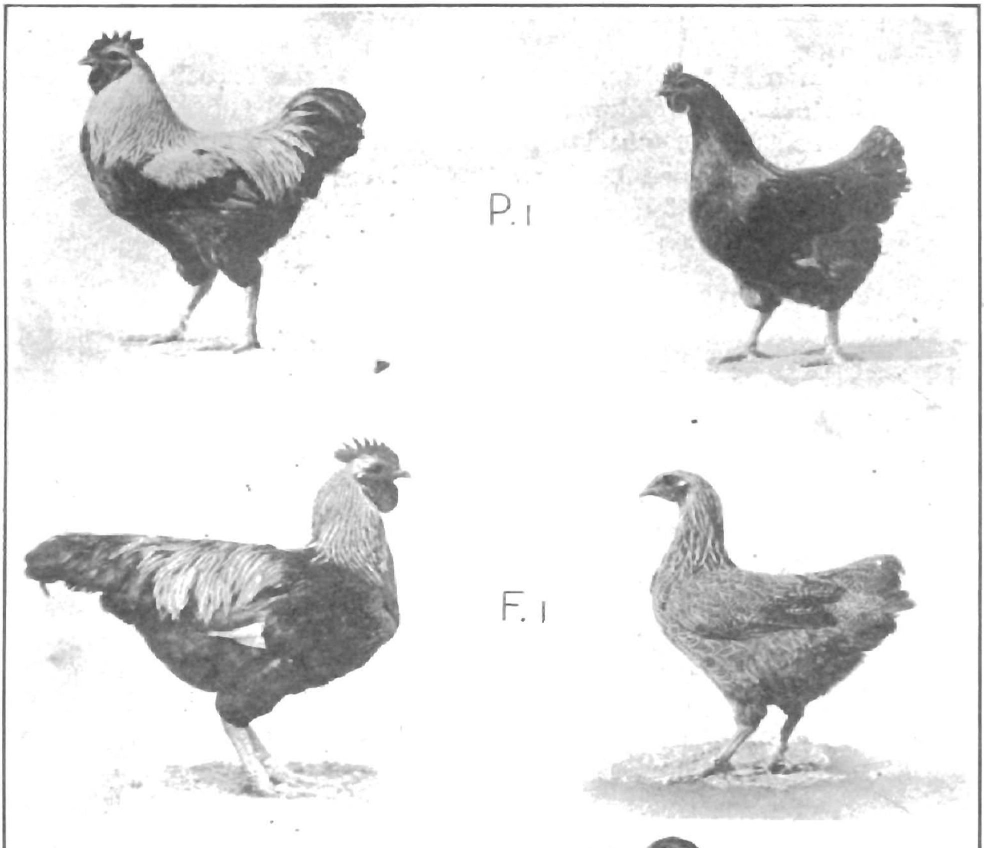

FIG. 26.—A Silver-Penciled Plymouth Rock ♂ x Partridge Plymouth Rock ♀ produce F_1 silver males and females. An F_1 ♂ x F_1 ♀ produce an F_2 generation in which the males are silver and one-half of the females are silver but the other half are nonsilver. (Photo by U. S. D. A.)

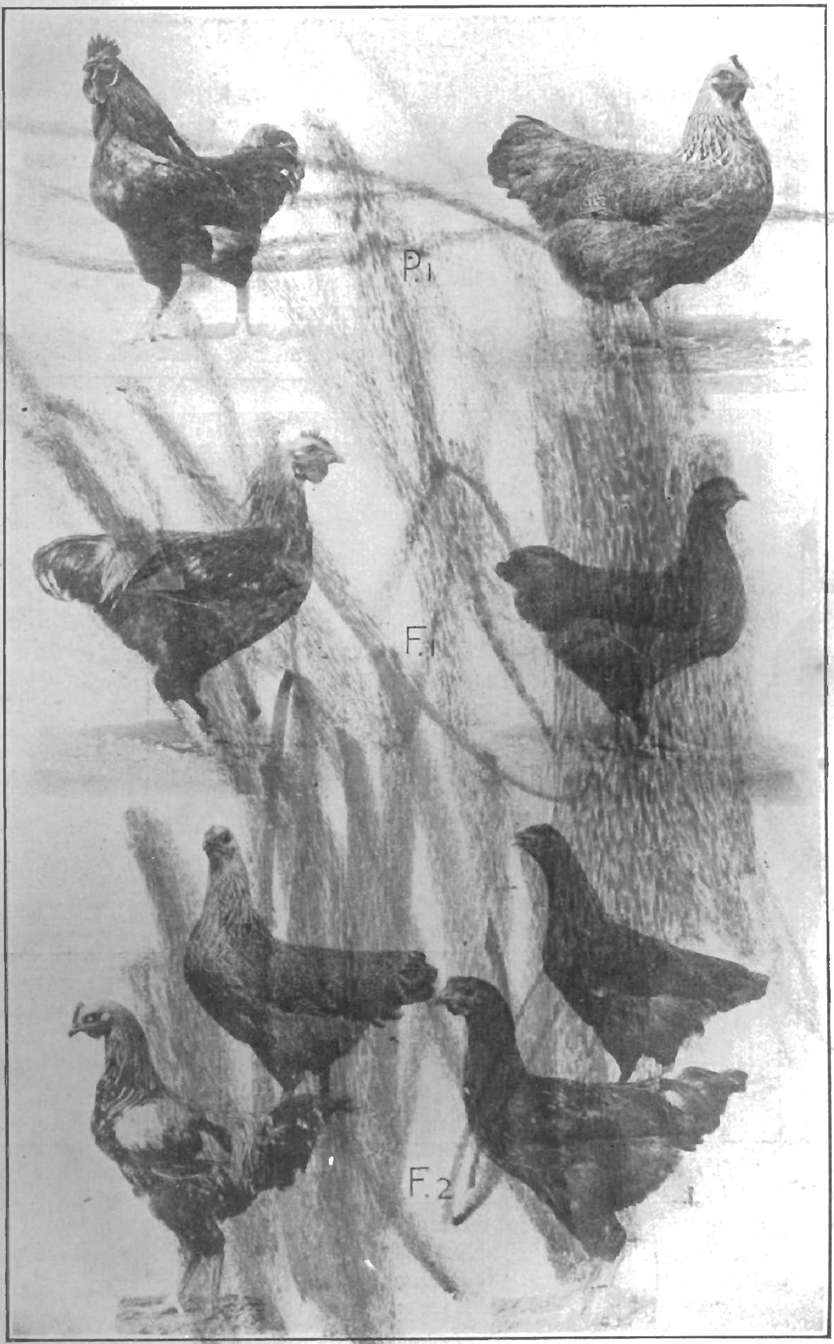

Fig. 27.—A Partridge Plymouth Rock ♂ x Silver-Penciled Plymouth Rock ♀ produce F_1 silver males but nonsilver females, the sex-linked gene for "silver" being transmitted from the dam to her sons only. An F_1 ♂ x F_1 ♀ produce an F_2 generation in which one-half of each sex is silver and one-half is nonsilver. In this sex-linked cross it is difficult to distinguish the sex of the chicks at hatching time. (Photo by U. S. D. A.)

The following table, taken from Warren (1930*b*) with a few minor changes, shows the color of the chicks at hatching time and their color when they become adults in various matings between silver and gold breeds and varieties.

TABLE 7. MATINGS INVOLVING THE SEX-LINKAGE OF SILVER WHICH MAKES IT POSSIBLE TO DISTINGUISH THE SEX OF CHICKS AT HATCHING TIME

Mating No.	Gold Males	Silver Females	Color of Chick	Color of Adult Progeny
1	Rhode Island Red.	White Wyandotte. Silver-Penciled Plymouth Rock. Silver-Penciled Wyandotte. Silver-Laced Wyandotte. Columbian Plymouth Rock. Columbian Wyandotte. Light Sussex. Dark Brahma. Light Brahma.	Males cream or white may show smokiness in down. Females buff or red color. Both sexes may show narrow striping.	Males columbian pattern. Females buff to red; may show some stippling or striping.
2	Buff varieties: Buff Leghorn. Buff Minorca. Buff Plymouth Rock. Buff Wyandotte. Buff Cochin.	Same as above.	Same as in mating No. 1 except female chicks generally lighter in color.	Same as in mating No. 1 except females usually buff.
3	Brown Leghorn. Partridge Plymouth Rock. Partridge Wyandotte. Golden-Laced Wyandotte.	Columbian Plymouth Rock. Columbian Wyandotte. Light Brahma. Light Sussex.	Same as in mating No. 1.	Same as in mating No. 1.

Warren (1930*b*) points out that the female chicks can be more easily distinguished from the male chicks at hatching time if the columbian pattern is involved in the mating. He also points out that if a Brown Leghorn male is mated to females of the silver-laced or silver-penciled varieties the chicks have such a broad dark stripe over the back that it is sometimes difficult to distinguish the sexes of the chicks. At the U. S. Animal Husbandry Experiment Farm, Beltsville, Maryland, Jull and Quinn (1931) found that when a Partridge Plymouth Rock male is mated to Silver-Penciled Plymouth Rock females it is impossible to distinguish the sexes at hatching time with any degree of accuracy, although the difference between the F_1 silver and gold birds in the adult plumage is quite marked, as shown in Fig. 27.

THE INHERITANCE OF EARLOBE COLOR

The color of the earlobe in the case of many breeds is a breed characteristic, by which is meant that all birds belonging to a certain breed must have the same color of earlobe. All Leghorns, regardless of variety, have white earlobes. Leghorns, Minorcas, and Anconas comprise most of the white-earlobe breeds, and Plymouth Rocks, Rhode Island Reds, Wyandottes, Orpingtons among many other breeds have red earlobes.

The inheritance of earlobe color has apparently received but little attention, since the only work that seems to have been done is that by Warren (1928). Crosses were made involving three varieties of Leghorns, the single-comb White, the rose-comb Brown, and the single-comb Buff, and the following varieties having red earlobes: Barred Plymouth Rock, Dark Brahma, White Wyandotte and Silver-Laced Wyandotte, single-comb Rhode Island Red, as well as the Jersey Black Giant breed. Earlobe color in the progeny of various crosses was determined at six months of age since Warren found that prior to this a change in color sometimes took place.

Warren found the inheritance of earlobe color to be very complex, and briefly it may be said that his results indicate that earlobe color is dependent upon the action of several genes, neither white nor red being dominant.

THE INHERITANCE OF EYE COLOR

In a study of the inheritance of down color in purebred Rhode Island Reds, Warren (1929) found no relationship to exist between chick down color and adult eye color, the inheritance of eye color not being studied although it was observed that the color of the iris varied from light gray to a reddish bay. Punnett (1923) has suggested that a close relation existed between down color and the presence of pigment in the iris in F_1 and F_2 chicks produced from a cross between

Golden-Penciled Hamburg males and Silver Sebright Bantam females.

Punnett also points out that when a Brown Leghorn male is mated to Black Langshan females the F_1 birds of both sexes have red to orange-red in the iris, whereas when a Black Langshan male is mated to Brown Leghorn females the F_1 males have a red iris but the F_1 pullets have a black iris.

THE INHERITANCE OF SKIN COLOR

Many breeds of poultry have yellow skin, many others have white skin, and one breed, the White Silkie, has black or violet colored skin. Yellow-skinned breeds include the Leghorns, Plymouth Rocks, Wyandottes, Rhode Island Reds, and many others. White-skinned breeds include Langshans, Orpingtons, Minorcas, Sussex, Dorkings, and others. The inheritance of skin color has been investigated only recently and only by a few investigators.

Yellow Versus White Skin.—The difference between yellow skin and white skin is due to the presence of lipochrome (animal fat) pigment in the former and its absence in the latter. Lambert and Knox (1927) made reciprocal crosses of Black Langshans × White Plymouth Rocks and Buff Orpingtons × White Plymouth Rocks. Observations on skin color were made after the birds had reached two months and in most cases four or five months of age. The results secured indicate quite clearly that white skin is dominant to yellow skin on a monohybrid basis and that skin color is not sex-linked.

In crosses of a Mottled Ancona male × Black Orpington females and a Black Minorca male × Mottled Ancona females, Asmundson and Milne (1930) secured results that likewise show that white skin is dominant to yellow skin and that one pair of genes accounts for the difference. White-skinned breeds have the genetic constitution *WW* and yellow-skinned breeds *ww*.

Black Skin.—Mention has been made of the fact that the skin of the White Silkie is black or violet colored, and in this respect the Silkie differs from all other breeds. Kuklenski (1916) has shown that the Silkie skin color is due to chromatophores distributed in varying density throughout the connective tissue, periost of the bones, and other organs. The epithelium, or outer layer of cells of an organ, is unpigmented, but the bird when plucked appears to be black because of the dark color of the underlying tissues.

In crosses between Silkies and Brown Leghorns, Bateson and Punnett (1911) explained their results by assuming that two genes are involved: (1) a dominant non-sex-linked gene for mesodermal pigment (*PP*), and (2) a dominant sex-linked inhibitor of mesodermal pigment (*DD*). On their hypothesis the Silkie male is *PPdd* and the Silkie female *PPd*—; the Brown Leghorn male is *ppDD* and the Brown Leghorn female *ppD*—.

Dunn and Jull (1927), from a cross between a White Silkie male and White Leghorn females, concluded that their data, although supporting the hypothesis of a sex-linked inhibitor of mesodermal pigment, indicate that the development of mesodermal pigment may be due to the effects of multiple genes or that in White Leghorns, in addition to *D* which inhibits the development of mesodermal pigment, the gene for barring apparently tends to modify the development of mesodermal pigment.

THE INHERITANCE OF SHANK COLOR

Since there are several shank colors among the breeds and varieties of the domestic fowl, as pointed out in Chapter I, it is natural to expect that the inheritance of shank color should prove to be a complicated problem.

Shank colors most frequently encountered include white, yellow, black, blue, gray, willow, pinkish white, and pearl. These colors are the result of the presence or absence of one or more different kinds of pigments in either one or both of the two layers of the skin. The outer layer of the skin is the epidermis and the inner layer is the dermis. The outer layer of the epidermis is modified into scales, which vary in size and shape. According to Hanau (1881) the epidermis is invariably thinner than the dermis.

The various colors of the shank are due to the presence of two kinds of pigment, which Hanau (1881), Jeffries (1883), and Gadow (1891) have called orange-yellow and brownish-black. The orange-yellow is a lipochrome pigment made up of animal fat cells, the pigment in concentrated form giving an orange color and in more dilute form a yellow color. The so-called brownish-black is in reality a melanic pigment.

The most intensive histological study of shank colors in the domestic fowl is that of Barrows (1914), although the inheritance of shank color was not studied. Among the more important observations of Barrows are the following: (1) White shanks are the result of lack of pigment. (2) Yellow shanks and various shades of yellow are due to the presence of lipochrome pigment in the epidermis, melanic pigment being absent from the dermis. (3) Willow shanks and green shanks are due to the presence of lipochrome pigment in the epidermis and melanic pigment in the dermis. (4) Black shanks are the result of melanic pigment in the epidermis and in some cases also in the dermis; if lipochrome is present the bottoms of the feet are yellow and if lipochrome is absent the bottoms of the feet are white. (5) Blue shanks are the result of the presence of melanic pigment in the dermis when it is absent from the epidermis and lipochrome pigment is absent from both dermis and epidermis. (6) All shades, except red and pink, are the result of various combinations of lipochrome and melanic pigment in the epidermis and dermis.

Among the earliest observations concerning the specific nature of shank-color inheritance are those of Punnett (1925). In a cross of a Brown Leghorn male × Gold-Penciled Hamburg females the F_1 birds of both sexes had light-colored shanks, whereas in the reciprocal cross the F_1 males had light-colored shanks but the F_1 females had dark-colored shanks. These results demonstrate that the brown Leghorn female carries an inhibitor for the development of dark shanks in a heterozygous form, the inhibiting gene being sex-linked.

The fact that Black Leghorn females frequently have black spots in an otherwise yellow shank whereas Black Leghorn males are usually free of such spots is accounted for by the fact that the female has the sex-linked inhibiting gene in a heterozygous form and the males have it in a homozygous form.

The sex-linked nature of the gene *B*, for barring, which inhibits the development of dark shanks is clearly demonstrated in a cross made by Jull and Quinn (1931) between a Rhode Island Red male and Barred Plymouth Rock females in which the F_1 males had yellow shanks and the F_1 females had black or very dark-colored shanks. It is easy to understand from this why purebred Barred Plymouth Rock females frequently have dark spots on their shanks but males are nearly all free of such spots.

According to Punnett (1923), highly developed epidermal pigment in the shanks seems to be associated with some form of black or dark-brown plumage. Warren (1928*a*) has pointed out that the genes for certain plumage colors also appear to affect the color of the shanks. Asmundson and Milne (1930) report that in crosses between each of two black-shanked varieties, Black Minorca and Black Orpington, and a yellow-shanked breed, Mottled Ancona, the F_2 generation consisted of birds with solid black plumage that always had black, bluish-black or greenish-black shanks, and birds with mottled plumage that had white or yellow shanks spotted with black.

Genes for Shank Color.—The inheritance of shank color has been most intensively studied by Dunn (1925). According to him there are two pairs of genes which tend to inhibit the development of pigment, one being sex-linked and the other not sex-linked. The gene *W* inhibits the development of lipochrome pigment in the epidermis and is present in birds with shanks that are white, pinkish white, pearl, blue, slate, or gray. *W* is practically completely dominant and is not sex-linked. The gene *D* tends to inhibit the development of melanic pigment in the dermis and is present in birds with shanks that are yellow, white, or pearl. *D* is nearly completely dominant and is sex-linked.

Accordingly, the genetic constitution of birds with the shank color indicated would be as follows, the symbol *D* used by Dunn and Jull (1927) being substituted for the symbol *Y* previously used by Dunn (1925):

Males	Females	
WWDD *WwDD* *WWDd* *WwDd*	*WWd–* *Wwd–*	white, pinkish-white, pearl, and light blue shanks (may show spots of dermal pigment, especially in females and in *Dd* males).
wwDD *wwDd*	*wwD–*	yellow shanks (may show spots of dermal pigment in females and in *Dd* males).
WWdd *Wwdd*	*WWd–* *Wwd–*	black, slate, blue and gray shanks.
wwdd	*wwd–*	black, bottoms of feet yellow.

Whether the genotypes given above cover all cases remains to be determined, since Punnett (1923) has suggested that there are indications that the presence of dermal pigment in certain instances is dominant to its absence.

Since it has been suggested that highly developed epidermal pigment is associated with black or dark-brown plumage, it is possible that the gene *E*, for the extension of melanic pigment throughout the plumage, may also affect the extension of melanic pigment to the shanks.

PROBLEMS

1. Give the genotypes and phenotypes for plumage color that are produced in the F_1 and F_2 generations in the following crosses:

White Leghorn male × White Minorca female.
White Wyandotte male × White Rose-Comb Bantam female.
White Silkie male × White Plymouth Rock female.
White Minorca male × White Silkie female.

2. What set of conditions give rise to the development of color in birds?

3. From the standpoint of barring only, give the results expected in the F_1 and F_2 generations in the following crosses:

Barred Plymouth Rock male × Black Hamburg female.
Black Hamburg male × Barred Plymouth Rock female.
Silver Campine male × Black Hamburg female.
Black Hamburg male × Silver Campine female.
Silver-Penciled Hamburg male × Black Hamburg female.
Black Hamburg male × Silver-Penciled Hamburg female.
Black Hamburg male × White Plymouth Rock female.

4. In testing for evidence of sex-linkage what backcross mating should be made?

5. What are the F_1 birds like in the following crosses:

Blue Andalusian male × Black Orpington female.
Blue Orpington male × White Leghorn female.
Blue Andalusian male × Blue Andalusian female.
White Minorca male × Blue Andalusian female.

6. Give examples of the following ratios: 9:7, 13:3, 9:4:3, 15:1, and explain how each of these ratios is produced.

7. Assuming that cockerels only are to be used for the production of broilers and roasters give a list of ten sex-linked crosses that could be made, placing the crosses in the order of their practical importance.

8. A strain of White Plymouth Rocks from year to year contains a few birds with greenish-colored shanks. Give the probable reason for this and explain how to eliminate this undesirable character from the strain.

9. (*a*) If a nonbarred male is mated with a barred female and an F_1 female from this mating is mated with her father and an F_1 male with his mother, what will be the appearance as to barring of the offspring of these two matings?

(*b*) Explain how it is that in the Cambar breed the sex of the chicks can be distinguished at hatching time.

10. What interesting situation exists regarding the feather pattern characters, barring, lacing, penciling, mottling, and spangling in their relation to black pigmentation?

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CHAPTER V

THE INHERITANCE OF MORPHOLOGICAL CHARACTERS

NUMEROUS breeds and varieties of domestic fowl are noted for the beauty and utility of their individual members, beauty sometimes being enhanced by a lovely color pattern, discussed in the preceding chapter, or by some striking morphological character which adds to the attractiveness of the individual.

Morphological characters are those relating to form or size. Breeds and varieties of domestic fowl differ a great deal in regard to structural characters such as the form or shape of comb, the presence or absence of a crest, the length of saddle coverts, presence or absence of feathers on the shanks, number of toes, body form, and many other characters. Two examples of structural or morphological differences in type of feathering are the "silky" feathers of the Silkie breed and the "frizzled" feathering of the Frizzle breed.

The inheritance of a number of morphological characters has been studied and the results as given in the following pages go to show how generally applicable is the principle of Mendelian inheritance to the great majority of characters possessed by domestic fowls.

THE INHERITANCE OF SILKINESS

The Silkie breed of fowls is noted for the "silky" appearance of its plumage, this condition being due to the hookless condition of the barbules of each feather. That the Silkie breed is of ancient lineage is attested by the fact that Taubert (1910), in his historical sketch of the breed, traces its lineage back to the time of Aldrovandus in 1600.

According to Jones (1921), there are five varieties of the Silkie breed. Wright (1891) mentions Silkies with single combs and non-feathered shanks, and Sturges (1909) describes blue-feathered Silkies, but whether these should be recognized as distinct varieties is doubtful because it is known that birds with "silky" plumage have appeared occasionally in numerous breeds. Individual specimens with "silky" plumage have appeared from time to time in many breeds in different parts of the world. Bement (1863) mentions "several instances of fowls of this description having sprung from those of the ordinary character." Tegetmeier (1873) mentions silky Cochins, and Jones (1921) gives several observations of various poultrymen who have recorded the appearance of silky birds in Rhode Island Reds, Black Orpingtons, White Wyandottes and other varieties.

The Gene for Silkiness.—Apparently the first reference to the inheritance of silky plumage is that of Darwin (1868), who observed that when Silkies were bred among themselves they produced nothing but silky-plumaged birds, but when Silkies were crossed with birds having normal plumage the F_1 offspring all had normal plumage. Davenport (1906, 1907), Bateson and Punnett (1908), Cunningham (1912), Bonhote (1914), Jones (1921), and Dunn and Jull (1927) studied the inheritance of silkiness and their results taken collectively give in the F_2 generation a total of 207 birds with normal plumage and 64 with silky plumage, expectation on a 3:1 basis being 203.25 to 67.75. The conclusion is justified that silkiness is differentiated from nonsilkiness by one pair of autosomal recessive genes.

The sporadic appearance of birds with silky plumage in breeds and varieties having normal plumage is readily accounted for on the assumption of a mating of two birds each of which has the gene for silkiness in a heterozygous condition.

THE INHERITANCE OF FRIZZLED PLUMAGE

The frizzled plumage character is peculiar to the breed known as Frizzles, the feathers of which curl upwards and forwards because of the absence or modification of the hooklets of each feather, a thickening of its barbules and barbs, and alterations in the direction of the barbules and barbs. The plumage has the appearance of being rubbed the wrong way.

An Old Character.—That the frizzled condition of plumage in the domestic fowl has persisted for a long time is borne out by the fact that a frizzled fowl was described by Aldrovandus (1600). From early times frizzled fowls have been reported in many parts of the world, including Java, Ceylon, East India, Southern Asia, Asiatic Russia, West Indies, Philippine Islands, and other parts. Its occurrence in England is reported by Tegetmeier (1867). By Buffon (1799) it was called *le coq frisée* and, according to Dürigen (1923), in Mauritius and Mozambique it was known as the Hurricane Fowl.

The Gene for Frizzling.—The genetics of the frizzled plumage character has been studied by Davenport (1906), Crew (1925), Wriedt (1925), Hutt (1930), and Landauer and Dunn (1930*a*). In a cross between a Frizzle fowl and a Silkie, Davenport secured results that showed that the frizzled character was dominant over non-frizzling. Crew and Wriedt each were led to believe that the frizzled character acts as a lethal in a homozygous condition, but this has been shown not to be the case by Hutt and by Landauer and Dunn.

In certain matings Hutt determined that he had secured two kinds of frizzled birds, one group with "ordinary" frizzling and one group with "extreme" frizzling. Five females with ordinary frizzling were mated to a White Leghorn male and produced 33 birds with ordinary frizzling and 29 with normal plumage. Five females with extreme frizzling were mated to the same White Leghorn male and produced 48 birds, all of them having ordinary frizzling. The five females with ordinary frizzling were heterozygous, and the five females with extreme frizzling were homozygous, for the frizzling character.

The results which Landauer and Dunn (1930*a*) secured confirm the observations of Hutt (1930), although the former make a distinction between what they call two types of heterozygous frizzles. One type they call "exhibition-type" heterozygous frizzling and the other "ordinary-type" heterozygous frizzling, the difference in frizzling being due to more conspicuous structural changes in the feathers of the exhibition-type birds. Landauer and Dunn observed that the exhibition-type of heterozygous frizzling is the kind of frizzling that private breeders exhibit at poultry fairs and that it "has been produced by selection and that it depends in its expression upon the presence of other genes beside the gene for frizzling."

The difference between frizzling and non-frizzling is due to a single pair of autosomal genes, frizzling being dominant. The homozygous type of frizzling is more extreme than the heterozygous type, and in this respect the inheritance of frizzling resembles the inheritance of blue plumage color in the Blue Andalusian breed.

THE INHERITANCE OF "HENNY-FEATHERING"

Among the various American standard breeds of chicken, the Campines and Sebright Bantams are known as "hen-feathered" breeds, inasmuch as in these breeds the male hackle and saddle feathers are of the same shape, color, and relatively the same length as in the female. The observation of Morgan (1919, 1920) and Punnett and Bailey (1921) go to show that hen-feathering is dominant to cock-feathering and is apparently inherited on a monohybrid basis. Jull and Quinn (1930), however, were led to believe that modifying genes are involved.

THE INHERITANCE OF COMB FORM

One of the most easily recognized structural or morphological differences existing among breeds and varieties is in the form or shape of the comb. In Chapter I it has been pointed out that there are single combs, rose combs, pea combs, walnut combs, V-shaped combs, leaf combs, and others.

Genes for Comb Form.—The inheritance of comb form, particularly as it applies to single, rose, pea, and walnut combs, has been studied intensively, and the results have brought to light a very interesting situation.

The results of the experiments of Bateson (1902), Hurst (1905), Davenport (1906), Bateson and Punnett (1908), and Dunn and Jull (1927) in crossing rose-comb birds with single-comb birds show that rose is dominant over single on a monohybrid basis, the F_2 generation segregating in the proportion of 3 rose to 1 single. It is well known, however, that there are different kinds of rose combs; the spike of the Wyandotte rose comb bends downward whereas the spike of the Hamburg rose comb projects straight outwards. Punnett (1923) observes that there are probably genes responsible for the particular type of rose comb common to a breed or variety, but this matter has never been investigated.

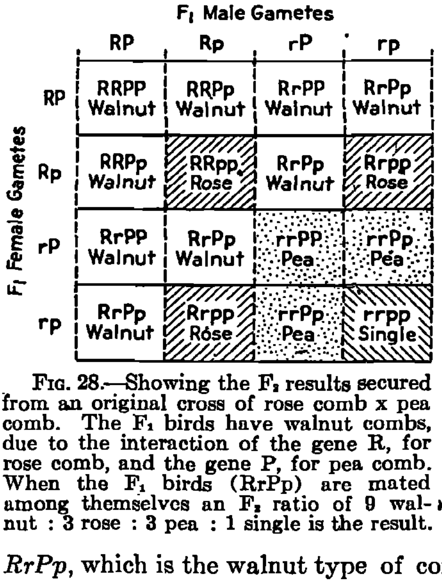
The rose comb of the Silkie differs from other types of rose combs, Dunn in Dunn and Jull (1927) having described the Silkie type of rose comb as follows:

> The comb of the Silkie is fleshier in the anterior parts, is shorter, and ends rather bluntly posteriorly in two or more points or papillae, whereas the ordinary rose comb is longer and is characterized by a single long posterior spike or point. Bateson (1909) describes the silkie comb as rose plus trifid element, but I am inclined to agree with Cunningham (1912) that the most important characteristic of the Silkie comb is its abbreviation and bluntness, the more so since it is not regularly trifid but may show from two to four or occasionally more posterior points.

When Silkies were crossed with White Leghorns it was found that all the F_1 birds had the Silkie type of rose comb, the majority having three points. The F_2 generation consisted of 139 birds with the Silkie type of rose comb and 32 birds with single combs. There was no indication that the truncated or multiple-point condition of the Silkie type of rose comb is inherited as a separate character.

In crosses between birds having pea combs and birds having single combs, Bateson (1902), Davenport (1906), and Bateson and Punnett (1908) have shown that pea comb is dominant to single comb on a monohybrid basis, the F_2 generation segregating in the proportion of 3 pea to 1 single. Punnett (1923) points out that, although some of the heterozygous pea combs are more or less like single combs, the fact that they are really pea combs is made clear when birds possessing them are mated to birds having rose combs.

A very interesting situation was found to exist in the inheritance of comb form when rose-combed birds were crossed with pea-combed birds. The results showed that all the F_1 birds had walnut combs, as found in Malays. The non-appearance of rose comb and pea comb in the F_1 and the appearance of only walnut combs shows that the genes for rose and pea act upon each other to produce a new type of comb.



	RP	Rp	rP	rp
RP	RRPP Walnut	RRPp Walnut	RrPP Walnut	RrPp Walnut
Rp	RRPp Walnut	RRpp Rose	RrPp Walnut	Rrpp Rose
rP	RrPP Walnut	RrPp Walnut	rrPP Pea	rrPp Pea
rp	RrPp Walnut	Rrpp Rose	rrPp Pea	rrpp Single

FIG. 28.—Showing the F_2 results secured from an original cross of rose comb x pea comb. The F_1 birds have walnut combs, due to the interaction of the gene R, for rose comb, and the gene P, for pea comb. When the F_1 birds (RrPp) are mated among themselves an F_2 ratio of 9 walnut : 3 rose : 3 pea : 1 single is the result.

Since rose comb is dominant to single on a monohybrid basis, the symbol *R* is used to designate the rose-comb character; and since pea comb is also dominant to single on a monohybrid basis, the symbol *P* is used to designate the pea-comb character. When a rose-combed and a pea-combed bird are mated together each has the recessive allelomorph of the other so that a rose-comb bird would be *RRpp* and a pea-comb bird would be *rrPP*. The F_1 birds would be *RrPp*, which is the walnut type of comb.

When the F_1 birds having walnut combs are mated among themselves both the males and the females produce the four kinds of gametes, *RP*, *Rp*, *rP*, and *rp*. The mating of these four kinds of F_1 gametes produces an F_2 ratio of 9:3:3:1, a result to be expected when F_1 birds differ in two pairs of genes. The F_2 ratio consists of 9 birds with walnut combs, 3 birds with rose combs, 3 birds with pea combs, and 1 bird with a single comb, as shown in Fig. 28.

It is clear, therefore, that the walnut type of comb is the result of the interaction of the genes *R* and *P*, and the combination of the recessive allelomorphs, *rr* and *pp*, produces the single type of comb.

A Pea and Walnut Inhibitor.—In a large number of matings involving the pea comb, Petroff (1929) observed a deficiency of pea combs in several of the matings. Combs were classified by their phenotypic appearance, and in this connection the observation of Punnett (1923), referred to previously, might explain why Petroff observed a deficiency of pea combs, for according to Punnett some birds heterozygous for pea comb might be mistaken for birds having single combs. The results of certain individual matings convinced Petroff, however, that certain of his birds carried a gene which inhibited the development of pea and walnut combs.

The Inheritance of Side-Sprigs.—A side-sprig, which is a well-defined, pointed growth on the side of a single comb, is regarded as a disqualification, as stated in Chapter I. Punnett (1923) points out that side-sprigs occur also on rose combs, although in such cases the defect is not regarded by exhibition breeders as of such a serious nature as to disqualify a bird. Punnett was led to believe that side-sprigs were dominant to the absence of side-sprigs.

The inheritance of side-sprigs in single-comb White Leghorns has been investigated by Asmundson (1926), who made the following observations: Males with side-sprigs mated to females with side-sprigs gave the following three groups, depending upon the genetic constitution of the parents: (1) all had side-sprigs, (2) three-fourths had side-sprigs, (3) equal numbers with and without side-sprigs and in some cases slightly more with than without, or approximately a 9:7 ratio. Males and females without side-sprigs produced chicks which did and did not have side-sprigs in the ratio of 1:3 and 1:1. Males without side-sprigs mated to females with side-sprigs produced progeny nearly one-fourth of which had side-sprigs. Since side-sprigs appeared in the progeny of all the types of matings used by Asmundson, it is apparent that the character is not sex-linked. Asmundson concluded that the presence of side-sprigs is due to the interaction of two dominant autosomal pairs of genes. These dominant genes are complimentary in their action so that, when both are present, either in the heterozygous or homozygous condition, side-sprigs are produced.

THE INHERITANCE OF CREST

Several breeds and varieties, including the Silkie, Houdan, and some of the Polish varieties, are noted for the development of a crest of feathers surmounting the head. Krautwald (1910) says that the crest occurs in the frontal region of the skull, is present in the chick, and is inherited.

Hurst (1905), Davenport (1906), Cunningham (1912), Bonhote (1914), and Dunn and Jull (1927) secured results which demonstrate that the presence of a crest is due to a single autosomal pair of dominant genes. The size of the crest is apparently due to multiple genes.

THE INHERITANCE OF CEREBRAL HERNIA

In the crested Polish breeds the frontal bones of the skull are raised into a dome-shaped protuberance, giving rise to a condition known as cerebral hernia, one of the first illustrations of which was given by Darwin (1868).

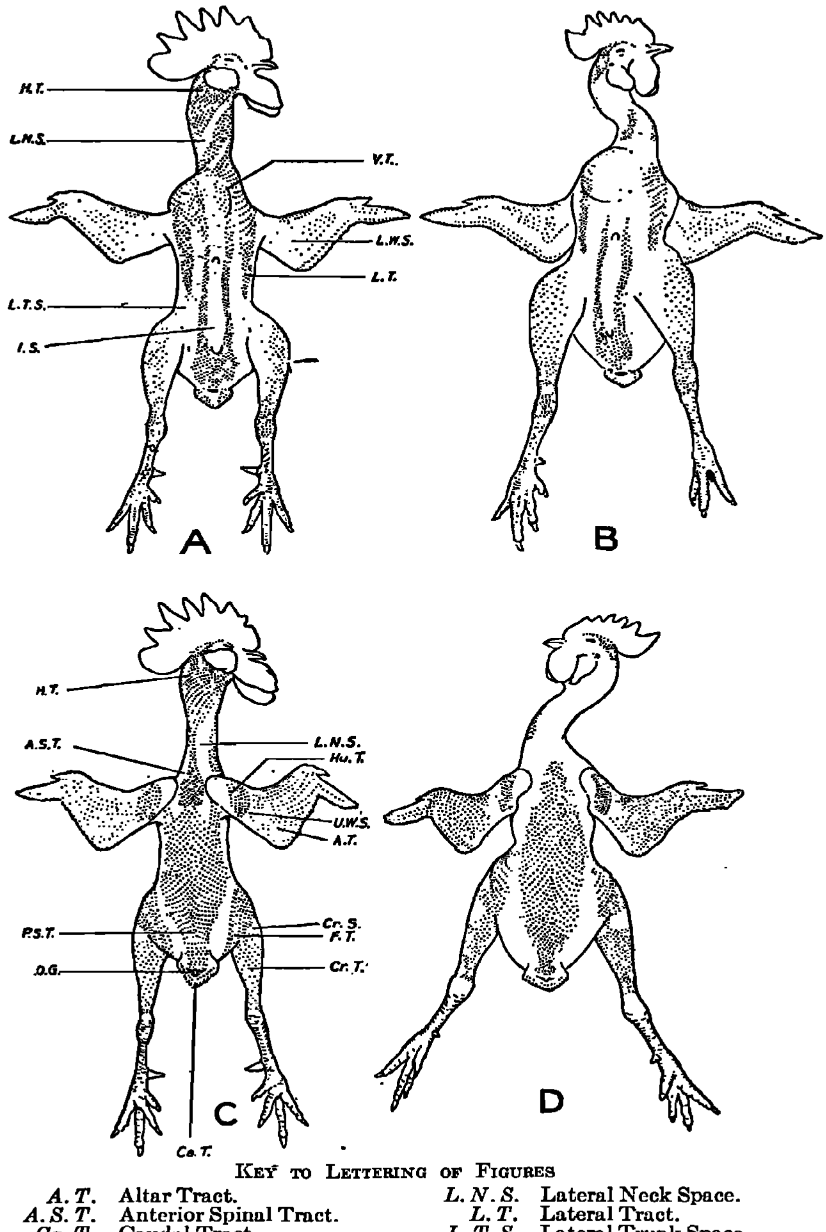
The results of investigations on the inheritance of this peculiar structural character are rather meagre. Davenport (1906) and Ghigi (1914) found that hernia behaved as a monohybrid recessive to normal cranium. Polish or Paduan fowls, which have cerebral hernia in both sexes, were crossed with fowls without hernia and in neither case was any relationship noted between sex and hernia. It is interesting to note, however, that hernia was apparently first confined to Polish females, for Darwin (1868) quoting Blumenbach (1805) states that at that time (circa 1805) the skull of the *hen* of the Polish fowl alone was protuberant. "Hence there can be no doubt that this remarkable character in the skulls of Polish fowls was formerly in Germany confined to the female sex, but has now been transferred to the males, and has thus become common to both sexes." (Darwin, 1868, p. 257.) Dunn and Jull (1927) crossed Silkies with White Leghorns and confirmed the previous observation that hernia is recessive to lack of hernia but they found some special predilection for its development in females rather than in males.

THE INHERITANCE OF MUFFS AND BEARD

These peculiar structural characters, common to certain continental breeds, have apparently been studied but very little. Davenport (1906) found that when the Mottled Houdan was crossed with the White Leghorn as well as with the Black Minorca, all the F_1 birds had muffs and beard. When F_1 birds were backcrossed to White Leghorns the progeny consisted of those with and those without muffs and beard in nearly equal numbers. The muffs and beard character is apparently recessive to absence of muffs and beard on the basis of a single autosomal pair of genes.

THE INHERITANCE OF THE NAKED-NECK CHARACTER

There is one breed of fowl that differs from all other breeds in having no feathers on most of the neck. By some this breed is known as the "Transylvania Naked-Neck"; by Crew (1922) and Greenwood (1927) it has been called the "Hackless" fowl; and by Punnett (1923)



Key to Lettering of Figures

A. T.	Altar Tract.
A. S. T.	Anterior Spinal Tract.
Ca. T.	Caudal Tract.
Cr. S.	Crural Space.
Cr. T.	Crural Tract.
F. T.	Femoral or Lumbar Tract.
H. T.	Head Tract.
Hu. T.	Humeral Tract.
I. S.	Inferior Space.
L. N. S.	Lateral Neck Space.
L. T.	Lateral Tract.
L. T. S.	Lateral Trunk Space.
L. W. S.	Lower Wing Space.
O. G.	Oil Gland.
P. S. T.	Posterior Spinal Tract.
U. W. S.	Upper Wing Space.
V. T.	Ventral Tract.

Fig. 29.—The feather tracts on the ventral side, A, and on the dorsal side, C, of the normal fowl and the feather tracts on the ventral side, B, and on the dorsal side, D, of the Naked-neck fowl. (Greenwood.)

and others it has been referred to as the "Bare Neck" fowl. A Naked-Neck male is shown in Fig. 30.

According to Wright (1891), this breed with such a peculiar structural deficiency originated in Transylvania, but birds with this character are now found in many parts of the world.

Not only are neck feathers absent but the area of skin lacking the feathers becomes loose, thickened, wrinkled, and deep red in color during the period of sexual activity. A careful examination of naked-neck birds has been made by Greenwood (1927), who observes that these birds have an incomplete covering of feathers, "the contour feathers of the head, neck, trunk, and limbs being restricted to more or less elongated narrow bands between which the skin is either naked or clothed only with down." The feathered bands have been called feather tracts or pterylæ by Nitzsch (1867), and the intervening naked bands have been called apteria. The illustrations in Fig. 29 show the extent to which normal and naked-neck birds differ concerning the feather tracts; Greenwood (1927) has further noted that in the naked-neck fowl the apteria were naked in all regions of the body, having no down or semiplumes like the apteria of normal birds.

The suggestion by Taubert (1910), Duerst (1911), and others that the naked-neck character is acquired is not supported by evidence. On the other hand, the evidence submitted by Greenwood (1927) makes it clear that the peculiar character is of genetic origin, arising probably as a mutation. Moreover, the breeding experiments of Davenport (1914) and Crew (1922) show that the naked-neck character behaves as a simple dominant to normal feathering, a single autosomal pair of genes being responsible for its development.

THE INHERITANCE OF "CROOKED-NECK" CHARACTER

In a study of the inheritance of hen-feathering in Brown Leghorns at the U. S. Animal Husbandry Experiment Farm, Beltsville, Maryland, there appeared seven birds in one of the matings in 1926 with decidedly crooked necks. A bird with this defect is illustrated in Fig. 30. The simultaneous appearance of seven such abnormal birds in one mating led to an analysis of the results, and it was found by Jull and Quinn (1931*a*) that these abnormal birds were produced by three different dams in a total population of 39. It became apparent at once that not only was the crooked-neck condition inherited but also that it was probably inherited on a monohybrid basis. Subsequent matings demonstrated such to be the case, the single pair of autosomal genes producing the condition being recessive.

THE INHERITANCE OF CLOSE FEATHERING

Certain breeds, such as the Cornish and Games, have short feathers that lie close to the body; certain varieties, such as Brahmas and Cochins, have feathers that do not lie close to the body, giving such birds what is termed profuse plumage.

In crosses between close-feathered breeds and others, it has been found that close-feathering is dominant. Bateson (1902) crossed what were then known as Indian Game (Cornish) with White Leghorn and observed that the F_1 progeny were close-feathered. Morgan crossed Game Bantams with Sebright Bantams and secured similar results. Punnett (1923) crossed the Aseel male with Brown Leghorn females and observed that the F_1 birds were as close-feathered as the Aseel male parent. Wassina (1926) crossed Indian Game (Cornish) with the Pavloff bantam and found that the F_1 birds were close-feathered and that the F_2 birds indicated that segregation had taken place on a simple monohybrid basis.

INHERITANCE OF SHANK FEATHERING

The information given in Table 1 in Chapter I shows that several breeds and varieties have feathered shanks as one of their characteristics. Brahams, Cochins, Langshans, Faverolles, and other breeds have feathered shanks, although it should be noted that some breeds differ from others in the amount or extent of shank feathering. Cochins, for instance, have much more profuse shank feathering than Langshans.

Studies on the inheritance of shank feathering have shown it to be an extremely complicated problem. In several cases relatively few birds were obtained in the F_1 and F_2 generations, but whenever a large F_2 population was secured it was found that there were gradations of feathering from a very slight degree of feathering to very profuse feathering. Another factor which has made it more difficult to interpret the results secured by various investigators was the appearance of birds in the F_2 population that were difficult to classify. Still another factor affecting the results secured in one or more experiments was that the parental stocks were of mixed origin. As a matter of fact, many breeds and varieties that are characterized as having nonfeathered shanks often have birds within the breed or variety with a few feathers on the shanks and stubs between the toes. Poultry breeders are obliged to exercise constant care in the selection of their breeding stock lest shank feathering, stubs, and down between the toes become firmly established in their particular strains. In spite of these difficulties the results that have been secured serve as a definite contribution to the problem of the genetics of shank feathering.

The Genes for Shank Feathering.—Although Hurst (1905) Davenport (1906, 1909), Cunningham (1912), Morgan and Goodale (1912) and Bonhote (1914), studied the inheritance of shank feathering, their results are inconclusive. Punnett and Bailey (1918), however, secured results that permitted drawing rather definite conclusions. They crossed Croad Langshans with Hamburgs and with Brown Leghorns and noted that the F_1 birds were shank feathered, but not so heavily as the Croad Langshan parents, and that the F_2 segregated into a 3:1 ratio of birds with feathered and nonfeathered shanks. The results they secured led them to conclude that shank feathering is dominant to absence of shank feathering, a single autosomal pair of genes being involved.

On the other hand, Punnett and Bailey concluded that two autosomal pairs of genes are responsible for the feathering in those breeds having more profuse shank feathering than their Croad Langshans. The results which Dunn and Jull (1927) secured in crosses between Silkies and White Leghorns, Brown Leghorns, and White Plymouth Rocks led to the conclusion that the Silkie should be added to the group of birds with profuse shank feathering, two dominant autosomal pairs of cumulative independent genes being responsible for the shank feathering as found in the Silkie.

From certain crosses made by Serebrovsky and his co-workers (1927) the same two pairs of dominant genes as reported by Punnett and Bailey were found to explain the results satisfactorily. The same was found to be true of crosses made by Lambert and Knox (1929) between Black Langshans and Buff Orpingtons and White Plymouth Rocks. Danforth (1929) crossed a Mille Fleur Bantam male with Golden Sebright Bantam females and reported that the Mille Fleur carries the two pairs of genes each in a homozygous dominant condition and that the Golden Sebright carries the two pairs of genes each in a homozygous recessive condition.

Lambert and Knox state that probably many Black Langshans are heterozygous for at least one of the two pairs of dominant genes. It is interesting to note that Punnett and Bailey (1918) in their crosses involving Langshans interpreted their results on the basis of a single pair of genes, whereas Lambert and Knox (1929) in their crosses involving Langshans interpreted their results on the basis of two pairs of cumulative independent genes. It is felt that much more work with larger numbers of progeny is necessary before the genetic analysis of shank feathering is placed upon a thoroughly sound basis.

Finally, aside from the fact that a few investigators are in agreement concerning the existence of two dominant autosomal pairs of cumulative independent genes, either pair of which produces shank feathering, it is obvious that much work is necessary before the genetics of shank feathering is completely solved.

The Inheritance of Stubs.—A stub is described by poultry breeders as the quill portion of a short feather and is regarded as a disqualification when it is present in breeds having nonfeathered shanks. It is well known, however, that stubs occur from time to time in individuals of numerous breeds having nonfeathered shanks. Stubs are usually found on the web of skin between the toes and on the toes although they may sometimes be found on the outer sides of the shanks. Frequently, instead of the quill portion of a feather, down may be present, the amount varying from almost complete absence as observed by the naked eye to a complete covering of the web between the outer toes.

Warren (1930) developed by selection a strain of White Leghorns in which a high proportion of the progeny had down and another strain of White Leghorns in which practically none of the progeny had down. These two strains were crossed and the results showed that the presence of down "is more or less recessive in its behavior" and that more than one pair of autosomal genes is involved.

THE INHERITANCE OF BRACHYDACTYLY AND SYNDACTYLY

By brachydactyly is meant a shortening of the fourth toe so that it is shorter than the second toe, the reverse being the normal condition. By syndactyly is meant a condition in which the third and fourth and sometimes the second and third toes are united by a web.

Aside from the observation of Davenport (1909) that syndactyly is dominant to absence of syndactyly, comparatively little work has been done on either of these two structural peculiarities except some research by Danforth (1919*a*, 1919*b*, 1929). The first suggestion put forward by Danforth (1919*b*) was to the effect that the three structural characters, shank feathering, brachydactyly and syndactyly, "are associated in heredity. All the available evidence points strongly to the conclusion that the three traits just mentioned are primarily caused by a single gene." After research work had determined that at least two autosomal pairs of dominant cumulative genes are responsible for the development of shank feathering, Danforth

(1929) confirmed this observation and suggested that each of the two pairs of genes tends to produce brachydactyly.

That Danforth's hypothesis is probably untenable has been suggested by Lambert and Knox (1929), who make the suggestion that linkage may exist between a pair of genes for brachydactyly and one of the pair of genes for shank feathering. In view of the fact that there are probably more than two pairs of genes for shank feathering, Danforth's original suggestion is ruled out and his second suggestion becomes less tenable, particularly in view of the fact that neither brachydactyly nor syndactyly has been observed with any degree of frequency by those who have investigated the inheritance of shank feathering.

THE INHERITANCE OF POLYDACTYLY

By polydactyly is meant the presence of an extra toe or toes. In Table 1, Chapter I, certain breeds are indicated as having five toes on each foot instead of four, which is the number common in most breeds. Among other breeds having five toes are the Houdans and Silkies, the extra toe occurring near the hallux or hind toe.

Several investigations have been undertaken over a period of years with the view of determining the nature of the inheritance of polydactyly, but the results are not very conclusive, so complex has the problem proved to be.

The observations of Bateson (1913), Bateson and Saunders (1902), Bateson and Punnett (1905 and 1906), Hurst (1905), Davenport (1906 and 1909), Barfurth (1908, 1909, 1911), Dunn and Jull (1927), and Punnett and Pease (1929) may be summarized by saying that polydactyly appears to be due to a pair of dominant autosomal genes, but that a four-toed bird may carry the gene for polydactyly and still be four-toed owing to the presence of a pair (or pairs) of genes which inhibit the development of polydactylism. Moreover, since the data examined by Punnett and Pease showed that polydactylous birds may also carry the inhibiting gene they suggested that such polydactylous birds also carry another pair (or pairs) of genes "rendering possible the manifestation of the polydactylous effect in spite of the presence of the inhibitor."

According to Hutchinson (1931), the results which Punnett and Pease secured may be accounted for by assuming that dominance is controlled by genes, as suggested by Fisher (1928*a*, 1928*b*), and that birds heterozygous for polydactyly but lacking all the genes favoring the dominance of polydactyly are four-toed birds. In other words, Hutchinson's suggestion is to the effect that four-toed birds occurring in the F_1, F_2, and backcross generations secured from a mating of polydactylous and normal birds may be due to a deficiency in one or both parents of genes necessary for the dominance of polydactyly.

THE INHERITANCE OF VULTURE HOCK

Two standard American breeds of chicken, the Sultan and the Mille Fleur Booted Bantam, have vulture hocks as a characteristic of their morphological feathering development and in this respect differ from most other breeds described in the American Standard of Perfection, although there are breeds in Europe with the same characteristic. The long feathers which constitute the vulture hock arise from the posterior area of the tibial feather tract, above the tibiometatarsal (hock) joint.

Jull and Quinn (1931*a*) mated a male with well developed vulture hocks with a pen of Rhode Island Red females, absence of vulture hocks being a characteristic of this breed, and secured an F_2 generation of 82 birds without vulture hock and 29 birds with vulture hock.

The evidence shows that not only is vulture hock recessive to absence of vulture hock, as Davenport (1906) suggested, but that an autosomal pair of genes is responsible for the development of the character.

THE INHERITANCE OF "LONG TAIL"

The Phoenix and Yokohama fowls of Japan have a very peculiar structural difference from practically all other breeds in that the males of these Japanese breeds have what is called a "long tail." As a matter of fact, however, the extreme length of the tail is due to the very long sickle feathers and saddle coverts in the male, although the main tail feathers in both males and females are longer than in most other breeds. (See Fig. 30.)

Cases have been reported where the sickle feathers of the Yokohama male have attained a length of over 20 feet. The literature dealing with the raising of these fowls makes it apparent that the particular diet given them has something to do with the ultimate length of feather attained, but it is apparent that the character is inherited.

The inheritance of the long tail has been investigated by Davenport (1906) and Bonhote (1914). Davenport crossed the Yokohama and the White Cochin Bantam and the Yokohama with the Dark Brahma and observed that in both crosses the F_1 male birds had saddle coverts, sickle and main tail feathers much longer than in the Cochin and Brahma parents but not so long as in the Yokohama

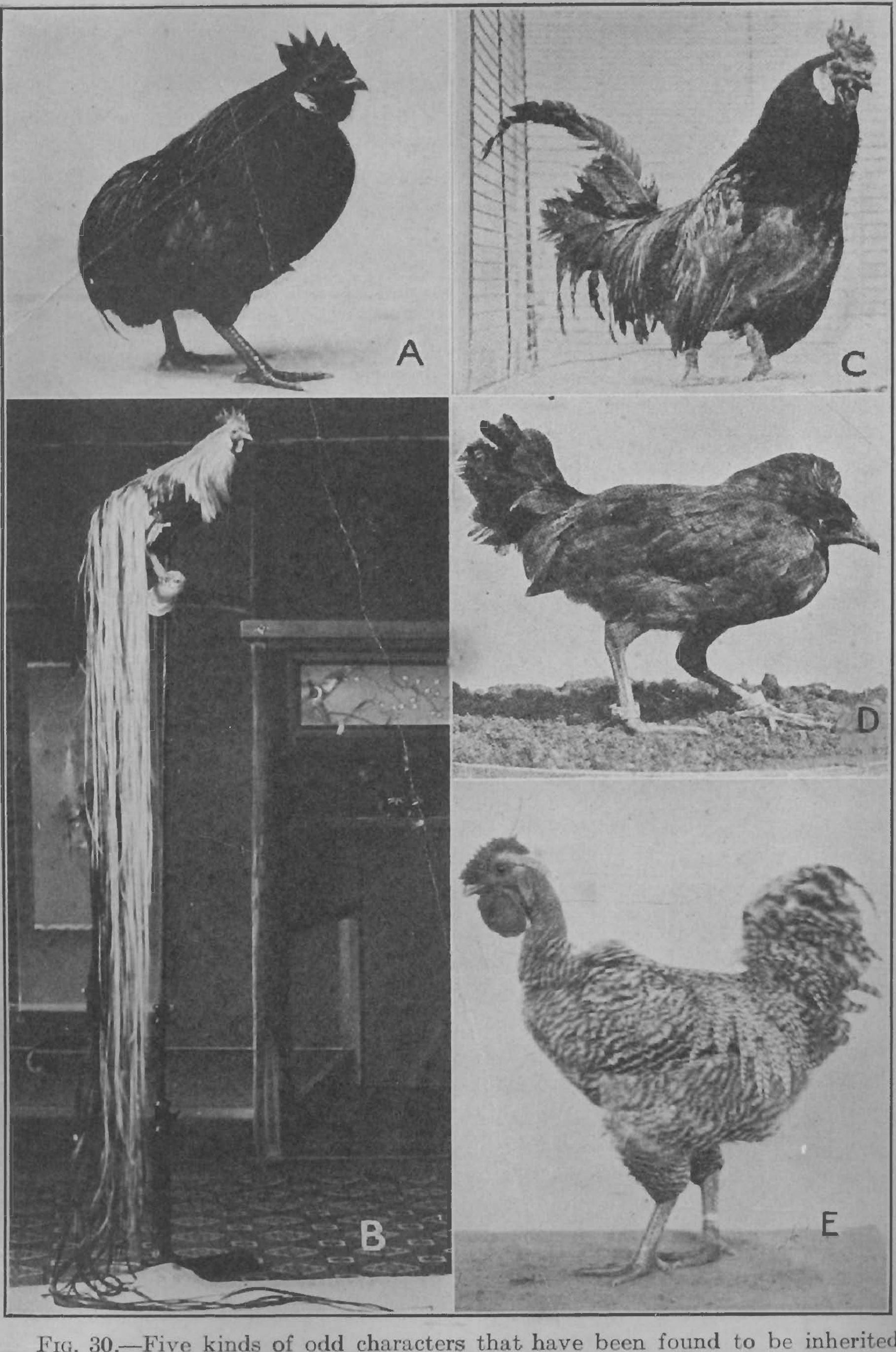


FIG. 30.—Five kinds of odd characters that have been found to be inherited in Mendelian manner. A, a rumpless bird (Photo by Ogiwara). B, A "long-tailed" bird. (Photo by Kinugawa.) C, A German Creeper. Note the "squatty" appearance, due to the short legs. (Photo by Landauer and Dunn.) D, A "Crooked-neck" bird. (Photo by U. S. D. A.) E, A "Naked-neck" bird. (Photo by U. S. D. A.)

parents. The same was true of the main tail feathers of the F_1 females. Bonhote crossed the Yokohama and the Silkie and secured similar F_1 results to Davenport's, and in the F_2 generation Bonhote secured 19 birds with long tail and 5 with short tail. These results indicate that the long-tail character is probably due to a pair of autosomal genes, but since the length of the saddle coverts, sickle and main tail feathers in the F_2 varied considerably, it would appear that multiple genes are probably involved.

THE INHERITANCE OF RUMPLESSNESS

One of the most unique structural variations existing among domestic fowls is the condition known as rumplessness, in which the birds have no tails. (See Fig. 30.) Rumpless fowls seem to have been in existence for hundreds of years, because Tegetmeier (1873) refers to a description of them by Aldrovandus in 1645. The observations of various writers make it appear certain that strains of rumpless birds have been bred for many years in widely scattered parts of the world, including Japan, South America, and many parts of Europe.

Three Types of Rumplessness.—The investigations of Landauer and Dunn (1925) and Landauer (1928) have shown that there are three types of rumpless birds. Live specimens of all three types resemble each other more or less closely, but differences among them are manifest from their breeding results, owing to the fact that in one type the trait is not inherited, whereas in the two types in which it is inherited there are differences in morphological structure.

The chief difference between a normal bird and a rumpless one is a deficiency in the latter of parts of the skeleton of the tail, the caudal vertebrae and the pygostyl being absent.

Landauer (1928) has observed, however, that there is an intermediate type of hereditary rumplessness that is somewhat different from the hereditary type that is completely rumpless. In the intermediate type a few tail feathers may be present and the backbones form a graded series from an almost normal condition to an almost completely rumpless condition, the outstanding difference between the intermediate and completely rumpless types being the presence of caudal vertebrae in the intermediate type. In the intermediate type one or two vertebrae of the synsacrum and all except the last two of the vertebrae of the pygostyl are absent.

The Genetics of Rumplessness.—The results of investigations conducted by Dunn (1925) led him to conclude that rumpless birds that sporadically appear in various flocks are usually of the nonhereditary type, that is, when mated to normal birds they produce nothing but normal offspring, a result similar to that secured by Davenport (1906).

Dunn also found that other matings of rumpless males to rumpless females produced progeny in the proportion of 3 rumpless to 1 normal bird. These results indicate the dominance of rumplessness on a monohybrid basis. Furthermore, when this same type of rumpless bird was mated to normal birds, rumpless and normal progeny were produced in approximately equal proportions. These results indicate that the hereditary type of rumplessness usually encountered is in a heterozygous condition. This fact makes it clear why Darwin (1868), Tegetmeier (1873), Dürigen (1886), and Wright (1902), among others, state that strains of rumpless birds produce some normal birds.

In further experiments on the inheritance of rumplessness, Dunn (1926) discovered that the homozygous rumpless condition is viable, a rumpless female upon being mated to a normal male produced rumpless progeny only, 17 in number. Completely rumpless birds mated to normal birds produced 245 rumpless and 267 normal birds, and intermediate rumpless birds mated to normal birds produced 135 completely or intermediate rumpless and 146 normal birds. Dunn states that the intermediate condition appears to be due to the interaction of the rumpless gene with a partially dominant, independent modifying gene.

THE INHERITANCE OF THE "CREEPER" CHARACTER

A class of fowl known as Creepers have two peculiar structural characters that distinguish them from all others. The wings and the legs are very much shortened, the development of the bones of the latter differing markedly from that in normal breeds. (See Fig. 30.) Cutler (1925) points out that all the leg bones are correspondingly shortened, that the tibia is usually bent considerably, and that the fibula is much better developed than in normal birds.

There are various names for the Creeper Fowl in various countries; in Great Britain they are known as Scotch Dumpies, in France as *Courtes pattes*, and in Germany as *Krüperhehn.* Investigational work has disclosed, however, that these Creeper fowls' in various countries are of the same genetic constitution.

The genetics of the Creeper fowl has been studied by Landauer and Dunn (1930*b*), who used Creepers from America, Germany, Scotland, and the Marquesas Islands. Their very interesting results are explainable on the basis of the Creeper character being determined by a single autosomal pair of dominant genes, which in a homozygous condition cause the death of the embryo in the early stages of incubation. Landauer and Dunn found that the characteristic lethal period is at the beginning of the fourth day of incubation, that very rarely does an embryo homozygous for the lethal gene live up to hatching time, and that it never hatches. Their data show that even when the gene is in a heterozygous condition it has a semi-lethal effect.

The lethal nature of the gene in a homozygous condition is demonstrated by the following facts:

1. Only birds in a heterozygous condition exist. This has been shown to be the case by numerous breeding tests.

2. In matings of Creeper by Creeper there is a segregation of 2 Creepers to 1 normal, giving a 2:1 ratio instead of a 3:1 ratio normally expected if the embryo carrying the gene in a homozygous condition were to live and hatch.

3. Approximately 25 per cent more embryos die during the first six days of incubation in matings of Creeper by Creeper than in matings of Creeper by normal fowls.

THE INHERITANCE OF BODY FORM

It is well known that breeds often differ greatly in their general appearance, Game breeds having an entirely different build of body from Cochins. The old adage of poultry breeders to the effect that "shape makes the breed" applies particularly to the shape of the bird as determined by feather contour. In this respect Langshans differ materially from Wyandottes, and Leghorns from Orpingtons. But if the birds of each of the breeds are stripped of their feathers the differences in body form may not be nearly so great as in the case of the shape of the same birds with their feathers. Practically nothing is known, however, concerning what constitutes typical body form in respect to any breed, from which it follows that the inheritance of body form is an unsolved problem.

One experiment on a limited scale has been conducted by Kopeć (1927) with a view toward determining the inheritance of body form in reciprocal crosses between White Leghorns and Buff Orpingtons. Measurements were made on the plucked carcasses, but inasmuch as Jull, Quinn and Godfrey (1932) found, as pointed out in Chapter X, that dressed carcass measurements do not serve as a very reliable index of skeletal structure and since Kopeć secured relatively few progeny, no conclusions are possible concerning the inheritance of body form in the domestic fowl.

THE INHERITANCE OF BODY WEIGHT

The problem of the inheritance of body weight is of considerable practical importance to all poultry breeders because the size of a bird, which is governed largely by the size of the skeleton, determines to a large extent the amount of flesh to be obtained for human consumption as well as the amount of feed to maintain the bird. The size of a female is also of practical importance from the standpoint of egg production, since, as pointed out in Chapter IX, it is apparent that a bird must be of a certain size before it can be expected to lay an egg of good size.

It is well known, of course, that the environmental conditions under which birds are reared sometimes affect the ultimate weight attained by the birds. The rations fed, the method of feeding, and general methods of flock management all have their influence on the rate of growth and the final weight attained by the individuals of any flock. On the other hand, where environmental conditions and methods of feeding and management are identical, the average weight attained by the members of one flock will nearly always be found to vary more or less from the average weight attained by the members of another flock, even when the two flocks are of the same breed or variety. In such cases the differences in weight are due to heredity.

Body weight is inherited, and it is largely on account of this fact that it is possible to maintain breeds differing very widely in body weight. The standard weight of the Jersey Black Giant cock is 13 pounds, whereas the standard weight of the Rose-Comb Bantam cock is 26 ounces, the weight of the former being exactly 8 times the weight of the latter.

Ghigi (1909), Goldschmidt (1913), and Phillips (1912, 1914) made different crosses for the purpose of studying the inheritance of body weight in poultry but for the most part their results were inconclusive.

Hamburg × Sebright Bantam Cross.—Punnett and Bailey (1914) crossed Golden-Penciled Hamburg males with Silver Sebright bantam females and observed that for each sex of the F_2 progeny "the range of variation is such that the smallest birds are smaller than the Silver Sebright bantam, while the largest are larger than the Golden Hamburg." The birds were weighed at 35 weeks of age. The problem was studied further by mating together one family of the largest of the F_2 progeny as well as by mating together each of two families of the smallest of the F_2 progeny. The family of large-sized F_2 birds produced F_3 birds of relatively large size, although there was considerable variation. The families of small-sized F_2 birds produced relatively small-sized F_3 birds, the family of smallest F_2 birds producing no F_3 progeny that weighed over 600 grams. The authors observed, "These F_2 results taken together suggest strongly that size in poultry depends upon definite factors, and that these factors segregate in gametogenesis."

Hamburg X Cornish Cross.—May (1925) crossed White Cornish and Silver-Spangled Hamburgs, data being obtained at 10 months of age from reciprocal crosses of the two breeds. The F_1 and F_2 progeny weighed on the average almost as much as the average weights of the Cornish according to sex. Moreover, the F_1 and F_2 progeny were not any more variable in weight than the purebred parental stocks. The number of birds in the F_2 families, however, was too small to allow of any deductions being drawn regarding the number of genes involved in the inheritance of body weight.

Leghorn X Orpington Cross.—Kopeć (1927) made reciprocal crosses between White Leghorns and Buff Orpingtons and observed that the F_1 females from the mating of Buff Orpington males and White Leghorn females weighed more than the F_1 females from the mating of White Leghorn males and Orpington females. In the case of the mating of Buff Orpington males and White Leghorn females the F_2 males weighed considerably less than the F_1 males whereas the F_2 females weighed considerably more than the F_1 females, although in the case of both F_2 males and females there was greater variability than in the case of the F_1 males and females, respectively.

Leghorn X Brahma Cross.—The original work of May (1925) was continued by Waters (1931) who crossed White Leghorns and Light Brahmas. Waters used the weights which his birds attained at 10 months of age, this being regarded as the age at which both purebred and crossbred birds attained their mature weight.

A point of particular interest in connection with the parental stock used by Waters is their great variability in weight. Some of the White Leghorn males weighed more than some of the Light Brahma females. Both parental stocks varied a great deal, indicating that each variety was apparently heterozygous for a number of genes that may be involved in the inheritance of body weight. This is a point that should be emphasized, particularly in view of the conclusions drawn by Waters from the results he secured.

Waters assumed that both his Leghorn and Brahma parental stock "approach a homozygous condition," an assumption hardly warranted in view of the great variability existing in both Leghorns and Brahmas that he used in his crosses. When some of the Leghorn males and females each weigh more than twice as much as others the stock could hardly be regarded as being homozygous for genes responsible for body weight, unless it is conceded that a considerable number of genes are involved. In such a case it might be possible for small Leghorns to be homozygous for a certain group of genes and large Leghorns homozygous for another group of genes, although both groups of genes might contain several similar pairs.

Since the adult sexes of practically all breeds and varieties differ significantly in body weight, it becomes necessary to employ a correction factor so that the weights of both sexes may be considered together in studies on the inheritance of body weight. Waters found that his males weighed on the average 1.28 times as much as his females, and so he used the factor 1.28 to transform the female body weight to make it equivalent to the male body weight.

Reciprocal crosses were made between White Leghorns and Light Brahmas. Waters states that both the F_1 males and the F_1 females from the mating of White Leghorn male and Light Brahma females are significantly heavier than the F_1 males and F_1 females from the mating of Light Brahma male and White Leghorn females.

The distribution of body weight among each group of parents, F_1 and F_2 birds indicates that both the White Leghorn and Light Brahma parental stocks were practically as variable as the F_1 birds and that the F_2 birds were somewhat more variable than the F_1 birds.

Waters concluded that segregation occurred in the F_2 generation, and he suggested that the difference in body weight between his White Leghorns and Light Brahmas was due largely to two pairs of autosomal genes, which have a cumulative effect.

The distribution of body weights which Waters actually secured in all of his F_2 populations indicates, however, that apparently more than two pairs of genes differentiate the weight of White Leghorns and Light Brahmas. Moreover, although Waters found that both small and large F_2 birds tended to reproduce their kind, it is observed that there was considerable variability among the F_3 progeny of each of these two kinds of matings. The actual variability in weights which Waters secured in his backcross populations indicates that apparently more than two pair of genes are involved.

The results which Waters secured indicate quite clearly the desirability of establishing as much homozygosity as possible in parental stock for genes which are responsible for body weight. Both the White Leghorns and the Light Brahmas which he used in his original matings showed so much variability in body weight that it would seem highly probable that he could have secured practically the same results in matings made within each breed as he secured in matings between the two breeds. For instance, if he had selected the smallest White Leghorns and bred them among themselves and had also selected the largest White Leghorns and bred them among themselves and then crossed the progeny of the two matings, he might have secured much the same results as he secured in crossing the two breeds.

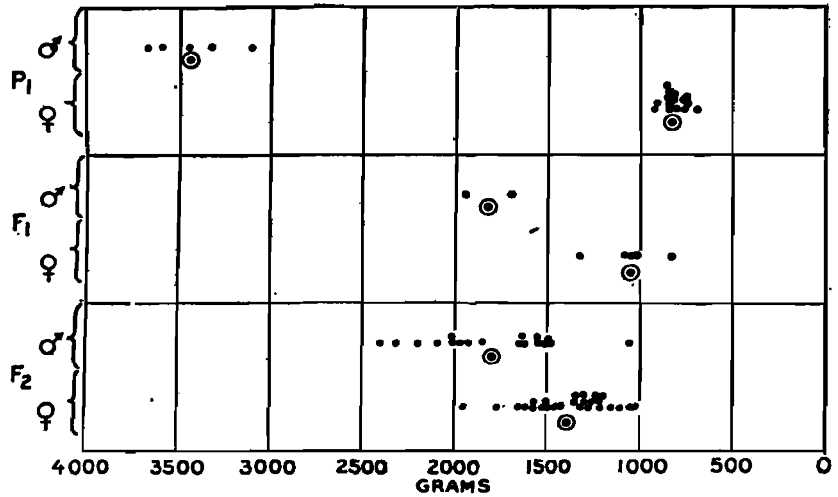
Barred Plymouth Rock × Rose-Comb Bantam Cross.—Additional data on the inheritance of body weight in the domestic fowl are available from reciprocal crosses made by Jull and Quinn (1931*b*) between Barred Plymouth Rocks and Black Rose-Comb Bantams.

Owing to the great difference in size between the Barred Plymouth Rocks and the bantams artificial insemination was practiced. Barred Plymouth Rock males were allowed to mate with Rhode Island Red females and immediately after mating took place the semen was extracted from the cloaca of the females and injected into Black Rose-Comb Bantam females. For the other cross, Black Rose-Comb Bantam males were allowed to mate with White Rose-Comb Bantam females and the semen was immediately extracted and injected into Barred Plymouth Rock females. Artificial insemination of the Rose-Comb Bantam females proved to be much more successful than that of the Barred Plymouth Rock females. All birds were weighed when approximately 9 months of age.

It is to be observed first that the original crosses made in this experiment involve breeds that differ more widely in body weight than the breeds used in any other crosses made in studies on the inheritance of body weight in the domestic fowl. Punnett and Bailey (1914) state that in their crosses the Silver Sebright Bantams weighed a little more than one-half as much as the Golden-Penciled Hamburgs. May (1925) states that the Silver-Spangled Hamburgs in his crosses weighed approximately two-thirds as much as the Cornish. Waters (1931) states that his Light Brahmas weighed approximately twice as much as his White Leghorns. In this experiment the Barred Plymouth Rocks weighed approximately from four and one-half to over five times as much as the Black Rose-Comb Bantams.

If the inheritance of body weight is Mendelian in nature it is reasonable to suppose that the more widely the two breeds that are crossed differ in body weight the greater the number of genes involved in the inheritance of body weight and consequently the greater the segregation in body weight in the F_2 progeny. Figs. 31 and 32 show, respectively, the mean body weights and the distribution of individual body weights of the parents and the F_1 and F_2 progeny in the 1928 and 1929 Barred Plymouth Rock male × Black Rose-Comb Bantam

A—1928 Matings



B—1929 Matings

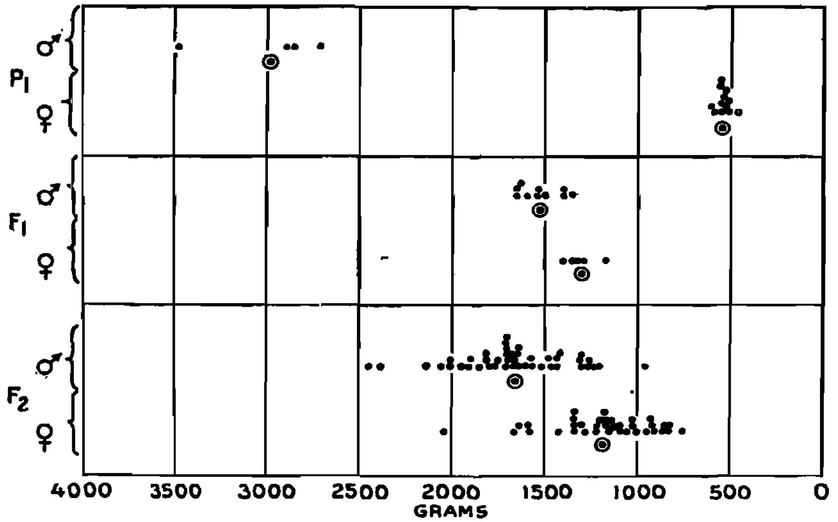


FIG. 31.—Showing the distribution of body weights in the P_1 (parental), F_1 (first-hybrid generation) and F_2 (second-hybrid generation) birds in the 1928 and 1929 matings of Barred Plymouth males x Black Rose-Comb Bantam females. (Jull and Quinn.)

female matings and in the 1929 Black Rose-Comb Bantam male × Barred Plymouth Rock female mating.

In all three matings the mean weight of the males and the females in the F_1 progeny is much nearer the mean weight of the bantam parents than the mean weight of the Barred Plymouth Rock parents. This suggests the partial dominance of one or more factors for small size, although Punnett (1923) observes in connection with the experiment by Bailey and himself that the same collection of weight genes on a Silver Sebright Bantam frame and on a Hamburg frame might produce birds of different weights. To whatever extent this is true then it becomes necessary to study the inheritance of body shape in crosses differing in body shape, and it also becomes necessary to study the influence of body shape on body weight.

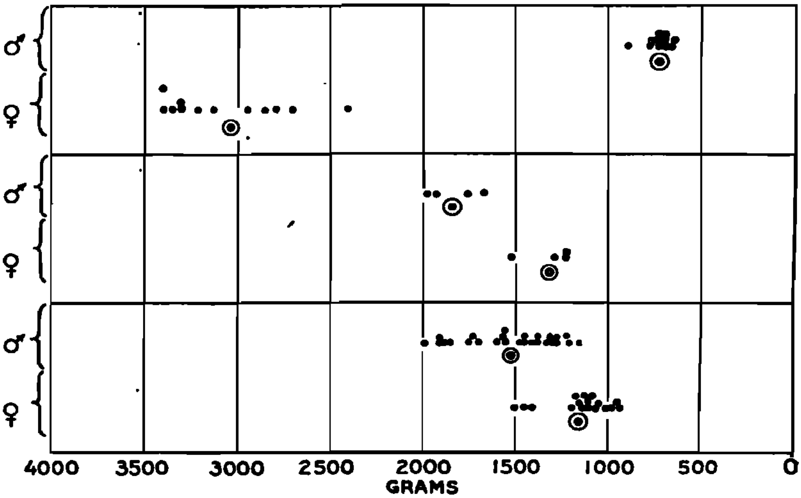


FIG. 32.—Showing the distribution of body weights in the P_1 (parental), F_1 (first-hybrid generation) and F_2 (second-hybrid generation) birds in the 1929 mating of Black Rose-Comb Bantam males x Barred Plymouth Rock females. (Jull and Quinn.)

The results secured by Jull and Quinn (1931*b*), however, are contrary to those secured by Punnett and Bailey (1904) and by May (1925), all of whom found that the F_1 generation approached the larger-sized parent in body weight more than the smaller-sized parent. In fact, May observed that there were no significant differences between the mean body weights of the Cornish parents and the F_1 progeny in the reciprocal crosses between Cornish and Silver-Spangled Hamburg, although in both sexes the data show that the F_1 progeny from the mating of Cornish male and Silver-Spangled Hamburg female was somewhat heavier than the F_1 progeny of the mating of Silver-Spangled Hamburg male and Cornish female. In a cross between Jersey Black Giants and White Leghorns, Warren (1926) observed that the F_1 progeny more nearly approached the size of the Jersey Black Giant parents, the larger of the two breeds. The results which Waters secured showed that the F_1 progeny from White Leghorn × Light Brahma matings were intermediate in weight between the parental stocks. He also found that both the F_1 males and the F_1 females from the Light Brahma dams were heavier than the F_1 males and the F_1 females from the White Leghorn dams.

The F_1 progeny in all three matings made by Jull and Quinn show considerable variability, a result to be expected from the fact that the parental breeds exhibited considerable variability, which is true of practically all breeds of poultry. The F_1 progeny in the crosses made by Punnett and Bailey, and by May and by Waters, also showed considerable variability. May found that from his Cornish × Silver-Spangled Hamburg matings the F_1 generation showed about the same amount of variability as his parental stocks. The data of Waters show the same situation concerning his F_1 generations and the parental stock.

The F_2 generation in May's experiments showed about the same amount of variability as his F_1 progeny and his parental stocks. Punnett and Bailey, however, found that the F_2 birds showed greater variability in body weight than the F_1 birds, and that among the F_2 birds there were some that were smaller than the Silver Sebright Bantams and some that were larger than the Golden-Penciled Hamburgs. It is unfortunate that Punnett and Bailey apparently did not consider the amount of variability in the parental Silver Sebright and Golden-Penciled Hamburg stocks from which they selected the two Silver Sebright females and the one Golden-Penciled Hamburg male used in the original mating. It is known, for instance, that the Silver Sebrights normally show considerable variability in body weight, and it is altogether probable that Golden-Penciled Hamburgs show no less variability than Barred Plymouth Rocks, Cornish, White Leghorns, Light Brahmas, and Black Rose-Comb Bantams.

At the same time, the results secured by Punnett and Bailey and by Waters and those secured by Jull and Quinn are in agreement in respect to the greater amount of variability in body weight among the F_2 progeny than among the F_1 progeny. On the other hand, although Punnett and Bailey secured some F_2 birds larger than the Golden-Penciled Hamburg male and smaller than the Silver Sebright Bantam females used in their original cross, none of the F_2 birds in all three matings made by Jull and Quinn were as large as the smallest of the Barred Plymouth Rocks nor as small as the largest of the Black Rose-Comb Bantams used in the original crosses. The difference in the two experiments may be accounted for by the fact that Punnett and Bailey secured a larger F_2 generation than did Jull and Quinn: the larger the number of genes involved in the inheritance of body weight the greater the number of progeny required in order to secure the extremes in body weight among the F_2 progeny.

If four independently segregating genes are involved in the inheritance of body weight in the domestic fowl, as Punnett (1923) has suggested, it would be expected that some of the extremes in body weight would be produced in an F_2 population of 124 individuals, as secured in the cross between Barred Plymouth Rock males and Black Rose-Comb Bantam females, although 256 individuals are necessary in order to secure the appearance of all possible combinations of weight characters. None of the extremes were secured by Jull and Quinn in their F_2 progeny, however, and the nature of the frequency distribution of the F_2 progeny on the basis of body-weight percentages of the mean suggests that probably more than four genes are involved. Indeed, many genes are probably involved.

This suggestion is in accord with the observations of Hutt (1929) in connection with his investigation concerning sex dimorphism and variability in the appendicular skeleton of the Leghorn, his observation being "that while there are genetic size factors affecting all parts of the body, there must also be special factors affecting only certain regions and certain individual bones."

The fact that the inheritance of body weight in the domestic fowl is an extremely complicated problem is borne out by the observations of Schneider and Dunn (1924), who have shown that body weight is from three to six times more variable than bone measurements. Moreover, as pointed out in Chapter X, Dunn (1928*b*) found that inbred families differed among themselves regarding average bone length and especially in the proportion of the length of different bones which he measured, which suggests that there are specific genes affecting bone length.

The results of the various experiments on the inheritance of body weight have shown that in nearly every case the F_1 birds have been intermediate between the parental stocks used and there has been greater variability in the F_2 progeny than in the F_1 progeny, these results indicating that body weight is inherited.

It is felt that the results of the various experiments on the inherit-

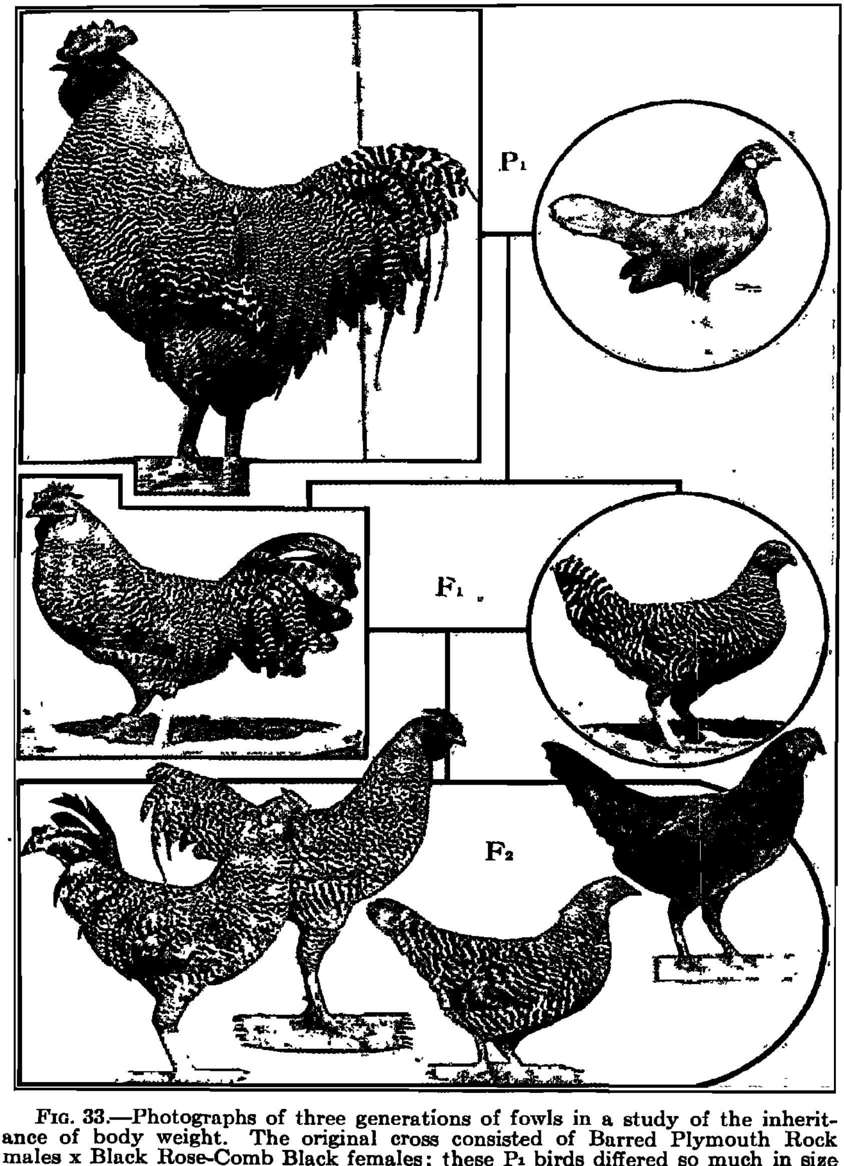


Fig. 33.—Photographs of three generations of fowls in a study of the inheritance of body weight. The original cross consisted of Barred Plymouth Rock males x Black Rose-Comb Black females; these P_1 birds differed so much in size that artificial insemination was practiced. The F_1 birds were intermediate in size. In the F_2 generation neither of the extremes of parental body weight were secured, indicating that several genes are involved in the inheritance of body weight. The results secured in this cross show that barring is dominant to nonbarring, the F_1 males and females being barred, and in the F_2 generation there are 3 barred birds to 1 black bird but all F_2 males are barred whereas one-half of the F_2 females are barred and one-half are black. (Photo by U. S. D. A. in Jour. Hered.)

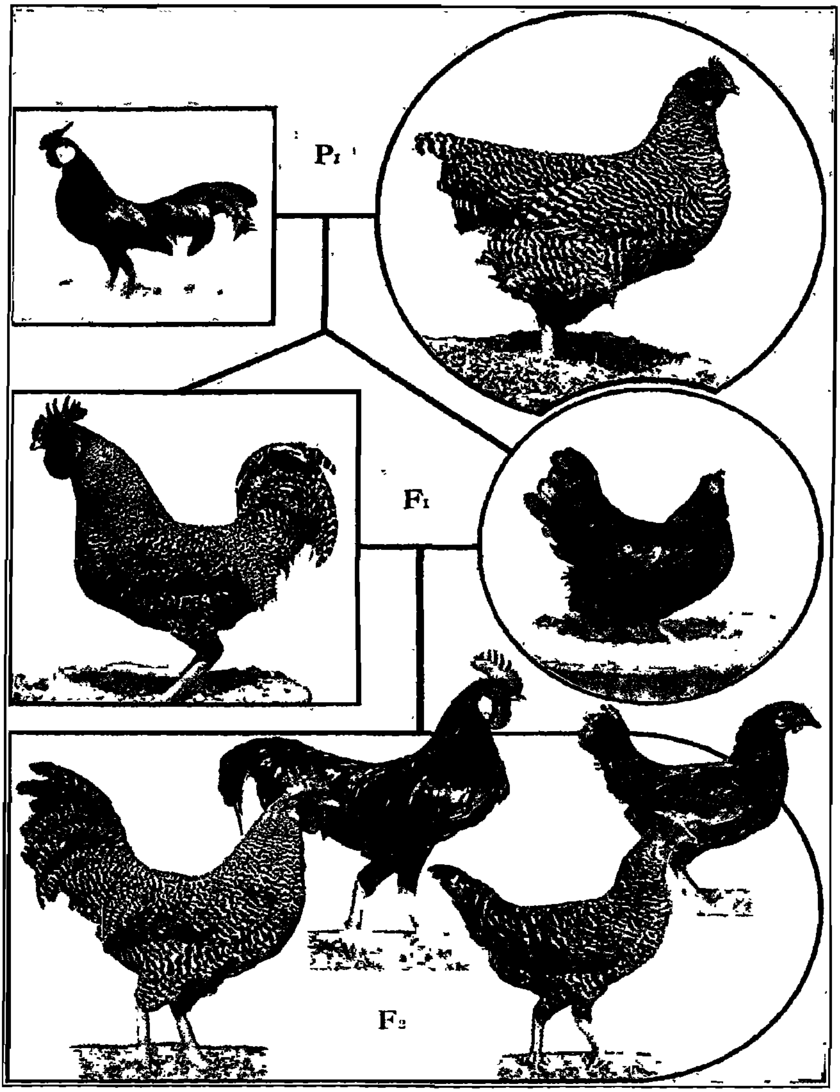


FIG. 34.—Photographs of three generations of fowls in a study of the inheritance of body weight. The original cross consisted of Black Rose-Comb Bantam males x Barred Plymouth Rock females, artificial insemination being practiced. The results secured were similar to those secured in the reciprocal cross, illustrated in Fig. 33. From the standpoint of plumage color inheritance, the results secured in this cross demonstrate the sex-linked inheritance of the gene for barring. The Barred Plymouth Rock female parent transmits barring to her sons only and in the F_2 generation one-half of the males are barred and one-half are black, and one-half of the females are barred and one-half are black. (Photo by U. S. D. A. in Jour. Hered.)

ance of body weight do not show that body weight in the domestic fowl is inherited in Mendelian manner, and it is apparent that in order to secure conclusive evidence on the matter large F_2 families should be raised from original crosses of highly inbred strains, the individuals of which are as uniform as possible in respect to skeletal structure and body weight.

PROBLEMS

1. A poultry breeder breeds White Wyandottes only and finds that a few of his chicks have single combs. Suggest matings that will enable him to detect and eliminate the breeders that are heterozygous for rose comb.

2. A White Silkie with its rose comb is mated to a single-comb White Leghorn. Using the symbols *RR* for rose comb, *rr* for single comb, *NN* for normal plumage, and *nn* for silky plumage, give the genotypes and phenotypes produced in the F_2 generation.

3. The same mating is made as in Problem 2, and the same symbols are used for rose and single comb and normal and silky plumage, and in addition the symbols *IICCOO* designate the dominant white of the White Leghorn and *iiCCoo* the recessive white of the Silkie, as explained in the preceding chapter. Give the genotypes and phenotypes produced in the F_2 generation.

4. Two males, No. 1 and No. 2, are mated to two females, No. 3 and 4. All four birds have frizzled plumage and pea combs. Male No. 1 with both females produces offspring all of which have frizzled plumage and pea combs. Male No. 2 with female No. 3 produces offspring all of which have pea combs but some have normal plumage and some have frizzled plumage. Male No. 2 with female No. 4 produces offspring all of which have frizzled plumage but some have single combs and some have pea combs. Use the symbols *FF* for frizzle plumage, *ff* for normal plumage, *PP* for pea comb and *pp* for single combs and give the genotypes of the two males and the two females.

5. What is the most effective method for the poultry breeder to employ in eliminating side-sprigs and stubs from his flock of White Plymouth Rocks or any other variety with single combs and nonfeathered shanks?

6. Suggest the possible origin of the three following characters: cerebral hernia, muffs and beard, and hereditary rumplessness.

7. A male homozygous for both rose comb and the naked-neck character is mated to a female homozygous for both pea comb and vulture hocks. Describe the appearance of the F_1 progeny and show by appropriate symbols for the different characters whether or not there would be produced in the F_2 a bird with a single comb, normal neck plumage, and absence of vulture hocks.

8. In each of the following crosses, what will be the comb character of the progeny produced?

$RRpp \times rrPP$
$RrPp \times RrPp$
$RrPp \times Rrpp$
$rrPp \times RrPp$
$RRpp \times rrPp$
$RRPp \times rrPp$
$Rrpp \times Rrpp$
$rrPp \times Rrpp$

9. (*a*) Do poultry breeders experience difficulty in maintaining uniform weights among all individuals of the same breed and variety? If so, explain why.

(*b*) Give an account of the probable origin of the small size of the various bantam breeds.

10. Give the proportion of birds of different body weights produced in the F_2 generation from two crosses in each of which two pairs of weight genes are involved, in one cross the genes having a cumulative effect on weight and in the other cross the genes not having a cumulative effect.

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CHAPTER VI

THE INHERITANCE OF PHYSIOLOGICAL CHARACTERS

In the two preceding chapters attention has been given to the inheritance of color characters and morphological or structural characters, but it is apparent that chickens differ in other respects than in the color of plumage, the color of shanks, the shape of comb, the number of toes, and similar features which can be determined rather precisely. Chickens also differ in factors affecting the reproduction of their kind, such as hatchability, rate of growth, constitutional vigor, and resistance to disease. These are all known as physiological characters because they involve various vital processes that take place within an organism, such processes determining, in part, the number of progeny secured or the length of life that may be attained.

Studies involving the inheritance of various physiological characters are of great practical importance because the results secured have an economic bearing on the development of strains that reproduce themselves most efficiently. For instance, if it can be shown that hatchability is inherited, it should be possible to breed strains that will eliminate much unnecessary wastage in dead embryos during the incubation period. Likewise, if it can be established that rate of growth is inherited, poultrymen would have the necessary information available for the selection of breeding stock for different purposes. Finally, if it can be established that constitutional vigor and the ability to resist disease are inherited, the information should be of considerable value to poultrymen from the standpoint of reducing losses usually occurring through mortality.

In spite of the fact that the physiological characters mentioned previously are all of great economic importance, relatively little definite information is available regarding the nature of their inheritance. This is readily understood when the fact is realized that physiological characters are determined by complex physiological processes. Of course, color and morphological characters are also determined by physiological processes, but in each case the heritable differences, being measurable in terms of color or form, can be determined rather precisely. For instance, a bird is either white or colored, it is either barred or it is nonbarred, it has either a single or a rose comb, and it has either feathered shanks or nonfeathered shanks.

With what are here called physiological characters, however, the case is different. For instance, although some eggs of nearly all hens hatch, relatively more eggs of some hens hatch than of other hens; and although all chickens live and grow to some extent, some grow faster than others and some live longer than others. It is a question of differences in degree, and sometimes these differences are very difficult to measure, particularly when environmental conditions affect the results, which may be true of such characters as hatchability, growth, length of life attained, and resistance to disease.

THE INHERITANCE OF HATCHABILITY

By the term "hatchability" is meant the ratio of the maximum number of eggs that hatch to a given number of fertile eggs, when presumably ideal conditions of incubation prevail. Hatchability is expressed in terms of percentage; for instance, when 23 out of 25 fertile eggs set from one hen hatch, that hen is said to have a hatchability of 92 per cent. Studies involving the inheritance of hatchability require that all eggs be incubated under uniform conditions, which should be as ideal as possible in order that all hatchable eggs may hatch.

Hatchability Is Inherited.—The fact that hatchability is inherited was apparently first indicated by Gowell (1903), who found that great variability existed among hens in the hatchability of their eggs. Pearl and Surface (1909) measured the variability and secured evidence showing that hatchability is inherited. Lamson and Card (1920) concluded that individual differences among hens was the most important cause of variation in hatchability. Dunn (1921-1922) reports that "recent studies of the causes and inheritance of variations in the hatching quality or hatchability of the eggs of the domestic fowl have indicated rather definitely that differences in the hatchability of eggs are determined by innate differences in the individual hens which lay them," and "that these differences are probably inherited." Dunn (1923*a*) found that periodicity of embryo mortality is inherited, some strains showing a relatively high rate of mortality at the early period of incubation whereas other strains showed a relatively high rate at a later period.

Apparently the first analysis of hatchability from the genetic standpoint was undertaken by Hays and Sanborn (1924). They compared the first and second year hatchability of the same group of birds and the hatchability of the dams with their daughters. In a group of 253 Rhode Island Reds that were bred as pullets and as yearlings, it was found that the average hatchability in the pullet year was 56.78 ± 1.13 and in the yearling year 47.91 ± 1.30. The difference in hatchability between the two years is 8.87 ± 1.72, a difference that is regarded as being significant since it is more than three times its probable error. This difference may have been due to slightly different conditions of incubation that may have prevailed during the two different years or to the influence of the different males to which the same hens were mated in the different years. At the same time, Hays and Sanborn found the coefficient of correlation between the hatchability of the two years to be 0.43 ± 0.03, which means that the birds that gave high hatchability as pullets also tended to give high hatchability as yearling hens, and that poor hatchers the first year tended to be poor hatchers the second year.

Hatchability from Year to Year.—The hatchability of the eggs of birds used in successive years has been investigated by Hyre and Hall (1931), the variety being single-comb White Leghorns. In a group of 202 birds the hatchability as pullets was 54.31 ± 0.12 and as yearlings 52.42 ± 0.11, the difference being 1.89 ± 0.13. The difference is slight but significant, although the coefficient of correlation between the hatchability of the two years was 0.40 ± 0.04, indicating that hens having good hatchability the first year are inclined to have good hatchability the second year. In another larger group, all birds were first used as breeders in their second year of egg production, all were again used in their third year and then some in their fourth year, some in their fifth year, and a few in their sixth year. The data in Table 8 give the hatchability results for the different groups of birds for the different years.

Table 8. Average Hatchability Each Year for S. C. White Leghorns that Were Used Two or More Years as Breeders

(Data by Hyre and Hall, 1931)

Number of Birds	Average Hatchability in Per Cent				
	2nd Year	3rd Year	4th Year	5th Year	6th Year
633	61.38	53.17			
219	62.08	54.82	46.35		
85	62.04	58.96	57.94	46.53	
34	64.80	57.48	57.64	56.36	47.82

The data in Table 8 show that hatchability tends to decrease each successive year that birds are used as breeders. At the same time, the coefficient of correlation between the hatchability of one year and the hatchability of the succeeding year was found to be positive and significant in every case, thus indicating that hatchability is inherited. At the same time, the results given in Table 8 indicate that there are certain physiological factors that cause a hen's eggs to hatch less well on the average each succeeding year that she is used as a breeder.

The fact that a study of the inheritance of hatchability is an extremely complicated problem is further demonstrated by additional data supplied by Hyre and Hall (1931), who found that in three groups having high hatchability in the second year there was a decrease in the hatchability in the third year, whereas in three groups having low hatchability in the second year there was an increase in hatchability in the third year. The difference cannot be accounted for on the basis of the influence of the males because apparently the same males were used on the high and low second-year hatchability groups and either the same males or males of the same breeding were used for the two years involved. It seems probable that the correct explanation is that some of the birds in the three groups showing low second-year hatchability were adversely influenced by environmental factors that affected the birds or the incubation of their eggs causing them to be grouped in the low hatchability group whereas they might genetically belong to the high hatchability group. The same adverse factors, of course, might tend to lower the hatchability of birds that are nevertheless placed in the high hatchability group. To whatever extent this condition actually prevails, then, the determination of the inheritance of hatchability becomes still more difficult to solve.

Hatchability of Dams and Daughters.—The relationship between the hatchability of dams and daughters was determined by Hays and Sanborn (1924) in their Rhode Island Reds. The hatchability records of 811 daughters were compared with those of their dams, the number of which was not given. Hatchability percentages were 70.64 ± 0.39 for the dams and 50.91 ± 0.73 for the daughters, the difference being 19.73 ± 0.81. Ths significant difference may be attributed to differences in conditions of incubation for the dams and daughters or to the fact that different males were mated to the dams and daughters, or to the fact that the dams represented a smaller and selected group as compared with their daughters. In spite of these possibilities it was found that the coefficient of correlation between the hatchability of dams and daughters was 0.20 ± 0.02. Although the coefficient of correlation is both positive and significant it is of a low order and indicates that the males mated with the dams exercised a considerable influence on the hatchability of the daughters.

Influence of Male.—The point should be made clear at this time that any influence which a male may exert on the hatchability of the eggs of a female to which he is mated may be something quite different from the influence a male exerts on the hatchability of the daughters produced by the female to which he is mated. Apparently the only way to determine so-called "hatchability of a male" is by comparing the hatchability of the females to which he is mated with the hatchability of their daughters.

The relationship between the hatchability of the dams of a group of males and 748 daughters of the same males was studied by Hays and Sanborn (1924), the average hatchability of sires' dams being 70.19 ± 0.47 and that of the sires' daughters being 50.96 ± 0.76. The difference, 19.23 ± 0.89, is significant and indicates that the females to which the males were mated tended to lower the hatchability of the daughters or the males were of different genetic constitution from their own dams or probably both conditions existed. The coefficient of correlation between the hatchability of the sires' dams and that of the sires' daughters was 0.059 ± 0.025, which is not significant, showing, therefore, that the hatchability of the sires' dams was not transmitted to the sires' daughters, probably for the reasons mentioned previously.

Theory of the Inheritance of Hatchability.—As a result of their investigations Hays and Sanborn proposed a theory on a genetic basis to explain the inheritance of hatchability. According to them one dominant pair of autosomal genes, *HH*, determine a hatchability of 85 per cent or more. Birds having a hatchability of from 55 to 84 per cent are of the constitution *Hh* and birds having a hatchability of less than 55 per cent are of the constitution *hh*. The gene *H* is supposed to have a cumulative effect.

If the inheritance of hatchability rests upon such a simple basis as that proposed by Hays and Sanborn, it should be possible to develop strains of fowls having an average hatchability of 85 per cent or over in a relatively short time. That such is hardly possible in actual practice is borne out by the results secured by experienced breeders, including those who have supplied the progeny test in an effort to improve hatchability from year to year.

In order to determine whether the theory of the inheritance of hatchability as propounded by Hays and Sanborn applies to the case of hatchability results secured with other flocks, the results secured in Rhode Island Red and White Leghorn flocks at the U. S. Animal Husbandry Experiment Farm, Beltsville, Maryland, were analyzed. It was found that the mean per cent hatchability of the 74 Rhode Island Red dams was 74.86 and that of their 148 daughters was 72.70, the coefficient of correlation being 0.21 ± 0.05.

In order to test the matter further, the Rhode Island Red dams are divided into two groups, depending upon whether the hatchability of their eggs was above or below the mean for the group as a whole, and then the mean hatchability of the eggs of the daughters from each group of dams is compared, as shown in Table 9.

TABLE 9. DIFFERENCE IN HATCHABILITY BETWEEN GROUPS OF DAUGHTERS, THE COMPOSITION OF THE GROUPS BEING DETERMINED BY HATCHABILITY OF DAMS, IN RHODE ISLAND REDS

(Data of Jull., 1930)

Range in Per Cent Dams' Hatchability	Number of Dams	Mean Per Cent Dams' Hatchability	Number of Daughters	Mean Per Cent Daughters' Hatchability
68.0–94.5	51	80.63 ± 0.45	105	75.10 ± 1.29
41.0–67.5	23	59.95 ± 0.78	43	66.36 ± 1.98
Difference		20.68 ± 0.90		8.74 ± 2.57

The results in Table 9 show that hatchability is inherited, the difference in the mean percentage of the hatchability of the two groups of daughters being significant, 8.74 being more than three times its probable error, 2.57.

It was found that the mean per cent hatchability of 60 White Leghorn dams was 74.31 and that of their 105 daughters 59.17, the coefficient of correlation being 0.16 ± 0.06.

In the White Leghorns, it is apparent from Table 10 that hatchability is inherited, although the coefficient of correlation is not significant, probably because of relatively too few observations being involved.

The results secured in the Rhode Island Reds and White Leghorns demonstrate that hatchability is inherited, but owing to the relatively low values of the coefficients of correlations in each breed it is apparent that possibly more than one pair of genes is involved.

TABLE 10. DIFFERENCE IN HATCHABILITY BETWEEN GROUPS OF DAUGHTERS, THE COMPOSITION OF THE GROUPS BEING DETERMINED BY HATCHABILITY OF DAMS, IN WHITE LEGHORNS

(Data of Jull, 1930)

Range in Per Cent Dams' Hatchability	Number of Dams	Mean Per Cent Dams' Hatchability	Number of Daughters	Mean Per Cent Daughters' Hatchability
74.0–94.5	36	81.24 ± 0.36	62	63.40 ± 1.92
53.0–73.5	24	64.36 ± 0.76	43	52.33 ± 1.94
Difference		16.88 ± 0.84		11.07 ± 2.73

If but one pair of genes for high hatchability is involved, as Hays and Sanborn have suggested, it would naturally be expected that a relatively high correlation would result between dam and daughter hatchability. The magnitude of the correlation in each breed suggests, however, that probably more than one pair of genes is involved in the inheritance of hatchability.

The Effects of Inbreeding.—Cole and Halpin (1916, 1922), Dunn (1923*a*), Jull (1929*a*, 1929*b*), Dunn (1930), and Dunkerly (1930) have all shown that close inbreeding tends to reduce hatchability, even when the selection of the progeny each succeeding year is from the dams showing the highest hatchability. Furthermore, Jull (1930) has shown that when highly inbred strains are intercrossed hatchability is increased above that of the last inbred matings. These results tend to show that undoubtedly certain physiological factors affect hatchability. The same would seem to be true in outcrossing or crossbreeding. Pearl and Surface (1910) and Warren (1927, 1930) crossed certain breeds and secured increased hatchability over purebred matings used as controls. A detailed discussion of the effects of inbreeding and crossbreeding is reserved for Chapter X.

In summarizing the evidence on the inheritance of hatchability, it may be said that, although hatchability is inherited, it is certain that physiological factors are involved that affect the results secured from any given mating. Inbreeding tends to decrease hatchability, whereas outbreeding tends to increase it. At the same time, it has been shown that hatchability is inherited, and the available evidence suggests that probably several pairs of genes are involved. The results which Axelsson (1932) secured at the Zoological Institute, Lund, Sweden, confirm this observation. It is felt that much more work of an extensive character must be undertaken to determine precisely the number of genetic factors involved in inheritance of hatchability.

Genes Having a Lethal Effect.—One of the surprising things revealed in recent studies on hatchability is that there are genes which when in a homozygous condition kill the embryo. A lethal gene occurring in the domestic fowl was first reported by Dunn (1923*b*). The first indications of the presence of such a gene appeared in the results Dunn obtained in a cross between a Pit Game male and White Wyandotte females. Breeding tests showed that one of the original White Wyandotte females carried the lethal gene in a heterozygous condition, *Ll*, and when she was mated to one of her sons it was found that he also carried the lethal gene in a heterozygous condition, *Ll*. This backcross mating produced 19 colored and 8 white birds, almost exactly a 2:1 ratio. The lethal effect of the recessive genes when in a homozygous condition, *ll*, being linked with the recessive genes for white, *cc*, explains why one-half of the embryos that would normally develop into white birds die, giving a ratio of 2 colored birds to one white bird.

The lethal effect of another gene has been demonstrated by Landauer (1930) and Landauer and Dunn (1930*a*) in the case of the Creeper fowl. It has already been pointed out in the preceding chapter that the Creeper character is due to a single pair of dominant autosomal genes. An F_2 generation from an original cross between Creepers and normal fowls would be expected to consist of 3 Creepers to 1 normal, but breeding tests by Landauer and Dunn have shown that the F_2 generation consists of the proportion of 2 Creepers to 1 normal. Table 11 shows the results secured in the F_2 and backcross generations.

TABLE 11. F_2 AND BACKCROSS RESULTS SECURED IN MATINGS INVOLVING THE CREEPER FOWL

(Data of Landauer, 1930)

	F_2 Generation		Backcross Generation	
	Creeper	Normal	Creeper	Normal
Observed	1966	985	486	477
Expected	1967.3	983.7	481.5	481.5

The fact that when the dominant gene for the Creeper character is in a homozygous condition the embryo never hatches accounts for the ratio of 2 Creepers to 1 normal instead of 3 Creepers to 1 normal.

Byerly and Jull (1930, 1932) observed an embryo defect in the F_2 progeny of a mating between a Rhode Island Red male and Barred Plymouth Rock females. The bones of the affected embryos are described as being so soft that at hatching time the pipping of the shell is impossible. Other abnormalities include unabsorbed allantoic and amniotic fluids, and the unabsorbed yolk is about twice that in embryos developing normally. An F_1 male mated to related females produced 242 normal embryos that hatched and 74 abnormal embryos that lived to the eighteenth day of incubation. The same F_1 male mated to the dam of the F_1 females that produced abnormal embryos produced 13 normal and 5 defective embryos. An examination of the defective embryos showed that approximately 60 per cent of them had the head under the left wing, this being a malposition which usually prevents hatching. The defective character is apparently due to a single pair of recessive genes, which are lethal in their effect when they are in a homozygous condition in the embryo.

Many Genes Determine Hatchability.—The various observations made in the preceding pages show that hatchability is a very complex character. Undoubtedly several pairs of genes determine hatchability, and it is apparent that different pairs of genes vary in their effects, ranging from the known Creeper genes that are lethal in a homozygous condition and the dominant genes in the Frizzle fowl that lower hatchability considerably when they are in a homozygous condition to several other pairs of genes that probably exercise varying effects in determining degrees of hatchability among normal breeding birds.

THE INHERITANCE OF THE RATE OF GROWTH

Although numerous observations have been made on the rate of growth in embryos during the 21 days of incubation and in birds from hatching time to maturity, very little is known concerning the inheritance of rates of growth either in embryos or in chicks.

Rate of Growth in Embryos.—Murray (1925) and Schmalhausen (1927) have shown that embryonic growth in the chick is roughly proportional to the ratio of surface to mass plotted against time; or, according to Schmalhausen, the cube root of weight plotted against time gives a straight line. According to Bucciante (1929), chick embryos have a rather definite number of cells at particular morphological stages, regardless of the time required to reach those stages. Murray (1925) and Needham (1927) have submitted data on the daily growth of the embryos of White Leghorns from the first to the twenty-first days of incubation but the embryonic growth rates of different strains of White Leghorns are not considered.

The observations of Iljin (1917) and Byerly (1930*a*) show that, as embryo development proceeds, the correlation between embryo weight and initial egg weight increases, which is to be expected, since the albumen and then more and more of the yolk are assimilated by the embryo. Fangauf (1928) found that the ratio of albumen to yolk in the unincubated egg was 56.0 to 33.0, whereas on the sixth day of incubation the ratio of albumen to yolk was 22.5 to 62.1, on the thirteenth day 17.4 to 33.4, and on the twentieth day 0.0 to 23.3. At the same time, Fangauf observes that even as early as the sixth day of incubation the albumen is absorbed by the yolk and the two are assimilated by the embryo in this combined form.

The relationship between the mean weight of eggs at the commencement of the hatching period and the mean weight of chicks at hatching time has been studied by a few investigators. Halbersleben and Mussehl (1922) found that chicks hatched from brown-shelled eggs weighed 64.90 per cent and those hatched from white-shelled eggs 62.50 per cent of the original egg weight. Jull and Quinn (1925*a*) found that, in Barred Plymouth Rocks and Rhode Island Reds, there is no significant difference in the percentage chick weight (in either sex) of egg weight in yearling hens as compared with pullets. They found that the mean percentage chick weight of egg weight was approximately 65.00 in the Barred Plymouth Rocks and approximately 66.00 in the Rhode Island Reds. Upp (1928), working with Rhode Island Red pullets, found that chick weight averaged 68.00 per cent of egg weight. Hays and Sanborn (1929) observed in Rhode Island Reds that the chick weight was 61.00 per cent of the egg weight. Jull and Heywang (1930) observed that the chick weight was 68.43 per cent of the egg weight in White Leghorns.

In order to determine whether any differences exist in respect to the mean percentage chick weight of original egg weight and the mean percentage yolk weight of chick weight between eggs differing in size, Jull and Heywang (1930) analyzed the results secured from 251 eggs laid by 11 White Leghorn hens and found that the smaller the egg the smaller is the chick and the smaller is the absolute amount of yolk weight in the chick at hatching time. It was also found that the rate of assimilation of yolk material by the embryos from different hens is sometimes of a different order.

Embryo Growth in Different Breeds.—The relation of breed to the rate of growth in chick embryos has been investigated by Byerly (1930*b*), who studied eggs from matings of single-comb White Leghorns, single-comb Rhode Island Reds, and reciprocal crosses between the two varieties. It was found that up to the tenth day of incubation the White Leghorn and crossbred embryos were heavier than the Rhode Island Red embryos, but after the tenth day the Rhode Island Red and crossbred embryos became heavier than the White Leghorn embryos in most cases. Yet, the chicks from the four different sources weighed approximately the same at hatching time.

Byerly was led to conclude that differences in the size of embryos of the same age and from eggs of the same size, regardless of the breed, are slight, and although Rhode Island Red and crossbred embryos are somewhat heavier than White Leghorn embryos during the latter half of the incubation period, this difference decreases by hatching time, owing to the limitation of food.

The influence of breed on the rate of embryo growth was also studied by Henderson (1930). The rate of embryo growth was studied in embryos in eggs from White Leghorns, Dark Cornish, and their reciprocal crosses. Henderson observed "little if any constant significant difference in the growth of embryos from the different strains and breeds used in this investigation." Moreover, Kaufman (1930) found that the rate of growth in pigeon and fowl embryos is the same.

Rate of Growth in Chicks.—That the rate of growth of the male chicken differs to a considerable extent from that of the female is indicated by the data of Jull (1923) and by Ackerson and Mussehl (1930), who showed that males were significantly heavier at one week of age and the significance increased thereafter.

Practically no information is available concerning the inheritance of the rate of growth in the chicks of the different breeds and varieties. This is readily understood when the fact is realized that the inherent ability to grow is affected by such environmental factors as the kind of ration fed, seasonal influences throughout the growing season, the number of chicks per brooder and per house, general conditions of flock management, and the presence of parasites and disease, all of which may vary from year to year. There is no reason to believe that rate of growth is not inherited, but it is very difficult to secure evidence bearing on the point. It is well known, of course, that such breeds as Leghorns usually reach maturity much earlier in life than such breeds as Brahmas, but it is also known that some strains of Leghorns mature earlier than other strains, and the same is true of Brahmas.

THE INHERITANCE OF THE RATE OF FEATHER GROWTH

During the growing period of the chicken there are rapid and frequent changes in plumage, these changes resulting from the replacement of old feathers by new ones and by the appearance of new feathers from newly developed follicles, which are embedded in certain regions in the skin, giving rise to what are called "feather tracts," as illustrated in Fig. 29.

In White Leghorns, Rice, Nixon, and Rogers (1908) observed that the down of the chick is succeeded during the first few weeks by definitive feathers which are replaced, for the most part, at about 8 weeks, this second plumage being replaced by a third plumage at about 16 weeks, the third plumage being retained until about 5 or 6 months, when a full molt usually takes place and the birds assume the fourth or adult plumage, which is retained for approximately a year. Dunn and Landauer (1930) observed, however, that the processes of molting are almost continuous during growth and take place at different times in different feather tracts.

Feather Growth Affected by Endocrine Secretions.—According to the observations of Heinroth (1898) and Dwight (1900), the same feather follicle at different times may produce feathers with different colors or patterns. Goodale (1916) has shown that endocrine secretions directly affect the type of plumage produced; and Greenwood and Blyth (1928-1929) have shown that in the Brown Leghorn the plumage of the male is a reflection solely of a certain level of functioning of the thyroid gland, whereas the plumage of the female is modified male plumage, the modifications being induced by the thyroid gland and the ovary.

Juhn, Faulkner, and Gustavson (1931) have shown that there is a direct relation between the growth rate of male feathers in the Brown Leghorn and the concentration of the female hormone essential to female plumage modification. It was also found that males differ from females in the growth rate of regenerating feathers in the back, saddle, and anterior and posterior breast. Additional evidence tending to show that the development of a feather, including its pattern, is not determined entirely within the follicle has been given by Pearl and Boring (1914). They found that when feathers were pulled from Barred Plymouth Rocks the regenerated feathers tended to lose their characteristic barring effect; the more frequent the regeneration of a new feather the more progressively was the black and white bar broken up. In feather regeneration experiments with Silver-Spangled Hamburgs, it was found by Landauer and Dunn (1930*b*) that the spangled pattern is retained with considerable regularity in successively regenerated feathers, but that there is variability in regard to spangle size, particularly in different regions of the body. Landauer and Dunn were led to conclude that the degree of variability in spangle size is determined by the constitution of the individual and not by the properties of the feather follicles.

Heritable Differences in Feather Growth.—On the other hand, Kruimel (1916), Danforth and Foster (1927), and Danforth (1928, *1929a, 1929b*) have shown by means of skin-transplantation experiments that the feather follicle has within itself the power of self-differentiation with respect to the pattern of the feather it produces. Successful skin grafts between males and females and between individuals differing in the color, form, or pattern of the feathers (except for secondary sexual differences), showed that for the most part the transplanted skin produces feathers characteristic of the donor in color and pattern.

According to Dunn and Landauer (1930) the processes underlying feather differentiation are under a dual control: (1) the genetic constitution of the follicle itself, and (2) general agencies within the body as a whole. In their studies on the development of spangling in Silver-Spangled Hamburgs they came to the conclusion that the genetic constitution of the follicle is only one factor in the reaction which produces the spangled pattern.

It will be recalled that in Chapter IV it was shown that various feather markings, such as barring, lacing, mottling, and spangling, are apparently determined genetically. These feather markings and plumage colors in general are inherited according to Mendelian principles. Recent experiments have shown that the rate of feathering in certain breeds and varieties is also inherited according to Mendelian principles.

The barring character in Barred Plymouth Rocks is sex-linked, as shown in Chapter IV, but Martin (1929) has shown that there is a difference in the rate of feathering between males and females, feather growth in males being slower than in females. According to the American "Standard of Perfection" (1930), standardbred Barred Plymouth Rocks are expected to have black and white bars of equal width in both sexes, each feather ending with a tip of black, and both sexes are expected to be of an even shade. Martin has pointed out, however, that poultry breeders have found that the males are nearly always lighter in shade than the females. Many poultry breeders resort to the double-mating system involving the use of two separate breeding flocks, one for the production of standardbred males and the other for the production of standardbred females. Such a practice, however, is out of the question for the farmer or poultry breeder who is desirous of securing the greatest economic returns from his flock.

Moreover, Martin has shown that there is a general tendency for many of the best specimens of standardbred Barred Plymouth Rocks, as judged by the "Standard of Perfection" to feather slowly and to be poor layers. On the other hand, many flocks of Barred Plymouth Rocks bred primarily for egg production usually lack the desirable type of barring found in standardbred birds.

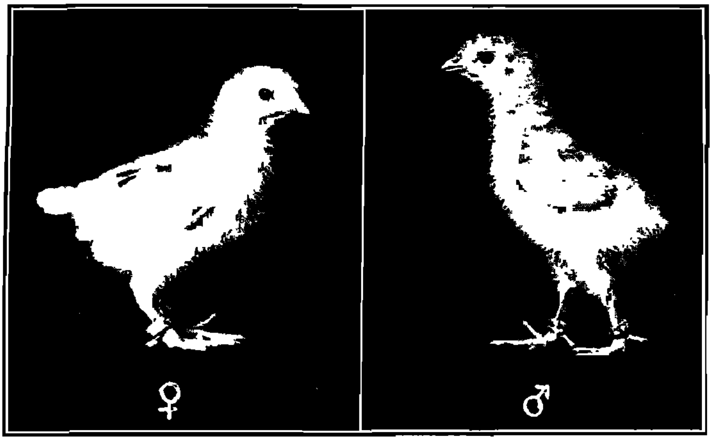

FIG. 35.—Sex-linkage of rate of feathering. Ten-day old chicks from a mating of White Leghorn male x Jersey Black Giant female. The male chick has inherited the dominant sex-linked gene for slow wing and tail feathering from its dam. (U. S. D. A.)

Martin compared the rate of feather growth and egg production between standardbred and production-bred flocks. Rate of feathering was determined principally on the basis of the degree of feathering over the back at the age of one, two, and three months, respectively, and comparisons in egg production were made on the basis of winter egg production, from November to February inclusive, as well as first-year egg production.

It was found that standardbred chicks grew at a slower rate than production-bred chicks, and that the rate of feather growth over the back is closely related to the rate of the growth of the birds. There is a greater tendency in standardbred chicks to be largely bare of feathers for several weeks than in production-bred chicks.

Among standardbred birds it was found that slow-feathering cockerels and pullets more nearly approached the standard type of barring than did the rapid-feathering cockerels and pullets. Among both standardbred and production-bred birds it was found that females that feathered slowly over the back were poor layers, whereas females that feathered rapidly were good layers.

Slow Versus Rapid Wing and Tail Feathering.—It is a well-known fact that purebred Leghorn chicks acquire their first feathers somewhat sooner than purebred chicks of such breeds as Brahmas, Orpingtons and Plymouth Rocks. Apparently the first case of the sex-linkage of rate of feathering was that reported by Serebrovsky (1922) in a cross of Russian Orloffs × Barred Plymouth Rocks. Warren (1925) crossed White Leghorn males × Jersey Black Giant females and observed that the sons were all of the slow-feathering type, whereas the daughters were all of the rapid-feathering type. In this case the Jersey Black Giant females transmitted slow feathering to their sons but not to their daughters. The opposite cross, Jersey Black Giant males mated to White Leghorn females, produced sons and daughters that were all slow feathering. These two matings made by Warren demonstrate that slow rate of feathering is sex-linked and dominant to rapid rate of feathering.

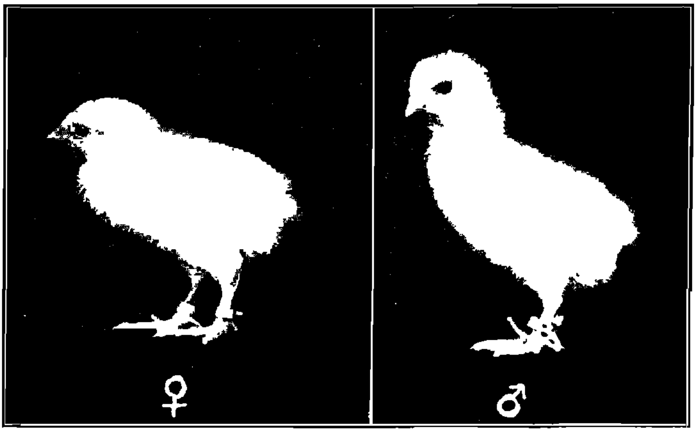

Fig. 36.—Ten-day old chicks from a mating of Jersey Black Giant male x White Leghorn female. Both sexes have inherited slow rate of wing and tail development from the sire. (U. S. D. A.)

Moreover, Warren (1925) found that when Leghorn males were mated to the first generation hybrid females obtained from a mating of Jersey Black Giant males × White Leghorn females all the female progeny were rapid feathering and all the male progeny were slow feathering. Such a mating is called a "backcross" mating, males possessing the recessive character in a homozygous condition (the male being homozygous for sex) being mated to females possessing the heterozygous dominant character (since the female is heterozygous for the sex character); and since only rapid-feathering males and slow-feathering females were secured, the results prove that slow rate of feathering is a sex-linked character.

Saharova (1926) crossed a Cochin male with Indian Pavloff females and observed that all the progeny were of the slow-feathering type, whereas an Indian Pavloff male mated to Cochin females produced slow-feathering cockerels and rapid-feathering pullets.

Kinugawa (1927) found that the male progeny invariably were slow feathering and the female progeny rapid feathering when White Leghorn males were mated to females of the following varieties: Black Orpington, Barred Plymouth Rock, White Wyandotte, Rhode Island Red, Light Brahma, and Nagoya. He also found that the same results were obtained when Rhode Island Red females were mated to Ancona males and Black Orpington females mated to Silver-Spangled Hamburg males. The fact that rate of feathering is inherited as a sex-linked character has also been demonstrated by Horn (1927).

Warren (1930*a*) points out that from crosses involving the use of males possessing the gene for rapid rate of feathering and females possessing the gene for slow rate of feathering the sexes may be identified accurately by the extent of the growth of the primary and secondary wing feathers at hatching time and by the presence or absence of tail feathers at ten days of age. At hatching time the primary or flight feathers in female chicks from such a cross as between White Leghorn males and Rhode Island Red females are much more developed than those of male chicks from the same cross. The sexes can be separated, according to the development of the flight feathers, with little inaccuracy as soon as the chicks are fluffed out. The identification of the sexes according to the development of tail feathers at ten to fourteen days of age serves as a check on any errors made in the identification of the sexes at hatching time according to flight feather development.

THE INHERITANCE OF CONSTITUTIONAL VIGOR

Practically every poultryman knows in a general way that birds often differ a great deal in vigor. At the same time, very few poultrymen know what constitutional vigor really involves. Practically no one seems to know the proper basis for comparing the difference in vigor between any two birds.

That constitutional vigor implies physical fitness is generally understood, but some poultrymen think that physical fitness means one thing and others that it means something else. To some poultrymen vigor means the ability of the male to hold his own in mortal combat with his fellows, whereas to other poultrymen vigor means good hatchability of eggs, the ability to lay, or the ability to live a long life.

For the sake of a clear understanding of what is implied in the term constitutional vigor in this book, the following suggestion is made: *A bird with an abundance of constitutional vigor is one so well endowed with health and physical fitness as to be able to withstand unfavorable environmental conditions, to resist disease, to produce offspring most efficiently, and to be capable of living a relatively long life.*

There are a number of external, visible evidences of constitutional vigor which show considerable variation from birds of strong constitutional vigor to birds of very weak constitution. Before a bird can be abundantly vigorous, however, it must have good health. A bright eye and glossy plumage are indicative of health. The body must be of good proportions, good breadth in proportion to the length indicating strength.

For a detailed discussion of physical characters of a bird indicating constitutional vigor, see Rice, Hall, and Marble (1930).

Importance of Constitutional Vigor.—That constitutional vigor is of paramount importance in laying stock is evidenced by the fact that a 4-pound Leghorn and a 6-pound Rhode Island Red each laying 216 eggs of standard size, 2 ounces each, would produce a weight in eggs equivalent to six times the weight of the Leghorn and four times the weight of the Rhode Island Red. High egg production constitutes a heavy drain on the bird's digestive and reproductive systems and a female must possess abundance of constitutional vigor to stand the strain of continuous production.

A point of great practical importance to poultry breeders which they often overlook is the relatively high cost to them of lack of vitality in their breeding and laying stock. Even under the best of circumstances the span of life of the average chicken is relatively short, so that frequent replacement is necessary. The average poultryman is obliged to replace approximately two-thirds of his laying flock every year, but if his layers were profitable producers for several years the annual cost of the replacement would be reduced considerably. Then again, lack of vitality often means increased embryo mortality during incubation and increased mortality in the laying flocks, thus requiring many poultrymen to incubate more eggs and rear more pullets every year than a poultryman whose flock possesses abundance of constitutional vigor.

Determining the Mode of the Inheritance of Constitutional Vigor, a Very Complex Problem.—Reference has already been made to the fact that there are not only numerous external evidences of constitutional vigor but that the various processes in the reproduction of the flock from year to year must be taken into account. It is clear that there is no single criterion for constitutional vigor. A male may not be aggressive as a fighter but his daughters may lay well. A female may be a poor layer but during the breeding season practically all her eggs may hatch, or a hen's eggs may hatch poorly but the daughters that are reared may be good layers. For these and other reasons it is clear why so little is known concerning the inheritance of constitutional vigor.

Inbreeding experiments with poultry, the detailed results of which are discussed in Chapter X, have shown that different traits, such as hatchability of eggs, livability or viability of chicks, egg production, and body size, are affected in different ways. For instance, close inbreeding probably affects hatchability more seriously than many other traits.

Other valuable data bearing on the problem of the inheritance of constitutional vigor are obtained from the results of crossbreeding experiments, the details of which are discussed in Chapter X. At this time, it is sufficient to say that crossbreeding has usually resulted in increased hatchability over that of each of the pure breeds crossed. Other experiments, as, for instance, those of Warren (1930*b*), tend to show that crossbreeding produces greater viability in the chicks, faster rate of growth and better egg production than in pure breeds.

The term "hybrid vigor" or "heterosis" is used to denote the greater vigor of the progeny of purebred stocks that are crossed as compared with the vigor of the purebred stocks themselves. Apparently a beneficial physiological result occurs when different pairs of genes from the different purebred parents are brought together in the hybrid progeny.

Studies on the inheritance of constitutional vigor within purebred flocks are very limited. The general effects of inbreeding have already been mentioned. Few other observations have been made, except that Dunn (1922) and Jull (1928) found no relationship between embryo mortality during incubation and chick mortality during the first few weeks, and Hays and Sanborn (1928) found that egg production for the most part is not related to vigor. On the other hand, it was found that mortality among the layers was due largely to lack of vigor.

THE INHERITANCE OF RESISTANCE TO DISEASE

It is well recognized that diseases of various kinds cause an enormous loss annually in the poultry industry. It is estimated, for instance, that in the United States, the annual loss from mortality in growing chicks is at least $18,000,000 and the annual loss in the mortality among laying hens is at least $20,000,000. Some of these losses are due to parasites of various kinds and part of the losses are probably due to diseases over which man has yet been able to exercise little or no control, several diseases of major importance having proved to be very stubborn in regard to control measures.

It has become apparent that chickens differ among themselves in respect to infection from disease and that to some extent the differences are due to genetic dissimilarity, which produces differences in general physiological constitution. Crew (1926) maintains that immunity from disease is an hereditary character that can be developed in a strain of animals by selection. Lambert (1929) observes that an animal in order to be most useful must not only be kept under the best possible environmental conditions but must also be equipped with a good heredity in order to withstand the attacks of disease.

Probably the first observation on the hereditary resistance to a specific poultry disease is that of Frateur (1924). Experimental work was conducted with bacillary diphtheria, the results of which led Frateur to conclude that the resistance to this disease is due to the presence in a bird of a gene and that by proper selection the development of disease-resistant strains of poultry should be possible.

Regarding the inheritance of resistance to pullorum disease (bacillary white diarrhea), Roberts and Card (1926) state that chicks from certain hens were found to be much more resistant to infection with Salmonella pullora, which cause the disease, than are the chicks from other hens. The results they secured led them to believe that it may be possible to develop strains of the domestic fowl that will be highly resistant to the disease.

The inheritance of resistance to fowl typhoid has been studied by Lambert and Knox (1928), who found that resistance to infection with fowl-typhoid bacteria was transmitted by sires as well as by dams to their chicks. It was also found that sires differed markedly in their ability to transmit resistance to their progeny, a situation to be expected if resistance to this disease is an inherited character.

In conclusion, it may be said that the rather meagre though highly *interesting results secured on the general problem of the inheritance of resistance to disease should stimulate further research on this very important economic problem.*

PROBLEMS

1. Outline a comprehensive ten-year project for the purpose of ascertaining the number of pairs of genes determining hatchability.

2. If increased knowledge concerning the inheritance of hatchability would lead to an increase of 5 per cent in hatching results, what would this increase be worth to a poultryman maintaining a flock of 1,000 birds, and what would the increase be worth to the poultry industry of the country as a whole?

3. Account for the origin of lethal genes.

4. Since body weight is inherited, as shown in the preceding chapter, and since newly hatched White Leghorn, Rhode Island Red, Barred Plymouth Rock, and Light Brahma chicks would weigh approximately the same if the eggs set from the different varieties were of the same size, how do you account for the fact that the adult weights of the four varieties differ considerably?

5. Should the males and females in the different breeds and varieties differ to the same extent in body weight, or should some of the standard weights in the American Standard of Perfection be altered to conform to existing knowledge concerning the inheritance of growth? For instance, the standard weights of the Leghorn cockerel and pullet are 5 pounds and 4 pounds, respectively, and the standard weights of the Plymouth Rock cockerel and pullet are 8 pounds and 6 pounds, respectively; using the weights of the two pullets as the basis of comparison should the weight of the Plymouth Rock cockerel be 7.5 pounds, or should the weight of the Leghorn cockerel be 5.3 pounds? Compare the standard weights of males and females among the following breeds: Cornish, Minorcas, Orpingtons, Wyandottes, Jersey Black Giants, and Sussex.

6. Since practically all slow-feathering breeds lay brown eggs and since some markets show a preference for white eggs, tell how a slow-feathering, white-egg breed might be developed.

7. Is it possible to combine standard quality of barring in Barred Plymouth Rocks and maximum efficiency in rate of growth and egg production?

8. What are the different traits in males and in females that should be taken into consideration in measuring constitutional vigor and in determining its inheritance?

9. What steps would be necessary in replacing strains of birds throughout the country that do not possess hereditary resistance to a specific disease with birds that possess it?

10. To what extent might the science of genetics contribute toward a solution of some of the more important economic problems facing the poultry industry? Confine the discussion to economic problems involving physiological characters.

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CHAPTER VII

THE INHERITANCE OF LINKED CHARACTERS

Two of the fundamental principles of Mendelian inheritance—dominance and the independent assortment of the genes—have been fully discussed in Chapter III. Numerous illustrations involving both principles have been given in Chapters IV, V, and VI in the discussion of the inheritance of color and of morphological and physiological characters. Dominance and recessiveness have been shown to be clear-cut in many pairs of characters. The independent assortment of the genes has also been found to hold good in respect to many pairs of genes, giving the 3:1, the 9:3:3:1, and other ratios in the F_2 generations.

✓ On the other hand, many cases have been established where independent assortment of the genes does not take place, so that in the F_2 generation a normal Mendelian ratio is not obtained. In several instances in the domestic fowl when parents differing in two pairs of characters have been crossed the F_2 generation, instead of consisting of a 9:3:3:1 ratio, contains an excess of birds having the same combination of characters as the original parents and a relatively small number of birds showing the new combination of characters. In other cases the reverse is true.

The Principle of Linkage.—These apparently abnormal F_2 ratios are due to the phenomenon known as linkage, which simply means that genes giving rise to certain characters tend to remain together instead of assorting themselves independently of each other when the gametes from the two sexes unite. For instance, if genes *A* and *B* are completely linked so that they never separate, different results are produced in the F_2 generation from those which would be obtained if *A* and *B* separated freely, as shown in Fig. 37.

The cases of linkage that have been investigated in the domestic fowl have shown that linkage is rarely complete but is usually partial, that is, a given pair of genes tend to remain together but do separate to a certain extent, although less frequently than in the case of independent assortment.

When *A* and *B* exhibit partial linkage the proportion of birds in the F_2 progeny having the same combination of characters as the parents and those having the new combinations of characters varies according to the way the original cross is made. If the original cross is of the nature $AABB \times aabb$, each F_1 individual is of the constitution $AaBb$ and forms the four kinds of gametes AB, Ab, aB, and ab, but the two parental combinations, AB and ab, are more numerous than the new combinations, Ab and ab. If the original cross is of the nature $AbAb \times aBaB$, each F_1 individual is of the constitution $AaBb$

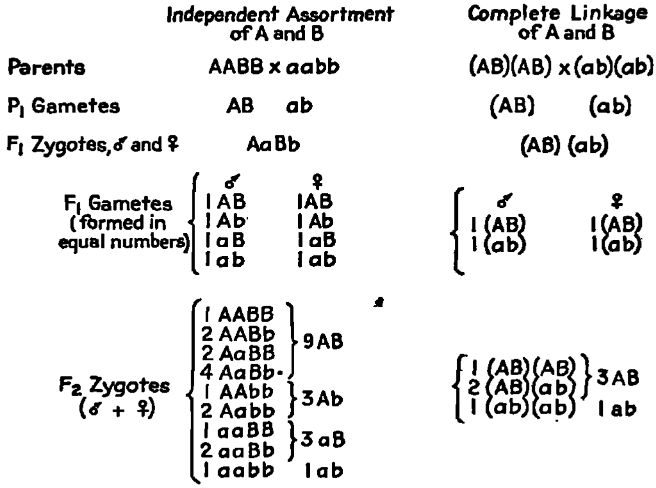

FIG. 37.—Showing the difference in the results secured in the F_2 generation when two genes show independent assortment in one case and complete linkage in the other case. In the case of the independent assortment of A and B, similar results would be secured if the original cross was AAbb x aaBB instead of AABB x aabb, shown above.

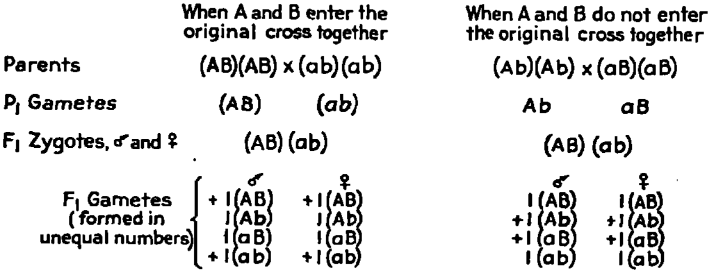

FIG. 38.—Showing different proportions of F_1 gametes formed by F_1 individuals when A and B enter the original cross together and when they do not enter the original cross together, partial linkage being involved in both cases.

and forms the four kinds of gametes *AB*, *Ab*, *aB*, and *ab*, but the two parental combinations, *Ab* and *aB*, are more numerous than the new combinations *AB* and *ab*. In the first cross, *AB* and *ab* are more numerous than *Ab* and *aB*, whereas in the second cross *Ab* and *aB* are more numerous than *AB* and *ab*. Different results are secured depending upon the way the original cross is made, as shown in Fig. 38.

Owing to the fact that some characters are dominant over others, the F_2 ratio does not give a direct index of the kinds of gametes produced by the birds of the F_1 generation in cases of linkage. But a backcross of an F_1 bird heterozygous for each of two pairs of genes to the parent with both pairs of genes in a homozygous recessive condition provides an accurate index of the constitution of the gametes of the heterozygous F_1 bird.

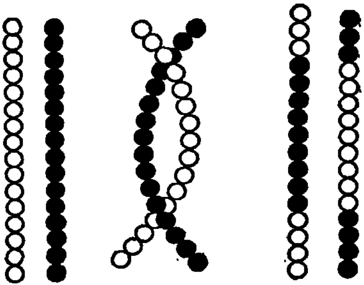

FIG. 39.—Diagram illustrating the manner in which crossing-over is supposed to take place. A, a pair of chromosomes composed of hypothetical genes. B, the pair of chromosomes in contact with each other at two places. C, the chromosomes have separated, each chromosome "breaking" at the points of contact with each other so that the genes of one chromosome have crossed over to the other chromosome. (After Agar, 1920, by permission Macmillan & Co.)

The Principle of Crossing Over.—Genes that are located in the same chromosome, whether it be autosome or sex chromosome, should always be inherited together as linked genes if the chromosome remains intact in inheritance. But it has been observed previously that linkage is rarely complete, thus indicating that frequently the chromosome is not inherited intact. Investigational work has established the fact that the gametes go through various stages of development and division in order that a gamete from the male may unite with a gamete from the female. During at least one of these stages of development each pair of chromosomes in a gamete lie side by side or even coil around each other and, occasionally, instead of separating intact, both chromosomes may break at the same place and the anterior portion of one chromosome of the pair becomes joined to the posterior portion of the other chromosome of the pair. This is supposed to give rise to an interchange of parts of the same pair of chromosomes; hence the suggestion that crossing-over takes place. The genes of one chromosome are said to cross over to the other chromosome of the pair, as illustrated in Fig. 39.

Suppose that the genes *A* and *B* from one parent enter into an original cross and that they are located at opposite ends of the same chromosome. Suppose also that the genes *a* and *b* enter the same cross from the other parent. An F_1 bird will have the constitution *AaBb,* and the genes *A* and *a* and *B* and *b* will be in the same relative positions in each chromosome of the same pair. If crossing-over takes place, then each of the newly formed chromosomes will have *A* and *b* and *a* and *B* instead of *A* and *B* and *a* and *b*. The combinations *A* and *b* and *a* and *B* are new, whereas *A* and *B* and *a* and *b* are the parental combinations.

On the other hand, if the genes *A* and *b* enter the original cross from one parent and *a* and *B* from the other parent and crossing-over takes place, then *A* and *B* and *a* and *b* are the new combinations and *A* and *b* and *a* and *B* are the parental combinations. The parental or original combinations are noncross-overs and the new combinations are cross-overs.

Determining Linkage Value.—It has already been pointed out that if no crossing-over takes place linkage is complete, but that if crossing-over takes place linkage is not complete. It is obvious, therefore, that the amount of crossing-over that takes place is determined by the degree of linkage, or the degree of linkage is determined by the extent to which crossing-over takes place. Regardless of which is cause and which is effect, crossing-over is the corollary of linkage.

Each pair of linked genes exhibits a characteristic proportion of noncross-overs and cross-overs, the degree of linkage being determined in terms of the percentage of cross-overs in the gametic series. This is called the linkage value.

Under independent assortment the noncross-overs and cross-overs are approximately equal in numbers, whereas under linkage the noncross-overs are always more numerous than the cross-overs. Linkage may vary from slightly over 50 per cent to nearly 100 per cent noncross-overs of the total number of progeny. This is another way of saying that crossing-over may vary from about 50 per cent to less than 1 per cent. In other words, linkage strength varies inversely as the cross-over value increases.

The degree of linkage which exists between any two genes is not influenced by the way in which the linked genes enter the cross. Suppose, for instance, that genes *A* and *B* exhibit 90 per cent linkage or 10 per cent crossing-over. Then the proportion of phenotypes in the F_2 generation of an original cross between a bird of the constitution (*AB*) (*AB*) and one of the constitution (*ab*) (*ab*) can be predicted in advance. The F_1 birds from the original mating would be of the constitution (*AB*) (*ab*), and instead of producing a gametic ratio of equal numbers of *AB*, *Ab*, *aB*, and *ab*, expected under independent assortment of *A* and *B*, they would produce gametes in the following proportions:

$$\left.\begin{array}{l}45\text{ per cent }AB\\45\text{ per cent }ab\end{array}\right\}90\text{ per cent linkage or noncross-overs}$$

$$\left.\begin{array}{l}5\text{ per cent }Ab\\5\text{ per cent }aB\end{array}\right\}10\text{ per cent cross-overs.}$$

The results that would be secured in the F_2 generation produced by the F_1 birds of the constitution (*AB*) (*ab*), the genes *A* and *B* having entered the cross from the same parent, mated among themselves can be predicted in advance. In case of independent assortment of two pairs of genes an F_2 phenotypic ratio of 9 *AB* : 3 *Ab* : 3 *aB* : 1 *ab* is produced, since the gametes *AB*, *Ab*, *aB*, and *ab* are produced in equal numbers by both the male and the female F_1 birds of the constitution *AaBb*. In 90 per cent linkage or 10 per cent crossing-over, the F_1 gametes (*AB*) and (*ab*) are each 9 times (45 as to 5) as numerous as the gametes (*Ab*) and (*aB*), so that the F_2 phenotypic ratio is quite different from that produced under independent assortment of the genes. A still different F_2 phenotypic ratio is produced in the case of 90 per cent linkage or 10 per cent crossing-over when the genes *A* and *B* enter the original cross from different parents, (*AA*) (*bb*) being mated to (*aa*) (*BB*).

The results in the F_2 generation can be predicted for any cross involving linkage, providing the linkage value is known, the linkage value being most readily determined by backcrossing. It should be noted, however, that there are cases where certain genes affect the amount of crossing-over that takes place between other genes.

Double and triple crossing-over has been reported in poultry, in which cases the pair of chromosomes have broken twice and three times, respectively, instead of only once as in single crossing-over.

Crossing-Over of Sex-Linked Genes.—From the time of the first demonstration of Goodale (1917) of crossing-over between two sex-linked genes, other investigators, including Haldane (1921), Serebrovsky (1922), Agar (1924), and Warren (1924), have verified the result and have extended the list of sex-linked genes that exhibit the trait. Apparently crossing-over of sex-linked genes does not take place in the female fowl, in all probability on account of the absence of the second sex chromosome.

Although a number of investigators, including Hertwig and Ritterhaus (1929), Hertwig (1930), Serebrovsky and Petrov (1930), Serebrovsky and Wassina (1927), and Warren (1928), have reported results purporting to show the crossing-over percentages in four groups of sex-linked genes in the domestic fowl, it should be noted that their results are not in entire agreement and that in some experiments the observations were based on relatively few birds. In view of this situation, it is felt that the publication of the results secured should await the compilation of more convincing data.

Linkage Between Autosomal Genes.—The fact that linkage occurs between genes in the autosomes of different animals and plants has been established for some time, although only relatively recently for the domestic fowl.

Dunn and Jull (1927) secured evidence indicating linkage between the genes for hernia and polydactyly, between the genes for hernia and colored plumage, and between the genes for polydactyly and colored plumage. The linkage evidence was based on rather limited data, however, and further work is necessary to determine whether or not the genes for hernia, polydactyly, and colored plumage constitute one linkage group. Dunn and Jull also secured evidence indicating linkage between the genes for rose comb and crest, but additional evidence supplied by Jull (1930) shows that there is probably no linkage between the two genes.

Other evidence purporting to establish linkage between autosomal genes has been provided by Serebrovsky (1926), Serebrovsky and Petrov (1928), Warren (1929), and Serebrovsky and Petrov (1930). Serebrovsky's data for 1926 are for the most part included with additional data given by Serebrovsky and Petrov in their 1930 paper, in which the most conclusive evidence of linkage is that between the gene for rose comb and the gene for the "creeper" character.

Warren (1929) tested for linkage among the following seven groups of autosomal genes: (1) naked-neck and normal neck-feather development, (2) rumplessness and normal number of caudal vertebrae, (3) yellow shank color and white shank color, (4) rose comb and single comb, (5) black plumage and columbian plumage pattern, (6) feathered shanks and nonfeathered shanks, (7) pea comb and single comb. The first four groups showed independent assortment, and group 5 showed independent assortment with groups 1, 2, and 4. Group 6 showed independent assortment with group 4. The foregoing crosses were arranged for testing crossing-over in the male.

Suttle and Sipe (1932) have reported results indicating linkage between the gene for crest and the one for frizzling.

Double crossing-over in the domestic fowl has been reported by Serebrovsky (1927), Warren (1928), and Hertwig and Ritterhaus (1929), who have also reported triple crossing-over in the sex chromosomes. Such a condition would indicate a sex chromosome of considerable length, which is in keeping with the cytological evidence supplied by Hance (1926), whose observations are given in Chapter II.

Mapping the Chromosomes.—It has already been pointed out that the fact that linkage exists between any two genes demonstrates that the two genes are in the same chromosome. In general, the greater the distance between any two genes the greater is the tendency for crossing-over to take place. Conversely, the closer together the two genes are the less liability of crossing-over taking place, or in other words, the greater is the linkage strength.

The distance between two genes in the same chromosome is determined by the crossing-over percentage, the distance being expressed in terms of units.

Where it has been determined that three or more genes are located in the same chromosome, their relative positions can be indicated according to the crossing-over percentages exhibited between each pair. Suppose, for instance, that genes A, B, C, and D are in the same chromosome and that the crossing-over percentage for each of the pairs is as follows: A and $B = 40$, A and $C = 20$, B and $C = 20$, A and $D = 10$, and C and $D = 10$; then it is apparent that B is four times as far from A as is D, that C is half way between A and B, and that D is half way between A and C. Such a procedure is called mapping the chromosomes.

The relative positions of some of the linked genes on the sex chromosomes and on one or more of the autosomes have been suggested by Serebrovsky (1926), Serebrovsky and Wassina (1927), Warren (1928), Hertwig (1929), and Serebrovsky and Petrov (1930). The suggestions are for the most part tentative, however, and it is felt desirable to withhold publication of chromosome maps in this book until more definite information is available regarding larger numbers of linkage groups.

It is of very great fundamental importance, however, to be able to map the chromosomes as completely as possible because the greater the number of linkage groups established the greater is the possibility of determining the existence of linkage between such characters as egg production and some of the color, morphological, and physiological characters, which have been discussed in Chapters IV, V, and VI. If it can be determined that certain of these visible characters are linked with egg production the task of the practical poultry breeder will be made much simpler.

PROBLEMS

1. What is the relationship between linkage and crossing-over?
2. Outline a breeding project with a view to determining the linkage strength between two genes whose linkage strength has not yet been determined.
3. What is the relationship between two genes when (1) there is no crossing-over and (2) when there is 50 per cent crossing-over?
4. From the information given in Chapter II regarding the number of chromosomes in the domestic fowl, how many linkage groups should it be possible to establish in the case of the male and in the case of the female?
5. What are some of the practical aspects involved in linkage?

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CHAPTER VIII

THE INHERITANCE OF EGG-LAYING CHARACTERS

Egg production is of greater practical importance to poultrymen throughout all parts of the world than any other character which domestic fowls possess, and for that reason the discussion of the inheritance of egg-laying is given a separate chapter. A thorough study of the heredity of egg-laying characters includes the problem not only of the inheritance of egg-laying ability but also of the inheritance of the kind of eggs that are laid. In other words, consideration must be given not only to the number of eggs that are laid but also to their size, shape, color, and interior quality. In this chapter the discussion is confined to the inheritance of egg-laying ability, the number of eggs laid per hen being the criterion; the discussion on the inheritance of egg characters is reserved for the next chapter.

The ability to lay eggs involves certain physiological processes, pertaining particularly to the formation of the egg, and certain genetic factors as a result of which there is variation among egg producers, thus making possible the development of highly productive strains through selection and the adoption of proper breeding practices. It follows, therefore, that due consideration must be given to the problem of the physiology of egg production before a complete understanding is possible concerning the problem of the genetics of egg production.

Moreover, the problem of the genetics of egg laying cannot be discussed without first determining the proper basis of comparing the inheritance of the egg-laying ability of any two hens. Egg production must be considered on a time basis, for the simple reason that a hen must lay a certain number of eggs in a given time in order to return a net income to her owner. The number of eggs that may be laid in any given time is affected by a variety of factors in addition to those of a genetic nature. Therefore, before discussing the inheritance of egg production due consideration must be given to the extent to which egg production is affected by such factors as season, climate, or weather, methods of housing, feeding and management, and the presence of disease. These factors are discussed under the general heading of the effect of external factors on egg production. Theories of the

Mendelian inheritance of egg production, and then the basis of improving egg production, are discussed. This chapter, therefore, is divided into five parts:

(1) The physiology of egg production.
(2) External factors affecting egg production.
(3) Annual production records serve as a basis of inheritance studies.
(4) Theories of Mendelian inheritance of egg production.
(5) The basis of improving egg production.

. THE PHYSIOLOGY OF EGG PRODUCTION

The new-laid egg is the end product of a number of physiological processes that take place in the ovary and oviduct, which have been described in Chapter II.

The possibility of producing eggs obviously depends upon the presence of ova in the ovary. At hatching time the ovary of a female chick usually contains a large number of ova, each ovum apparently being in a quiescent state ready to be developed into the yolk of a future egg. Each ovum begins as a minute body in the ovary and is similar to the reproductive cells of mammals. It is contained in a very thin envelope called the "follicle," which is attached to the ovary by a slender stalk or pedicel. The ovum consists of a finely granular protoplasm enclosed in a pellicle called the "vitelline membrane." Embedded in the protoplasm is the nucleus.

The number of visible ova in the ovary of each of a number of laying hens was determined by Pearl (1912*a*), who found that the number present in any hen appeared to bear no relationship to her egg-laying ability, although Pearl and Schoppe (1921) observed a general relationship between the average number of ova present and egg production in different orders of birds.

The Accumulation of Yolk.—As the female approaches laying condition, the immature ova begin to accumulate yolk, which is carried to the ovary by the blood and the lymph in the form of proteins and fatty acids. In each ovum the yolk granules are secreted in concentric layers, beginning with a layer of light yolk and then a layer of dark yolk, and this alternation of layers of physically different kinds of yolk continues until the ovum is ready to be discharged from the ovary. Riddle (1911) determined that the light yolk is accumulated during the night, the time of low blood pressure in the laying hen, whereas the dark yolk is accumulated during the day.

The increase in the size of each ovum takes place quite rapidly, although all the ova do not accumulate yolk granules at the same time but follow each other in successive order until each is sufficiently developed to be liberated from the ovary. The rate of growth of each ovum is not regular, for Riddle (1916*a*) observed that when the ovum of the domestic fowl reaches a diameter of 6 mm. the rate of growth suddenly increases about twenty-five fold until a size of approximately 40-mm. diameter is attained, this being about the size of the yolk of a normal egg. During the growth of the ovum the follicle enlarges and, when the ovum is ready to be liberated from the ovary, bursts along a streak called the "stigma." Subsequently, the ruptured follicle degenerates. The ovum as it escapes from the follicle is still contained in its vitelline membrane.

The Formation of the Vitelline Membrane.—The vitelline membrane is of composite structure, as shown by Lecaillon (1910), comprising a delicate non-cellular layer immediately surrounding the ovum, outside of which is a layer of degenerating epithelium, and outside of that again is a layer of connective tissue, the last two layers having been contributed by the follicle.

Ovulation.—The ovum just before being liberated from the follicle of the ovary is embraced by the mouth or funnel of the oviduct, which normally lies pressed against the ovary, although Pearl and Curtis (1914) have shown that the pressure from the funnel is not necessary for ovulation, a term used with reference to the passage of the ovum from the ovary. Moreover, Lillie (1919) has observed that the funnel of the oviduct is able to grasp ova that have dropped into the body cavity. If ova that are dropped into the body cavity are not taken up by the oviduct, they may be absorbed or they may cause serious and fatal disturbances.

The Secretion of Albumen.—Immediately after entering the funnel, the ovum is passed down the four remaining sections of the oviduct by peristaltic action. Gadow (1891), Patterson (1910), and Pearl and Curtis (1912, 1914) give detailed accounts of the formation of the various parts of the white or albumen of the egg and the shell membranes and shell, all of which serve to protect the germinal disc in the yolk. The ovum requires approximately three hours to pass through the albumen-secreting portion of the oviduct, during which time the chalazae and the dense albumen are secreted.

The two chalazae are dense portions of the albumen twisted in opposite directions and, according to Gadow (1891), attached on opposite sides of the yolk to a dense layer of albumen surrounding the yolk. The chalazae serve the important function of mooring and steadying the yolk in the albumen, thus serving to protect the embryo from violent jarrings.

Immediately surrounding the thin layer of dense albumen to which the chalazae are attached there is a thin layer of watery albumen, which in turn is surrounded by a thick layer of dense albumen.

According to Pearl and Curtis (1912), the outer fluid layer of albumen is secreted in the isthmus and uterus portions of the oviduct. This observation has been confirmed by Chomkovic (1926, 1927) for ducks. Approximately from two to three hours are required by the ovum and the albumen already secreted to pass through the isthmus of the oviduct.

The outer watery layer constitutes from about 50 to 60 per cent of the total weight of the albumen, and most of it is secreted in the uterus, since about 50 per cent of the total weight of the albumen is secreted in this portion of the oviduct. From about five to seven hours are required for the secretion of the albumen in the uterus, although the egg remains there about sixteen to seventeen hours, during most of which time the shell is being formed.

Concerning the secretion of albumen, it is interesting to note that Pearl and Surface (1908) removed a section of the albumen-secreting portion of the oviduct by operation and observed that there was little or no effect on eggs subsequently laid.

The Formation of the Shell Membranes.—As early as 1847 Coste showed that the shell membranes are deposited in the isthmus, only those parts of the egg that lie within the isthmus at that time being surrounded by the shell membrane. Pearl and Curtis (1912) were of the opinion that the shell membranes were completely formed in the isthmus, whereas Giersberg (1921, 1923) believed that there is some increase in shell membranes after the egg enters the uterus. Nathusius (1893, 1896) went still further and stated that there is an increase in the formation of shell membranes after the deposition of the shell. On the other hand, judging from the results which Asmundson (1931*a*) secured when a portion of the isthmus was removed by an operation, it is apparent that the shell membranes are completely formed in the isthmus.

Since the formation of the shell membranes takes place for the most part in the isthmus, it should be observed at this time that the outer fluid layer of albumen, which is secreted in the isthmus and uterus, passes through the shell membranes by osmosis.

The shell membranes lie very close together except where the air cell appears in the egg, usually at the blunt end. According to Hays and Sumbardo (1927), the outer shell membrane is about three times as thick as the inner one, both being composed of organic fibers.

The Formation of the Shell.—The shell is composed of two layers and a cuticle or bloom.

The inner or mammillary layers consist of very minute particles of calcium carbonate so arranged as to provide air spaces for the passage of gases. The outside layer is composed of crystals of calcium carbonate arranged with their long axes perpendicular to the surface, according to Needham (1931). The cuticle, on the outside of the egg, is apparently structureless but is porous.

The porosity of the shell and the shell membranes is necessary to allow the embryo chick to respire by exhaling carbon dioxide and by inhaling oxygen. The porous character of the shell also allows water to evaporate from the egg.

Rizzo (1899) counted 1.23 pores per square millimeter on the surface of the shell, whereas Hays and Sumbardo (1927) found that the number of pores in the equatorial region varied from 413 to 601 per square centimeter. Romanoff (1929) observed that eggs with thick shells have more pores than eggs with thin shells.

Romanoff also observed that the average thickness of the shell of the eggs he examined was 0.311 millimeters, but it should be pointed out that evidence has been submitted from time to time showing that the kind of diet fed to the laying hens sometimes affects the thickness of the shell of the eggs laid. For instance, Taylor and Martin (1928) found that hens receiving an insufficient supply of vitamin D laid eggs with thinner shells than hens receiving an abundance of vitamin D; and Hendricks, Lee, and Godfrey (1931) found that feeding cod-liver oil or administering ultraviolet irradiation to laying hens that did not have access to direct sunlight increased the thickness of the egg shells. Similar observations on the part of other workers are reported by Taylor and Martin.

Herrasti (1916) found that the average breaking pressure of brown-shelled eggs was 154.8 pounds and of white-shelled eggs 112.4 pounds, but it should be noted that he used an apparatus which could not be expected to measure shell-breaking strength accurately. Romanoff (1929) reports that the breaking strength of egg shells was 4,460.00 grams. Morgan (1931) reports that the mean weight to crush the shells of Barred Plymouth Rock eggs was 3,498.50 grams and of White Leghorn eggs 3,787.17 grams. Morgan also found that the higher the percentage of shell of total egg weight the more pressure required to break the shell. The breaking pressure of egg shells is undoubtedly influenced by the kind of diet fed the hens and may also differ according to the breed, since Taylor and Martin (1928) found that Barred Plymouth Rocks and White Leghorns laid eggs differing significantly in shell percentage, the White Leghorn eggs having a slightly higher percentage of shell.

Calcareous salts are deposited in the uterus to form the shell, and, according to Giersberg (1923), the pigment and cuticle, or bloom, are also completed in the uterus. Substances for the formation of pigment and cuticle are liberated in the albumen-secreting portion of the oviduct and pass down the oviduct with the egg; in the uterus the pigment becomes embedded in the shell and the cuticle settles as a film on the outside of the shell. Asmundson (1931*a*) found, however, that the isthmus influences the pigmentation of the shell.

The extensive observations of Tarchanoff (1884), Weidenfeld (1897), Pearl and Surface (1909*a*), and Pearl and Curtis (1914) are in agreement in showing that the stimulus which activates the shell-secreting glands in the uterus is mechanical in nature.

The Completed Egg.—According to Asmundson (1931*a*), the vagina takes no part in the formation of the egg. At the time of laying, the egg is of very complex structure, the yolk being composed of concentric layers of white and yellow yolk and containing the blastoderm or germinal disc, the vitelline membrane surrounding the yolk, and albumen consisting of four kinds or parts—the chalazae and a thin layer of dense albumen surrounding the yolk, a thin layer of fluid albumen, then a thick layer of dense albumen, and then an outside layer of fluid albumen—the inner and outer shell membranes, and finally the shell with its pigment and cuticle. All these parts, except the inner thin layer of albumen, are shown in Fig. 8.

The egg is essentially a reproductive cell, and its complex structure serves to ensure that the embryo chick as it develops within the egg is given every possible protection as well as being provided with food. The egg may be regarded as a complete entity, and as Needham (1925) so well points out it is a "closed" system.

Hormones and Egg Formation.—Experiments have been conducted with various specific substances to determine their effect on the physiology of egg production. Ductless or endocrine glands and extracts from them have been used, the specific substance in each case being a hormone, which, in many cases, is known to have a considerable influence on avian physiology.

Pearl and Surface (1914*b*) found that ovulation ceased when large doses of the extract of corpus luteum were injected intra-peritoneally, but that smaller doses showed little effect. The resting ovaries of molting hens were not activated by extracts of the anterior lobe of the pituitary in experiments conducted by Pearl and Surface (1915) and Pearl (1916). Fresh anterior hypophysial substance injected intraperitoneally by Walker (1925) inhibited ovulation. Riddle (1924) claimed that a deficiency of thymus results in soft-shelled eggs being laid, but Ackert and Morris (1929) removed the thymus from young pullets and observed no effect on the shells of eggs subsequently laid. Asmundson (1931*b*) injected as much as 2.25 cubic centimeters of an aqueous solution of follicular hormone into a Leghorn pullet with apparently no effect on either the number or weight of eggs subsequently laid.

Several investigators have fed thyroid in different forms, the results on feather development having been discussed in Chapter II, and for the most part the results on egg formation and egg production have been negative. Asmundson (1931*b*) fed small amounts of desiccated thyroid to Leghorn pullets and found that the size of eggs was apparently reduced or the eggs did not increase in weight as would be expected normally. It was found that the size of the yolk was affected more than the albumen and the shell.

EXTERNAL FACTORS AFFECTING EGG PRODUCTION

The production of 300 or more eggs by the modern domestic fowl is something quite different from the production of some 12 to 30 eggs by the wild ancestor. Egg production sufficient for the reproduction of the species in the wild fowl has been developed in the domestic fowl into egg production primarily for the purpose of supplying mankind with a highly important article of diet.

Whether or not the wild fowl would lay many eggs under modern methods of poultry keeping has apparently never been determined, but it is apparent that the onset of broodiness which naturally occurs after about 12 to 30 eggs have been laid is a factor determining the limited production. That the onset of broodiness may be retarded in wild birds is indicated from three citations by Pearl (1912*a*). Although the wild Mallard duck normally lays from 12 to 18 eggs, Austin (1908) observed that it will lay as many as from 80 to 100 eggs if each egg is removed from the nest daily and the duck is confined in a pen at night. Hanke (1908) by removing an egg daily from the common wryneck's nest secured 48 eggs, and Wenzel (1908), using the same method with the house sparrow, secured 51 eggs. Undoubtedly the progenitor of the domestic fowl would lay more eggs except for the onset of broodiness, especially if food were more abundant and there were no chicks to rear.

The Influence of Climate.—The natural breeding season of wild birds, including the progenitor of the domestic fowl, is in the spring of the year, but it is interesting to note that in the northern and southern hemispheres the seasons are reversed, so that in the northern hemisphere maximum egg production occurs from about March to June whereas in the southern hemisphere it occurs from July or August to October or November.

Rice, Hall, and Marble (1930), from data supplied by Good (1924) and Huttar (1928), state that the optimum temperature for maximum egg production is apparently about 50 to 60 degrees Fahrenheit in northern parts of the United States and about 60 to 70 in southern parts of the United States, and that there is a close relationship between the temperature on a particular day and egg production 3 or 4 days later.

Weather conditions have an influence on egg production, especially if the temperature fluctuates greatly in a short period of time, as Musson (1913), Card (1917), and Graham (1930) have shown. Good egg production is possible during either very cold or very warm weather, providing there are no sudden changes, this fact being borne out by the egg records obtained in such widely separated parts of the globe as Japan, Mexico, Australia, Northern Canada, South Africa, and the Philippine Islands. As a matter of fact, the remarkable adaptability of the domestic fowl to a wide variety of climatic and other environmental conditions is one of the principal reasons for the universal extent to which poultry raising is carried on.

Housing Conditions Influence Egg Production.—Conditions may vary from practically no house to a tightly built, well-protected, heated house. Heywang and Jull (1930) have shown, for instance, that, in certain parts of southwestern United States, good egg production is possible where the laying hens are allowed to roost outdoors. On the other hand, in many parts of the United States and in various other countries the houses must be built to provide as far as possible against sudden changes in temperature. Good ventilation is imperative; open-front houses are preferable in order to admit as much sunlight as possible, and the houses should be of sufficient depth to avoid drafts. In certain sections the heating of the houses during cold weather has proved to be profitable, since a small amount of heat tends to check the serious effect of a decided drop in temperature outside.

One very important management factor involving housing which affects the average number of eggs produced per bird, even when the birds are of the same breeding, is the size of the flock. The larger the flock the lower the average egg production per bird, where the different flocks are of the same breeding. This explains to some extent why poultrymen with flocks of from fifty birds up to several hundred could not expect to secure such good results as are secured in numerous egg-laying contests with ten birds per flock or in single-bird contests, such as have been conducted in Australia.

The Kind and Amount of Feed Influence Egg Production.—It is well recognized by poultrymen everywhere that maximum egg production is not possible unless the hens are fed liberal amounts of a well-balanced ration. A deficient diet prevents a bird from laying the number of eggs she is potentially capable of producing.

Heavy laying requires relatively large amounts of feed, but in latitudes very far north and south of the equator the amount of daylight during the winter months is relatively short, so that egg production may be retarded through an insufficient intake of feed. This may be overcome by the use of artificial lights so that the birds have about twelve hours in which to feed.

In this discussion on the influence of the kind and amount of feed on egg production, the important point to be brought out is that, in studies on the inheritance of egg production, the kind of rations fed and methods of feeding from year to year should be as uniform as possible. It should be borne in mind, however, that good feeding will not make up for poor breeding.

Time of Hatching Influences Egg Production.—In order to be able to compare the egg records of dams and daughters or of sisters they should be hatched at relatively the same time each year because time of hatch influences egg production.

Goodale (1918*a*) has shown that Rhode Island Red pullets hatched at the Massachusetts Agricultural Experiment Station in March gave an average winter production of 42.65 eggs per bird, those hatched in April 35.40, and those hatched in May 22.50 eggs per bird. Card (1917) concluded that, in Connecticut, Leghorns should be hatched during late April or early May. Vickers and Cray (1925) report that in 150 farm flocks in Ohio the pullets which were hatched before the first of May laid an average of 152.9 eggs each, and those which were hatched after the first of May laid an average of 143.4 eggs each in their first year of production. Upp and Thompson (1927) show that, in Oklahoma, pullets hatched not later than the first week in April lay much better during the first year of production than those hatched after the first week in April. Berry and Walker (1927) found that pullets hatched in April in New Mexico laid better than those hatched either in March or May or any other month of the year.

Knox (1932), in Iowa, studied the relationship between date of hatch and annual egg production in White Leghorns which were hatched from February 8 to June 8 inclusive and found the best egg production was obtained from the birds which were hatched from the latter part of March to the latter part of May.

At the same time, there are some commercial poultrymen who hatch their chicks during December and January in order that their pullets may commence laying early enough to enable them to take advantage of the relatively high egg prices that usually prevail during the late summer and early fall.

Parasites and Disease Influence Egg Production.—External parasites, such as lice and mites, tend to reduce egg production especially if they become numerous. Internal parasites, such as roundworms, tapeworms, and cæcum worms, have the same effect. Disease in general tends to reduce financial returns in one of two ways, by decreasing egg production until the birds are completely recovered, or by death.

Thompson (1913) says, "It would appear that ovarian trouble must be considered as almost a necessary concomitant to high egg production." From data on the frequency of tumors, about one-half of which were associated with the ovary and oviduct, in birds at the Harper Adams egg-laying trials in England, in birds at the Storrs egg-laying contest in the United States, and in a farm flock in Massachusetts in the United States, Schneider (1926) points out that the higher the mortality from all causes the higher the mortality from tumors. An increase in the frequency of tumors was noted in the second half over the first half of the pullet year, and the data indicate that heavy antecedent egg production is associated with a rise in tumor rate.

Disturbances Influence Egg Production.—Just as sudden changes in temperature frequently cause a decrease in egg production, so may disturbances to the flock result in decreased production. Disturbances may be of the nature of bodily injury, fright, or moving the birds from one place to another. The manner in which the development of ova is affected by such disturbances has never been clearly determined.

Some very interesting observations have been made, however, on the direct effect of injury to the ovary. Pearl and Schoppe (1921) observed that, when part of the ovary was removed by an operation, "The total number of oocytes (ova) developing to a visible size in the lifetime of a bird is caused to increase from 33 to 68 per cent over the number which develop in the normal unoperated bird." Steggerda (1928) found that by injuring or partially removing the ovary certain birds were apparently stimulated to lay more eggs than control birds which were not operated upon. In later experiments involving the removal of the membrane over the ovary and withdrawing 10 cubic centimeters of blood from the wing every two weeks for a period of twelve weeks, Steggerda (1929-1930) observed no significant change in egg production as compared with control birds. When a portion of the ovary in six-week-old pullets was removed, it was found by Steggerda (1931) that they commenced laying on the average four days earlier than control pullets not operated upon. The number of birds tested by Steggerda was quite small so that no definite conclusions can be drawn. Moreover, Hutt and Grussendorf (1932) secured results contrary to those of Steggerda.

Stieve (1918) has shown that birds accustomed to range, upon being confined, stop laying as the result of a cessation of ovulation. That the functioning of the oviduct as well as the ovary may be affected when laying birds are unduly disturbed is indicated by the results of an experiment conducted by Warren (1930). An interesting observation noted by Warren was that laying activity was more affected among the birds that laid on the day of the disturbance. These observations on the effect of disturbances to the laying stock suggest that studies on the inheritance of egg production require that birds be disturbed as little as possible and that conditions of management be kept as uniform as possible from year to year.

ANNUAL PRODUCTION RECORDS SERVE AS BASIS OF INHERITANCE STUDIES

It has been pointed out in the preceding sections of this chapter that numerous complex physiological processes are involved in the formation of the egg and that numerous internal and external factors influence the number of eggs that a hen is potentially capable of laying. It is perfectly clear, therefore, that an analysis of the inheritance of laying ability presents an extremely complex problem.

Studies on the inheritance of egg production must take into consideration such factors as rate of ovulation and albumen secretion as they may be influenced by internal and external parasites, disease, and general methods of flock management from year to year. To whatever extent environmental conditions under which the flock is kept are variable from year to year the problem of determining the nature of the inheritance of egg production becomes all the more difficult. In spite of these seemingly insurmountable difficulties considerable progress has been made, nevertheless, and the discussion in the following pages brings together what is known to date concerning the inheritance of egg-laying ability.

Ways of Measuring Egg Production.—A bird usually lays an egg a day for a few or a large number of days in succession and then misses one or more days, the number of eggs laid on consecutive days being called a "clutch." That the number of eggs laid in each clutch is a definite characteristic of each hen has been determined by Goodale (1918*a*), Hays and Sanborn (1927*a*), and Atwood (1929). The observations of Atwood are particularly interesting inasmuch as he has shown that egg production follows a definite rhythm, the interval in hours between the laying of eggs on consecutive days depending upon the size of the clutch, although Atwood uses the term "cycle" in discussing his data. The data in Table 12 show that the larger the clutch the shorter the interval between layings.

TABLE 12. MEAN INTERVAL IN HOURS BETWEEN LAYINGS ACCORDING TO SIZE OF CLUTCH IN FIRST-YEAR PRODUCTION OF 172 WHITE LEGHORNS

(Data of Atwood, 1929)

Number of Eggs per Clutch	Number of Clutches	Number of Birds	Mean Interval in Hours Between Layings
2	485	139	28.03 ± 0.03
3	355	137	26.84 ± 0.02
4	138	82	25.93 ± 0.04
5	46	36	25.48 ± 0.07
6	21	17	25.21 ± 0.25
7	6	6	25.08 ± 0.29
8	4	3	24.57 ± 0.21
9	1	1	24.75 ± 0.73
10	3	3	24.41 ± 0.11
11	2	2	24.70 ± 0.30
26	1	1	24.16 ± 0.08

Atwood found that the correlation between mean interval length in hours between layings within clutches during August and first-year egg production was —0.41±0.04, indicating that the shorter the interval between layings the greater the annual production.

A short period of egg production, which may include several clutches, followed by a non-productive period has been termed a "litter" by Curtis (1914*a*) and others.

A "cycle" of egg production has been defined by Goodale (1918*a*) as a period of production alternating with a period either of decreased production or cessation of production, although during recent years cycles of production have been considered from the seasonal standpoint, as, for instance, winter, spring, summer, and fall cycles. It should be observed at this time, however, that these so-called cycles of production are purely arbitrary designations and may have no particular significance for the problem of the inheritance of egg production.

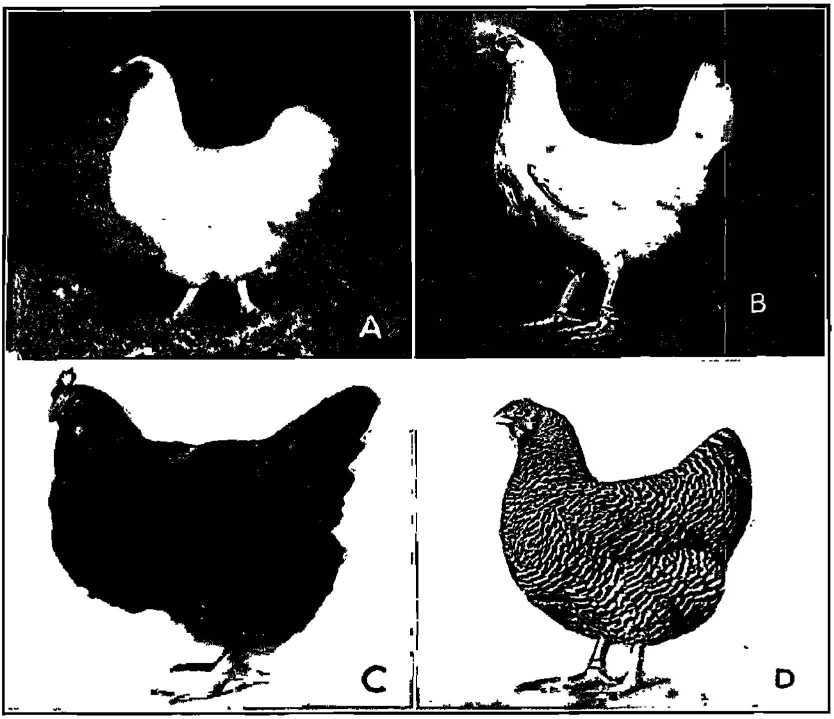

FIG. 40.—Records of 300 eggs or more in one year have become of fairly common occurrence during recent years. A, White Wyandotte that laid 305 eggs in a Storrs international egg-laying contest. (Photo by Storrs Agr. College.) B, White Leghorn that laid 351 eggs, 223 of them consecutively, in a Canadian egg-laying contest. (Photo by Univ. of British Columbia.) C, Black Orpington that laid 354 eggs in an Australian egg-laying contest. (Photo by P. Rumball.) D, Barred Plymouth Rock that laid 358 eggs at the University of Saskatchewan, Canada. (Photo by Univ. of Sask.)

The most common way of measuring egg production has been the number of eggs produced in one year.

First-year Production.—The basis of determining the egg-laying ability of a bird has been the number of eggs laid during her first year of production. Frequently the first-year production has included the number of eggs laid from the first of November to the last of October;

again, first-year production has included the number of eggs laid from the day of laying the first egg to 364 days thereafter. Both these methods of determining first-year egg production are somewhat arbitrary, the first being more arbitrary than the second.

It is true, of course, that birds entered in egg-laying contests must of necessity have an arbitrary time limit set for the beginning and end of the so-called year's production for the simple reason that the contests must start and end on certain dates. On the other hand, a much sounder basis for determining first-year production, especially from the biological standpoint, is from the day of laying the first egg. It is possible, also from the biological standpoint, that the end of the first-year production should terminate when laying ceases just prior to the first annual molt. In studies on the inheritance of egg production, however, the usual method of determining first-year production has been from the day of laying the first egg to 364 days thereafter.

Some High Records.—Only a few of the highest official trapnest records, by which is meant records obtained under the supervision of some official agency such as an agricultural college, experiment station, or government institution, are given here. They are taken from the "American Poultry Record," by Robinson and Althouse (1930) and appear in Table 13 together with two other high official records made after the publication of the "American Poultry Record."

TABLE 13. SOME OF THE HIGHEST OFFICIAL FIRST-YEAR EGG PRODUCTION RECORDS MADE IN RECENT YEARS

(Data by "American Poultry Record," 1930, and the author)

Eggs Laid	Year	Variety	Country
361	1929–1930	Black Orpington	New Zealand
358	1928–1929	Barred Plymouth Rock	Canada
357	1929–1930	White Leghorn	United States
354	1926–1927	Black Orpington	Australia
353	1928–1929	Black Orpington	New Zealand
351	1925–1926	White Leghorn	Canada
345	1929–1930	Rhode Island Red	United States

The records in Table 13 are given merely with the idea of showing what has been accomplished in securing unusually high first-year records. That such high records should be the aim of any breeder is not suggested since there are several other things that should be taken into consideration besides number of eggs produced.

From the reports of egg-laying contests during the past twenty-five years it would appear that high egg production is possible with almost any breed or variety. It should be observed that the practical poultryman is primarily interested in a good flock average rather than in high individual records of only a few birds in his entire flock. Through the use of trap nests at the various egg-laying contests it has been established most clearly that great variation in ability to lay exists not only among birds of the same variety but also among birds of the same strain. Since some birds in the laying contests were shown to have laid poorly while others laid well, poultrymen became convinced that the laying qualities of their flocks could best be improved by selecting each year as breeders those hens which had laid best the previous year. Trap-nesting, therefore, served a very useful purpose.

Four Assumed Cycles.—In a number of cases in the early studies on the inheritance of egg production it was customary to divide first-year egg production into four rather arbitrary periods, winter, spring, summer, and fall. Eggs laid during these periods were called "cycles of production." The interesting observations of Pearl (1911, 1912, 1914, 1915*a*, 1915*b*) and Pearl and Surface (1909*a*, 1909*b*, 1911) in their extensive analyses of egg-production records in Barred Plymouth Rocks at the Maine Experiment Station were largely responsible for the adoption of so-called "winter cycle" as a criterion of inherent laying capacity among birds. Prior to the time of their investigations it was rather unusual for birds in the United States to lay many eggs during the winter months, and since they found that the best winter layers were usually the best annual layers also, they concluded that the winter cycle of production, from the first of November to the last of February, was of considerable significance in determining the inherent laying capacity of a bird.

However, after a comprehensive study of records of production in White Leghorns at the Utah Experiment Station, reported by Ball, Turpin, and Alder (1914) and by Ball, Alder, and Egbert (1916), Ball and Alder (1917) were led to believe that the winter cycle does not represent correctly a biological entity. They also state that a record of production of three years is a safer guide than the record for the pullet year only in determining the inherent laying ability of a bird. Goodale (1918*a*) found no evidence of the existence of a winter cycle among Rhode Island Reds at the Massachusetts Experiment Station. Brody (1921), from an analysis of the first year of production of 4,210 Barred Plymouth Rocks at the Maine Agricultural Experiment Station and 1,000 White Leghorns in the Storrs egg-laying contests, found that the production of eggs is of the same general order as the growth of organisms, with no indication of the existence of cycles, as shown in Fig. 41. Harris and Lewis (1922*a*), from an analysis of records of production in White Leghorns, conclude that "there is no evidence of special factors which distinguish the 'winter cycle' from any other period of the year." Then, again, Dunn (1924*a*, 1924*b*, 1924*c*, and 1927) found no evidence of definite cycles of production in Plymouth Rocks, Rhode Island Reds, Wyandottes, and White Leghorns entered in the Storrs egg-laying contest over a period of nine years.

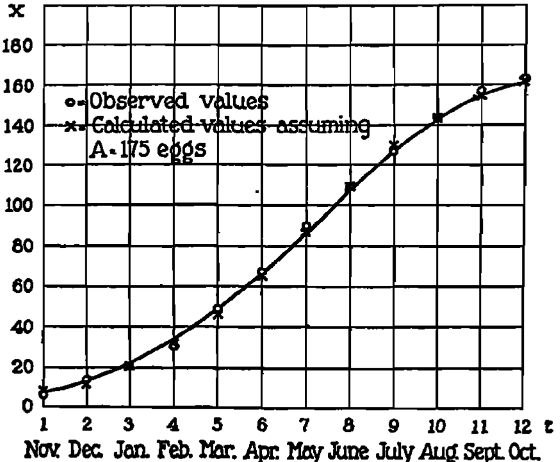

FIG. 41.—Curve showing the average number of eggs laid by White Leghorns at the seventh Storrs international egg-laying contest. Ordinates represent the number of eggs laid (x) for the time (t); abscissæ represent the time (t) from November 1, the beginning of the observation to any time of the year. (After Brody, 1921.)

Harris and Lewis (1922*b*), in analyzing the first- and second-year records of production of 443 White Leghorns, found no evidence of special factors which distinguish the winter cycle of production from that of any other period of the year. Moreover, Harris, Kirkpatrick, Blakeslee, Warner and Card (1921), from an analysis of the first-year production records of 1,840 Storrs contest White Leghorns, and Harris, Kirkpatrick, and Blakeslee (1921), from first-year records of 415 Storrs contest White Leghorns, as well as Harris and Goodale (1922), from 1,658 first-year records made by Rhode Island Reds at the Massachusetts Experiment Station, have shown that the annual egg records of a series of birds may be predicted with a reasonable degree of accuracy when their production for a single month is known. They have also shown that a somewhat higher accuracy of prediction is possible when the production of two or more months is taken into consideration.

Other evidence tending to show that there are no "cycles" of egg production is supplied by the observations of Voitellier (1930) and Dudley (1930-1931). From an analysis of egg-production records of birds entered in the French national laying competition at Versailles it was found by Voitellier that the annual production of a bird could be predicted quite accurately on any one of the following three methods of recording the layings of each bird:

1. One day each week.
2. Two consecutive days each week.
3. One week in every four weeks.

Of the three methods, the records taken one week each month gave the most accurate information concerning annual production, and the records taken on two consecutive days each week gave slightly more accurate results than the records taken on one day each week. The results which Voitellier secured indicate that egg production throughout the year follows a methodical rate and is not of a cyclic type.

Dudley analyzed the records of production of 198 White Leghorns which had completed 12 lunar months in an experiment at the English National Institute of Poultry Husbandry, 245 White Leghorns and 305 White Wyandottes entered in the Harper Adams egg-laying trials, which lasted 48 weeks, and found that the production records of one day each week or of four consecutive days in the middle of each lunar month served as a reliable index of annual production. Dudley's observations also indicate that egg production throughout the year is of a methodical rate.

Decline in Annual Production.—Brody, Henderson, and Kempster (1923) have shown that each year's egg production is 88 per cent of the preceding year's production. (See Fig. 42.) In other words, a first-year production of 200 eggs would be followed by a second-year production of 176 eggs, and a first-year production of 100 eggs would be followed by a second-year production of 88 eggs.

Hall and Marble (1931) have submitted data on the relationship between egg production in the first year and that of the second and later years in a large group of White Leghorns, records for three years being obtained from 1867 birds and from fewer birds each successive

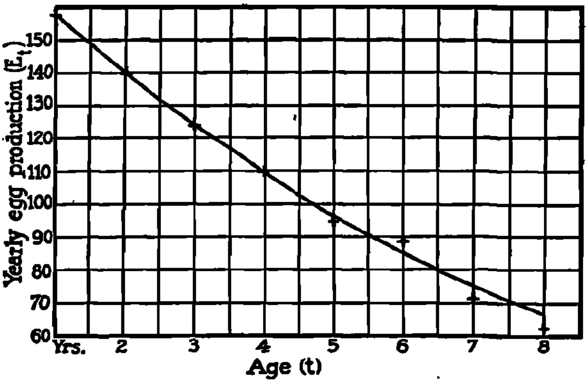

FIG. 42.—The decline in egg production with age in the domestic fowl. The smooth line represents the computed values; the crosses represent the observed values. The values for the seventh and eighth years are not reliable due to the small number of individuals represented in the averages. (After Brody, Henderson, and Kempster, 1923.)

year up to and including the eleventh year. The data are given in Table 14.

TABLE 14. ANNUAL EGG PRODUCTION IN SUCCESSIVE YEARS IN WHITE LEGHORNS AS A PERCENTAGE OF THE PRECEDING ANNUAL PRODUCTION

(Data of Hall and Marble, 1931)

Year	Number of Birds	Mean Egg Production per Bird	Per Cent of First-year Production	Per Cent of Preceding Year's Production
1	1867	168.85	—	—
2	1867	145.85	86.37	86.37
3	1867	124.42	76.68	85.30
4	957	108.79	64.42	87.43
5	450	95.49	56.55	87.77
6	232	86.14	51.01	90.00
7	152	65.55	38.82	76.09
8	80	67.07	39.72	102.31
9	48	50.77	30.06	75.69
10	23	41.04	24.30	80.83
11	5	46.32	27.48	113.06

The data in Table 14 show that, in the same group of birds under observation for three years in succession, the second-year production was 86.37 per cent of the first-year production and the third-year production was 85.30 per cent of the second-year production. These results are in close agreement with that secured by Brody, Henderson, and Kempster (1923).

On the other hand, Jull (1928) and Hall and Marble (1931) have shown that in Plymouth Rocks, Rhode Island Reds, and Wyandottes, egg production in the second year declines to a greater extent than in the White Leghorns of Hall and Marble. It has been shown quite definitely that the higher the first-year production the greater the relative decline in second-year production.

The fact that in such varieties as Plymouth Rocks, Rhode Island Reds, and Wyandottes, second-year egg production as compared with first-year production declines to a greater extent than in White Leghorns is made apparent from data submitted by Hall and Marble, as shown in Tables 14 and 15.

TABLE 15. ANNUAL EGG PRODUCTION IN SUCCESSIVE YEARS IN BARRED PLYMOUTH ROCKS, RHODE ISLAND REDS, AND WYANDOTTES AS A PERCENTAGE OF THE PRECEDING ANNUAL PRODUCTION

(Data of Hall and Marble, 1931)

Year	Number of Birds	Mean Egg Production per Bird	Per Cent of First-year Production	Per Cent of Preceding Year's Production
1	372	191.60	—	—
2	372	137.91	71.97	71.97
3	132	109.72	57.27	79.56
4	42	91.36	47.68	83.27
5	14	84.86	44.29	92.89
6	7	63.57	33.18	74.91

That there is a sensible relationship between second-year egg production and first-year egg production has been demonstrated by a number of workers, although the statements of Gowell (1903), Pearl and Surface (1909*b*), Ball, Turpin, and Alder (1914), and Ball, Alder, and Egbert (1916) were not in accord with this view. Nixon (1912) and Harris and Lewis (1922*b*, 1922*c*, 1923) show quite conclusively, however, that the best first-year layers were inclined to be the best second-year layers. In fact, Harris and Lewis concluded that those birds which are most persistent in laying at the close of the first year are inclined to be the first in the resumption of laying in their second year.

To whatever extent the ability to lay well over a period of years can be developed in a flock by selection and breeding, to that extent the cost of reproducing the flock annually will be reduced. The inheritance of the ability to lay well over a period of years is of immense practical importance and is deserving of much more consideration than it has received up to the present.

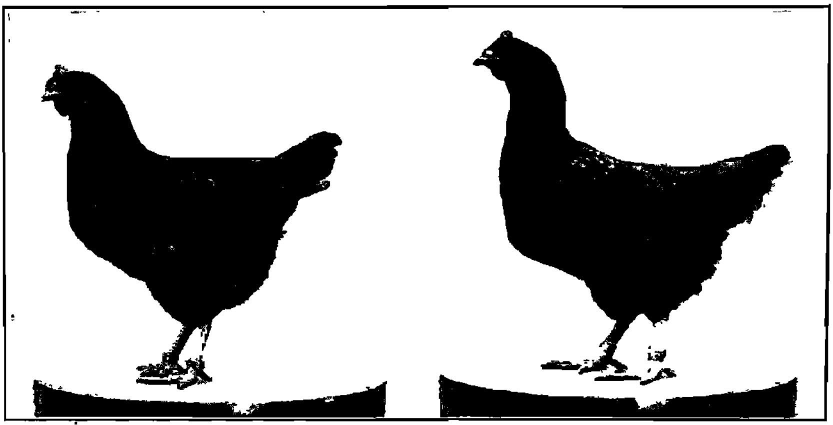

FIG. 43.—Good egg production for several years is eminently desirable. The Rhode Island Red at the left laid 213, 206, and 203 eggs during her first, second, and third year, respectively. The Rhode Island Red at the right laid 260 and 207 during her first and second year, respectively. (Photo by U. S. D. A.)

THEORIES OF MENDELIAN INHERITANCE OF EGG-LAYING CHARACTERS

The fact that egg-laying characters are inherited has been amply demonstrated by the results of investigational work and by the results which poultry breeders in all parts of the world have secured during the past quarter century. If it were not for the fact that egg-laying characters are inherited it would hardly have been possible for practical breeders to develop flocks laying an average of 200 eggs or more per bird. When one realizes the vast difference in the average number of eggs laid by the wild fowl and the average production per bird of many modern flocks, the significance of the inheritance of egg-laying characters is fully appreciated.

Apparently the first piece of work attempted at a state institution to develop an egg-laying strain through the selection of female breeders based on trap-nest records was that of the Maine Agricultural Experiment Station with Barred Plymouth Rocks. The records of Gowell (1902, 1903) show that over a period of nine years the practice of selecting female breeders according to their first-year trap-nest records failed to produce an increase in the average egg production per bird of the flock each succeeding year. The results secured were very disappointing at the time, for they seemed to demonstrate the apparent futility of improving egg production by selecting as breeders the best layers of the previous year.

The work of Gowell, however, laid the foundations for later work which was to demonstrate the value of the progeny test in breeding for increased egg production. Furthermore, the results which Gowell secured paved the way for the development of the three theories of the Mendelian inheritance of egg production which have been advanced. Continuing the breeding work with the Barred Plymouth Rocks at the Maine Agricultural Experiment Station, Pearl developed the theory of the sex-linked inheritance of so-called "winter egg production." Shortly thereafter, Goodale, working with Rhode Island Reds at the Massachusetts Agricultural Experiment Station, developed a different theory to account for the manner in which egg-laying characters are inherited. The Goodale theory was advanced further by Hays, who continued with the same flock of Rhode Island Reds. Shortly after Goodale's earlier publications dealing with the inheritance of egg production, Hurst developed his theory based on the results he reported to have secured in White Leghorns and White Wyandottes.

The three theories of the Mendelian inheritance of egg-laying characters differ in several details, although they are in agreement in pointing out that egg-laying characters are complex and that the selection of breeding stock based on the progeny test is the only way in which progress may be achieved in the development of high egg-laying strains. In the space available in this chapter, only the essential features of each of the three theories can be given.

The Pearl Theory.—It has already been observed that Gowell failed to increase egg production in the flock of Barred Plymouth Rocks at the Maine station by the continued use of the highest producing dams. A different method of selecting the breeding stock in the same flock enabled Pearl to improve egg production to a considerable extent. An extensive series of papers by Pearl (1909*b*, 1911, 1912*a*, 1912*b*, 1914, 1915*a*, 1915*b*) deal with the results he secured in numerous matings of Barred Plymouth Rocks and in crossbred matings of Barred Plymouth Rocks × Dark Cornish, the latter variety being regarded by Pearl as lacking the gene necessary for a winter production record of 30 or more eggs. It will be recalled it was stated in Chapters II and IV that the barring of the Barred Plymouth Rock is sex-linked, the female transmitting barring to her sons only. The Dark Cornish is, of course, a nonbarred variety, and the results secured from reciprocal crosses between Barred Plymouth Rocks and Dark Cornish led Pearl to conclude that high fecundity is sex-linked.

Using the so-called winter cycle, to March first, of the pullet year, as a basis for the analysis of records of production in Barred Plymouth Rocks, Pearl proposed a theory to explain the inheritance of winter production. The theory rested upon a sex-linked basis, two pairs of genes being involved, L_1 and l_1 being the dominant and recessive genes, respectively, of the pair located in one of the autosomes, and L_2 and l_2 being the dominant and recessive genes, respectively, of the pair located in the sex chromosome. Pearl postulated that if a bird carried L_1 but not L_2, it would lay slightly less than 30 eggs up to March first, whereas if a bird carried L_2 but not L_1, it would also lay less than 30 eggs up to March first, but that if a bird carried both L_1 and L_2 it would lay more than 30 eggs up to March first. Since L_2 is sex linked, it is apparent that dams could transmit it only to their sons, or as Pearl says, "high fecundity is not inherited by daughters from their dam."

It is not surprising that such an interesting theory of the Mendelian inheritance of winter egg production should stimulate further inquiry along similar lines, particularly since Pearl believed that his results applied to annual production as well as winter production. Goodale (1916, 1918*a*, 1918*b*, 1919), Goodale and MacMullen (1919), and Goodale and Sanborn (1922) in an analysis of the records of production in Rhode Island Reds at the Massachusetts station observed that Pearl's theory of the inheritance of fecundity is inadequate.

Moreover, in crosses involving the sex-linked genes for silver and barring, Punnett (1930) secured results that indicate rather definitely that egg production is not sex linked in its inheritance. Punnett mated an Indian Game male from a strain showing low fecundity to a White Wyandotte female that laid 240 eggs in her first laying year and came from a strain showing high fecundity. The F_1 males were all silver-barred, indicating that the White Wyandotte female carried both silver and barring. An F_1 male was mated to Silkie females, showing low fecundity.

The results secured indicate the absence of sex linkage in the inheritance of egg production. The mean egg production per bird of the 21 barred females was 123.7 eggs; for the 18 nonbarred females it was 118.1 eggs; for the 28 silver females it was 113.0 eggs; for the 11 gold females it was 142.1 eggs. The number of birds in each of the four groups is rather small, but the results, taken together with other results secured by Punnett, certainly do not support the theory of the inheritance of egg production on a sex-linked basis.

A Light Sussex female that laid 200 eggs in her first year of laying was mated with the same Indian Game male which Punnett mated with the White Wyandotte female mentioned previously. The Light Sussex carries the sex-linked gene for silver, the female, of course, being heterozygous. The F_1 males carry silver, and one of them was mated to Silkie females.

The results obtained show that the gold females laid somewhat better than the silver females, exactly opposite to expectation on the assumption of sex linkage for egg production.

Punnett made still another mating to test the theory of the sex-linked inheritance of egg production. A Black Sumatra male was mated with a Barred Plymouth Rock female. An F_1 male, being heterozygous for barring, was mated to Silkie females. The progeny consisted of 20 barred females, having a mean egg production per bird of 80 eggs, and 20 nonbarred females, having a mean egg production per bird of 84 eggs. These results make it clear that the sex-linked gene for barring is not associated with the egg-laying character.

It may be said, therefore, from the critical evidence available, that the Pearl theory of the sex-linked inheritance of egg production is apparently untenable.

The Hurst Theory.—Although the Hurst theory of the inheritance of egg production was advanced after Goodale had put forth his theory, Hurst's theory is discussed first because it can be disposed of quite readily and, moreover, the observations made by Goodale have been added to from time to time up to the present by Hays.

Hurst (1921) apparently followed Goodale in regarding the annual egg production of a bird as being made up of several different characteristics. Hurst suggested five different heritable characteristics, to each of which he assigned a pair of autosomal genes, that determine the number of eggs that a bird is capable of laying.

i. Early sexual maturity was regarded by Hurst as being dominant to late sexual maturity. ii. Fast rate of winter production was regarded as being dominant to slow rate of winter production. iii. Fast rate of spring production was regarded as being dominant to slow rate of spring production. iv. Fast rate of autumn production was regarded as being recessive to slow rate of autumn production. v. Nonbroodiness was regarded as being recessive to broodiness. Maximum egg production would be possible when a bird contained the series of dominant genes in a homozygous condition and the two pairs of recessive genes in a homozygous condition.(for autumn production & broodiness)

The theory proposed by Hurst is quite interesting, but the evidence he supplied to substantiate his theory is wholly unconvincing to one fully appreciative of the complexities involved in determining the mode of inheritance of a quantitative character that involves various physiological processes.

Moreover, from evidence submitted in previous pages of this chapter, it appears quite certain that hens do not lay in so-called "cycles," as Hurst suggests. The various ratios which Hurst claims he secured are altogether too close to expectation to appear reliable. The observations made demonstrate the facility with which genes can be allocated to various birds in spite of insufficient evidence.

The Goodale-Hays Theory.—The breeding of Rhode Island Reds at the Massachusetts Agricultural Experiment Station over a period of years enabled Goodale to accumulate a mass of data dealing with the inheritance of egg production. In one of his first papers, Goodale (1918*a*) reported that his results did not indicate that egg production was inherited on a sex-linked basis inasmuch as he found quite marked correlation between the egg production of dams and the egg production of their daughters. In another paper (1918*b*) he emphasized the complexity of laying performance as a hereditary character. Goodale and MacMullen (1919) and Goodale and Sanborn (1922) developed the conception that the first-year egg production of a bird is determined by five different characteristics: (1) age in days that laying commences, popularly referred to as sexual maturity; (2) intensity of production, popularly referred to as rate during a given period; (3) the amount of broodiness; (4) a so-called "winter-pause" in production; (5) persistency of production, determined by the length of time that laying continues prior to the first complete annual molt. Goodale was led to believe that the same number of eggs might be produced by birds having different combinations of the five characteristics.

Breeding work with the Massachusetts station flock of Rhode Island Reds was continued by Hays, who has confirmed, for the most part, the observations of Goodale and has extended them into the most complete theory of the Mendelian inheritance of egg production that has yet been suggested.

In order that the reader may have a clear understanding of the theory developed by Hays and his co-workers, the complete theory is given here in comprehensive form, a discussion of various of its details being reserved for subsequent pages.

✓ *Genes for Earliness of Sexual Maturity.*—Hays (1924-1925) has suggested that the inheritance of earliness of sexual maturity, birds commencing to lay when less than 215 days of age, depends upon two pairs of genes, one pair of which is sex linked. The dominant gene of either of the two pairs of genes is capable of inducing earliness of maturity. The sex-linked genes are designated *EE* and the autosomal genes *E'E'*, the recessive genes in each case being *ee* and *e'e'*.

✓ *Genes for Rate of Laying.*—The inheritance of the intensity or rate of laying, rate being determined by the relative number of eggs laid from the time that laying commences to March first, has been reported to be determined by two pairs of autosomal genes designated *RR* and *R'R'*, the recessive allelomorphs being *rr* and *r'r'*. A production of over 50 per cent is attained when the two dominant genes *R* and *R'* are together in the same bird, the two genes being regarded as complementary to each other.

Genes for Broodiness.—The inheritance of broodiness was studied by Goodale, Sanborn, and White (1920), who believed two pairs of complementary genes, *A* and *a* and *C* and *c*, to be involved. Broodiness is due to the presence of both dominant genes *A* and *C*, neither of which is sex linked, according to Hays (1924-1925). Punnett and Bailey (1920) observe that more than one independent dominant gene could produce broodiness but believe that the genes involved are not complementary. Hays, however, has substantiated the views expressed by Goodale *et al.*, and Hays and Sanborn (1926, 1927*a*) point out that the degree of broodiness as well as the presence or absence of broodiness during the pullet year of production must be considered in the breeding program and that there is a somewhat higher winter intensity in broody than in nonbroody individuals. Hays and Sanborn (1927*b*) emphasize the importance of selecting as breeders nonbroody pullets that have a high winter intensity of production.

Gene for Winter Pause.—Long, continuous records of egg production are the exception rather than the rule, even in strains that have been bred for egg production for several years. Broodiness naturally makes a break in the record of production, but independent of this characteristic, Goodale (1918*c*) observed that many of his Rhode Island Reds exhibited a characteristic winter pause which lasted from a few days to as much as two months or more. Hays (1924-1925) found that the flock could be divided into two groups, those which exhibited a pause of one week or more and those which did not, and concluded that the winter pause is inherited and is due to the presence of a dominant autosomal gene *M*, from which it follows that birds showing a nonpause must be of the *mm* type, since the genes are borne in pairs. Hays and Sanborn (1927*b*) found no apparent association between winter pause and intensity.

Genes for Persistency.—Hays and Sanborn (1927*b*) found a very intimate relationship between persistency of production and annual production. High persistency of production is said to exist in birds that lay for 315 or more days prior to their first annual molt. Since persistency of production is so important, it is interesting to note that Hays (1927*b*) has suggested that high persistency is inherited in the ordinary Mendelian manner, the dominant gene *P* giving rise to persistency. Hays also points out that *P* is intimately associated with *E'*, previously described as the dominant non-sex-linked gene for early sexual maturity. It is apparent, therefore, that in order to develop a heavy laying strain, birds homozygous for *P* and for *E'* are necessary.

Genes for Annual Egg Production.—So far as the theories of the inheritance of the numerous characteristics affecting annual egg production, as developed largely by Goodale and Hays, represent a true picture of the problem, it is apparent that eight pairs of genes are involved, the only sex-linked pair being *EE*, for earliness of sexual maturity. They are as follows:

Characteristic	Dominant Pair	Recessive Pair
Early sexual maturity	*EE* S L.	*ee*
	E'E'	*e'e'*
Intensity	*RR*	*rr*
	R'R'	*r'r'*
Broodiness	*AA*	*aa*
	CC	*cc*
Winter pause	*MM*	*mm*
Persistency	*PP*	*pp*

Since the genes are borne in the chromosomes, which are in pairs, one of each pair of paternal and the other of maternal origin, it is obvious that a male homozygous for all eight desirable genes would have the constitution *EE E'E' RR R'R' aaccmmPP* and the best kind of a female would have the constitution *E-E' E' RR R'R' aaccmmPP*, being homozygous for all genes except the sex-linked gene *E*. The production of individuals possessing the combination of genes shown above is realized as a difficult and complicated task for the simple reason that, when eight pairs of genes are involved, the number of possible combinations is very large, with the result that the number of birds necessary to make the proper matings to determine the genetic constitution of any particular individual would be very large indeed.

The fact should be appreciated, of course, that the Goodale-Hays theory of the Mendelian inheritance of the egg-laying characters is an attempt to interpret the results they secured in the breeding of their Rhode Island Reds. In this respect it is unfortunate that more concrete evidence has not been made available dealing with the inheritance of the five different characteristics which their theory recognizes as determining the number of eggs laid during the first laying year. One of the few papers containing ratios reported to have been secured from various matings is that of Hays (1924), but it is unfortunate that the number of progeny secured in most of the matings is quite small.

Since egg production involves physiological characters and is otherwise a very complex problem, it is felt that relatively large numbers of progeny are necessary before definite conclusions are possible. Moreover, when a theory is proposed involving complementary genes, each pair of which is supposed to produce a similar effect, as *EE* and *E'E'* for earliness of maturity, the relative ease with which results can be assumed to correspond to expectation makes large numbers necessary in order to provide an adequate test for the theory advanced. Then again, the proposed theory should be tested from the standpoint of results secured in backcross matings, which apparently have never been made.

It is to be hoped that more extensive matings may be made in the near future in order to test the validity of the Goodale-Hays theory. Regardless of whether or not the theory explains in its entirety the Mendelian inheritance of egg production, the fact should be emphasized that the breeding work with Rhode Island Reds at the Massachusetts Agricultural Experiment Station has been of very great practical value to poultry breeders. The selection and mating of breeding stock has been carried out with a greater certainty of securing desired results, and poultry producers have benefited to the extent of hundreds of thousands of dollars through increased egg production.

THE BASIS FOR IMPROVING EGG PRODUCTION

Theories concerning the Mendelian inheritance of egg production are of little interest to poultrymen unless they can be applied in a practical way in the development of a profitable laying strain. Theories are of value, however, in presenting new points of view as well as in leading to an increase in existing knowledge.

The work of Pearl, Goodale, and Hays, and also that of Dryden (1921), demonstrate that egg production can be increased by suitable methods of selecting and mating the breeding stock. With this in mind the balance of this chapter is devoted to an analysis of egg-production records with the object of identifying the most suitable birds to be used as breeders to improve egg production.

Importance of Early Sexual Maturity.—From the purely practical standpoint it is obvious, of course, that the earlier in life a pullet commences laying the sooner she begins to yield financial returns to her owner. In other words, a pullet that commences to lay early in life costs less to rear up to the revenue-producing stage than a late-maturing pullet. At the same time, the relative size of egg laid by the early-maturing and late-maturing pullet is of economic importance, as pointed out in the next chapter.

A number of investigators have shown that the time of year that a pullet commences laying is important from the standpoint of the total number and value of eggs laid during the first laying year. Kempster (1926) showed that among 1,110 White Leghorns those that commenced laying from October 16 to November 15 produced eggs having a greater value than birds that commenced laying either before or after these dates, but it is unfortunate that Kempster's data are based on the number of eggs laid by the different groups during the calendar year, November 1 to October 31, rather than on the value of eggs laid from the time that laying commenced to 364 days thereafter. Jull (1923) found that among 411 Barred Plymouth Rocks those commencing to lay in October laid more eggs per bird, and the eggs had a greater relative value, than those commencing to lay in September, November, and December.

Maw and Maw (1928) analyzed the egg-production records of 5,324 Barred Plymouth Rocks entered in the Canadian Record of Performance work and found that those birds which commenced to lay in September, October, and November laid approximately 180 eggs each, those that started laying in December approximately 168 eggs each, those in January approximately 154 eggs each, and those in February approximately 135 eggs each.

That it is possible to have birds in some flocks commence laying too early has been clearly demonstrated by the observations of Knox (1930*b*) in the first-year records of 684 Single-Comb White Leghorns. The results which Knox secured show that the birds that commenced laying in October laid the best, and that the birds that commenced laying in September, November, and December laid much better than those that commenced laying in July, August, and January. That birds commencing to lay as early as July or August did not make as good records as birds commencing to lay during the next four months was probably explainable by the fact that the birds that commenced laying during July or August underwent a partial molt during the fall and early winter, thus causing a break in their annual production.

Rice (1915) has shown that, in White Leghorn pullets, there is an important relationship between earliness of sexual maturity and rate and persistency of production. Kempster (1925, 1926, 1927) reports that there is a significant negative correlation between sexual maturity and egg production for the first laying year. In other words, Kempster found that early-maturing pullets tend to make the highest annual records. Similar observations have been made by Ball and Alder (1917), Kennard (1921), Hervey (1923*a*, 1923*b*), Hays and Bennett (1923), Hays, Sanborn, and James (1924), Jull (1923*a*, 1924*b*), Parkhurst (1926), Knox (1927), and Buster (1927). On the other hand, Lippincott, Parker, and Schaumburg (1925), in a group of White Leghorn pullets, found no correlation between earliness of sexual maturity and annual egg production, but it is interesting to note that the White Leghorns whose records were studied were a selected group. Kempster (1926) points out that out of a flock of 120 birds the 60 which were culled at the end of 240 days required 20.05 ± 3.86 days longer to mature than did those which were retained by Lippincott, Parker, and Schaumburg because of their superior ability to produce eggs.

Knox (1930*a*) has shown that the best records in egg production for the 684 White Leghorns mentioned previously were made by those birds that commenced laying between 160 and 210 days of age, as shown in Fig. 44.

Marble and Hall (1931) have shown that selection for twenty years in succession of the best layers for breeding purposes in each year's flock of White Leghorns resulted in an increase of 52.24 eggs per bird in the average of the last three years' production over the average of the first three years' production. The net decrease in age at which laying commenced was 25.81 days per bird between the average of the first three and the last three years. In another group of White Leghorns fifteen years of selection of low producers for breeders resulted in a net increase of 32.58 eggs per bird between the average of the first three years' production and the average of the last three years' production. This increase in egg production was accompanied by a decrease in age at commencement of laying of 9.81 days between the average of the first three and the last three years. Marble and Hall concluded that with each group of White Leghorns approximately 50 per cent of the increase in egg production was due to earlier sexual maturity, the balance of the increase over the period of years being due to better management.

Harris and Lewis (1923*b*) observed that birds that commence to lay early are in general long, persistent layers. Hays and Sanborn (1927*b*) have suggested, however, that "the high yearly producer must be early maturing not because early maturity itself is of importance but because early maturity has some 'association' with high intensity and very intimate 'association' with persistency." It is difficult to understand why earliness of sexual maturity is not of primary importance because the ability to start laying early in life may well be the determining factor that enables a pullet to lay at a relatively fast rate and continue production for a relatively long time.

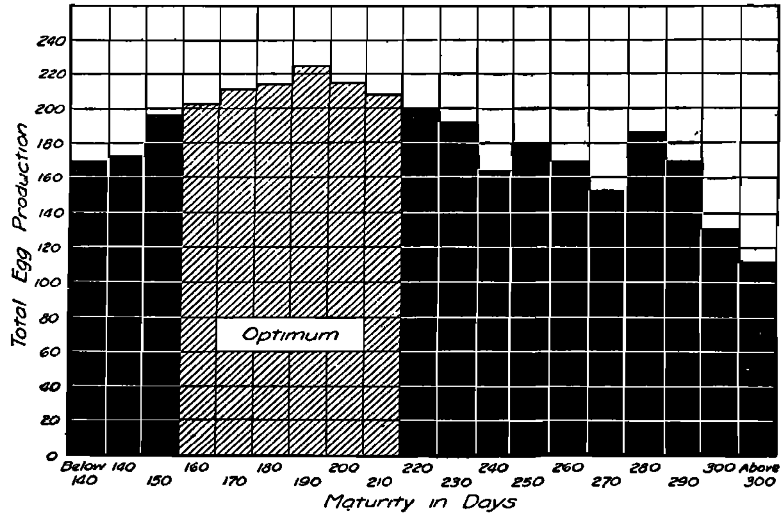

FIG. 44.—The highest annual egg production was secured from birds that commenced laying between approximately 160 and 210 days of age in this flock of 684 White Leghorns. (After Knox, 1927*a*.)

The importance of early sexual maturity in relation to first-year egg production is clearly indicated in the data given in Table 16, pertaining to the 1929 flock of Rhode Island Reds at the Massachusetts Agricultural Experiment Station, the data having been reported by Graham (1932).

The data in Table 16 show that in the 1929 flock of Rhode Island Reds, the best egg-production records were obtained from the birds that commenced laying at approximately 200 days of age. The data also show, however, that the earlier in life that laying commenced the

TABLE 16. THE EARLIER IN LIFE THAT LAYING COMMENCED OR THE SMALLER THE BIRD THE LESS THE MEAN ANNUAL EGG WEIGHT BUT THE GREATER THE MEAN ANNUAL PRODUCTION IN RHODE ISLAND REDS AT THE MASSACHUSETTS EXPERIMENT STATION

(Data of Graham, 1932)

1928 flock of 205 birds

Number of Birds	Mean Age in Days Laying Commenced	Annual Mean Egg Weight in Grams	Body Weight in Pounds	Mean Egg Production per Bird
8	(No data available)	49.5	4.00–4.49	247
50		53.8	4.50–4.99	210
78		54.9	5.00–5.49	208
52		55.7	5.50–5.99	202
12		54.9	6.00–6.49	196
5		58.7	6.50–6.99	184

1929 flock of 163 birds

Number of Birds	Mean Age in Days Laying Commenced	Annual Mean Egg Weight in Grams	Body Weight in Pounds	Mean Egg Production per Bird
27	190	52.3	4.50–4.99	227
55	187	53.4	5.00–5.49	214
39	215	55.4	5.50–5.99	204
27	243	57.2	6.00–6.49	169
10	280	58.2	6.50–6.99	133
5	298	58.8	7.00–7.49	121

lower was the first-year mean egg weight and the smaller was the size of the bird. The significance of these two factors is discussed in the next chapter.

The first-year egg-production records of a group of 1,013 Rhode Island Reds at the U. S. Animal Husbandry Experiment Farm, Beltsville, Maryland, have been analyzed from the standpoint of the relationship between various characteristics and the total annual production. The annual record included, for each bird, the number of eggs laid from the first egg to 364 days thereafter. No selection was made of the birds and no birds were removed except by death, which amounted to 9.18 per cent of the entire group. The mean first-year egg production was 192.03 eggs.

The data in Table 17 are arranged to bring out the relationship between age at which laying commenced and annual production, age at which laying commenced being classified on the basis of 10-day intervals, beginning with the period of 150 to 159 days and ending with the period of 230 to 239 days. Thus the table includes only the classes having 20 or more birds in each class according to age at commencement of laying, the total number of birds represented being 915. The table also contains data on the fall-winter rate of egg-production and on pauses in production, two factors that are discussed later.

Table 17. Fall-Winter Rate of Production, Pauses in Production, and First-Year Egg Production in Relation to Age in Days That Laying Commenced, in 915 Rhode Island Reds at the U. S. Animal Husbandry Experiment Farm, Beltsville, Md.

Number of Birds	Mean Age in Days Laying Commenced	Mean Fall-Winter Rate of Egg Production	Mean Number Days in Pauses	Mean Egg Production per Bird
34	155.2	56.94	22.12	203.81
71	164.4	57.14	20.96	210.17
94	174.6	56.33	24.80	206.79
148	184.7	57.06	22.61	202.95
201	194.4	51.31	30.14	188.41
140	204.4	56.62	20.98	195.73
119	214.1	59.30	17.27	190.72
71	224.1	55.64	18.20	177.84
37	234.0	57.72	13.33	179.52

The data in Table 17 indicate that there was relatively little difference in egg production among birds that commenced laying between 150 and 189 days and that their production was only slightly greater than that of the birds that commenced laying between 190 and 219 days.

From the information made available in Fig. 44 and in Tables 16 and 17, it is quite apparent that, in order to secure maximum egg production in Rhode Island Reds, age in days that laying commences is of considerable importance. In general, a first-year record of 200 or more eggs should be attained by birds commencing to lay at approximately 200 days of age or less providing that such birds do not commence laying too early in the year.

The first step in breeding for the purpose of improving egg production is to select pullets that commence laying in September, October, or November at approximately 200 days of age or less. It is important, however, that these pullets be of good body size and lay eggs of good size when they commence laying, the importance of these two points being discussed fully in the next chapter.

Importance of Good Rate of Laying.—The more eggs a bird lays in a given time the better the rate or intensity of production and the greater the net financial returns in egg production. Obviously a bird that maintains a good rate of production throughout the year lays more eggs than a bird with a poor rate of production. A determination of the rate of production is of little value, however, unless it can be used in the selection of pullets for future breeding purposes, assuming that rate of production is inherited.

It has been found that hens that lay a large number of eggs per clutch are usually better annual layers than hens which lay a small number of eggs per clutch. Hays and Sanborn (1927*a*) obtained a correlation coefficient of 0.35±0.01 between the mean number of eggs per clutch during the winter months and the total number of eggs laid per year in a group of 2,532 Rhode Island Reds. The mean number of eggs per clutch could be used as an index of rate of production but would be more difficult for the practical breeder to determine than rate based on the number of eggs laid in a given time.

Since it has been shown in previous pages that the number of eggs laid in any two consecutive months serves as a reliable index of the total number of eggs laid by a bird, a period of two months or more should be a satisfactory basis on which to compare rates of production among birds.

Several investigators have based their determinations of the rate of production on the number of eggs laid from the date of the first egg laid to March first divided by the number of days involved, the product being multiplied by 100. Hays and Sanborn (1927*a*) used this method for comparing rates of production in 3,863 Rhode Island Reds, except that they did not include in their calculations all pauses in the production of each bird of four or more days from November first to March first. On the basis of their calculation they obtained a coefficient of correlation of —0.23±0.01 between age at which laying commenced and rate of laying. On the other hand, the data given in Table 17 do not indicate a close relationship between age in days at which laying commenced and the fall-winter rate of production in the Rhode Island Reds at the U. S. Animal Husbandry Experiment Farm. The fall-winter rates of production as given in Tables 17 and 18 was determined on the basis of the number of eggs laid by each bird from the time that laying commenced to March first.

The importance of good fall-winter rate of egg production in relation to annual production is clearly demonstrated in Table 18, the data pertaining to 946 Rhode Island Reds at the U. S. Animal Husbandry Experiment Farm being arranged according to the classes of birds having a range of 5 per cent in rate of production to March first. The first class of 33 birds given in Table 18 had a range in rate from 25 to 29 per cent, and the last class of 29 had a range in rate from 80 to 84 per cent.

Table 18. Pauses in Production and First-Year Egg Production in Relation to Fall-Winter Rate of Production in 946 Rhode Island Reds at the U. S. Animal Husbandry Experiment Farm

Number of Birds	Mean Fall-Winter Rate of Egg Production	Mean Number Days in Pauses	Mean Egg Production per Bird
33	27.27	57.27	144.28
45	31.82	51.64	147.50
76	37.36	46.43	161.48
73	42.15	40.11	168.46
93	46.86	34.46	173.04
92	51.85	27.66	188.69
85	57.01	14.79	199.65
95	61.95	10.59	203.80
148	66.83	4.39	206.36
103	71.96	1.06	219.99
74	76.77	0.16	226.55
29	81.41	0.79	240.72

The data in Table 18 show quite clearly that the rate of egg production from the date of laying the first egg to March first has a very important bearing on the total number of eggs produced during the first laying year. Hays and Sanborn (1927*a*) obtained a coefficient of correlation of 0.48 ± 0.01 between fall-winter rate of production and total annual production for 2,528 Rhode Island Reds, indicating that a good fall-winter rate is quite significant. Knox (1927) obtained a coefficient of correlation of 0.34 ± 0.08 between rate of production, based on the two consecutive months of highest production, and the total annual production in 91 White Plymouth Rocks. That such a relationship should exist is naturally to be expected when it is borne in mind that rate is determined on a portion of the first-year production. Even in birds commencing to lay as late as December first the fall-winter rate is determined on three months' laying out of the first year's total production. The data in Table 18 show, however, that the fall-winter rate of production, apparently independent of age in days that laying commenced, serves as a valuable criterion in the selection of pullets to be used as future breeders for the purpose of improving egg production.

Importance of Nonpauses in Production.—It has been pointed out in the third section of this chapter that the production of eggs usually has a definite rhythm in each bird, the number of eggs per clutch being quite uniform throughout the year. For instance, one hen may have a characteristic clutch size of two eggs, whereas another hen may have a characteristic clutch size of six eggs. Whatever the size of the clutch that characterizes each bird's rhythm of laying, there is usually an interval of at least one day between two succeeding clutches. If several days of no production intervene between two succeeding clutches, the intervening periods are called "pauses" in production.

Pauses in production may be due to external influences such as a sudden change in temperature, fright, a temporary shortage of feed, a slight cold, or a host of other factors. Pauses also occur when birds become broody or undergo a partial molt. It is obvious, of course, that the longer the pause, or the more frequently that pauses occur, the less the total number of eggs laid up to the onset of the first annual molt, which usually means a complete cessation of egg production until after the annual molt is completed.

In an analysis of the egg-production records of Rhode Island Reds, Goodale (1918*b*) was led to suggest that a pause of ten days in production prior to the end of February was indicative of the end of the so-called "winter cycle" of production. However, it has already been pointed out in the third section of this chapter that from the biological standpoint of egg production there is apparently no such thing as a winter cycle of egg production. Hays (1924) considered a pause of one week or more in the fall and winter records of pullets a criterion of "winter molt" and acting upon this proposed the hypothesis of the Mendelian inheritance of "winter molt" on a monohybrid basis, the gene M, which determines a winter molter, being dominant to m, which is carried by birds which do not molt prior to March first. Later, however, Hays and Sanborn (1926*b*) considered a pause of five days or more as indicating the termination of the so-called "winter laying cycle."

Hays and Sanborn (1927*b*) secured a significant negative correlation between age in days that laying commenced and length of winter pause although the correlation was of low value. In this discussion concerning pauses it is understood that a four-day interval or less in

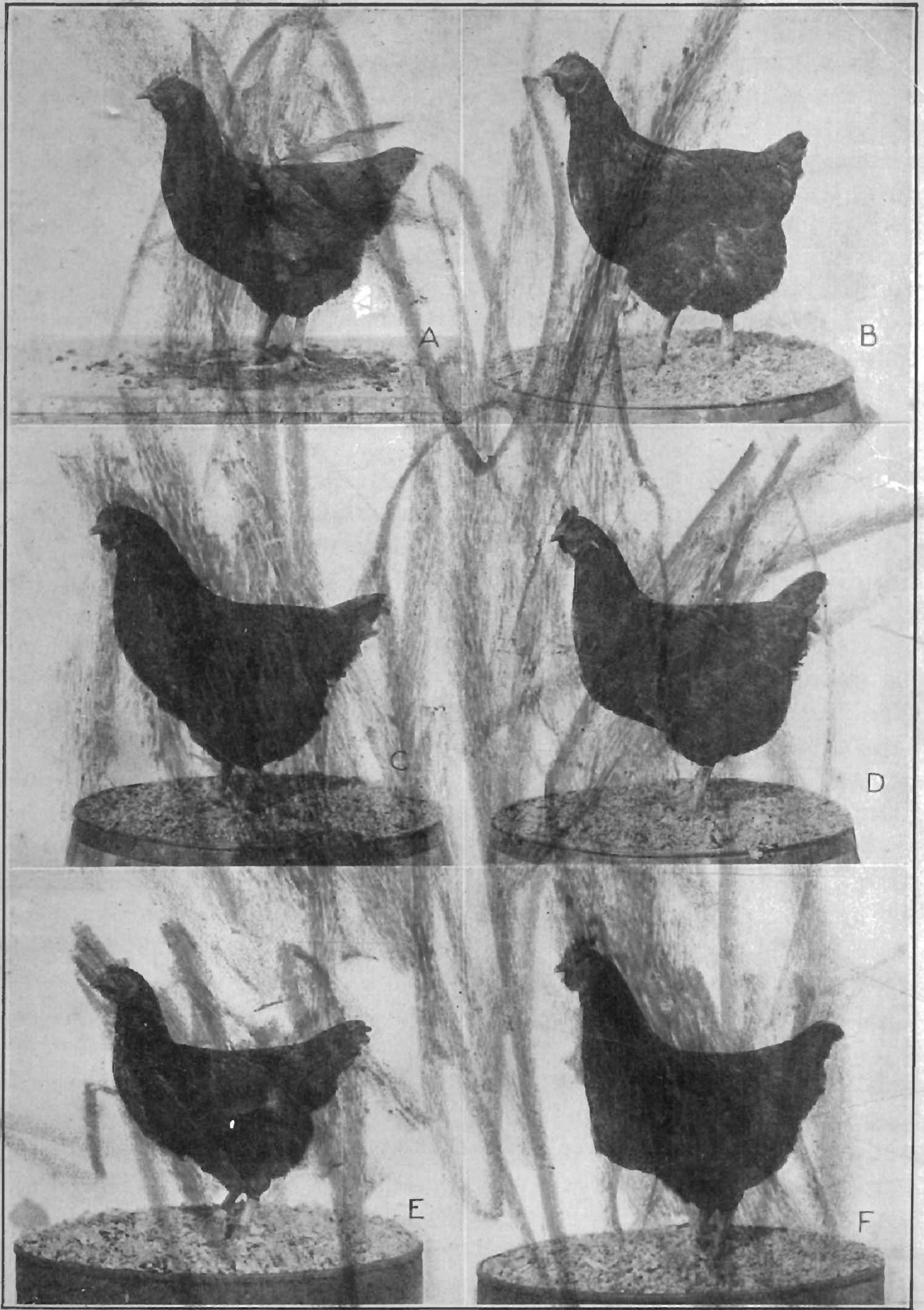

Fig. 45.—A dam and five daughters. The dam, A, laid 236 eggs. The first-year records of the daughters is as follows: B, 208; C, 229; D, 232; E, 246; F, 259. (Photo by U. S. D. A.)

a bird's record to March first does not constitute a pause, and that in the case of each bird showing one or more pauses in her record of production to March first the duration of the pause includes the total number of days occurring in all the pauses. The data in Table 17 do not indicate a significant relationship between age in days that laying commenced and mean days in pauses, although the later-maturing groups of birds given in the table show fewer days of pauses than the earlier-maturing groups.

In a group of 2,134 Rhode Island Reds, Hays and Sanborn (1926*b*) observed that the birds with the highest rate of production up to March first had fewer days of pauses than birds with lower rates of production during the same period. The data in Table 18, also on Rhode Island Reds, show that the higher the rate of production to March first the fewer the number of pause days, a situation to be expected regardless of whether pauses in production are due to external factors or to inheritance. Obviously an increase in the number of days of pauses means a lower rate of production during any given period.

Hays and Sanborn (1927*b*) observed "a tendency for short winter pause to be associated with a long period of broodiness," the latter tending to reduce the number of eggs laid. They also observed that the duration of the winter pause and persistency of production were not related but that there was a significant negative correlation between duration of winter pause and annual production. The data in Table 18 indicate that there is an important relationship between the rate of production to March first and number of days' pause, and since rate of production to March first is shown to be very important in its relation to annual production, it might be assumed that annual egg production is inversely proportional to the duration of pause. That such is not necessarily the case, however, is indicated by the data in Table 19, which gives the mean first-year egg production of different groups of Rhode Island Reds at the U. S. Animal Husbandry Experiment Farm, the groups being classified according to the number of days of pauses to March first. The total number of birds involved is 948, their classification being on the basis of intervals of pauses of 0 to 4 days for the first class and 65 to 68 days for the last class.

The data in Table 19 show that the number of days of pauses to March first apparently had little influence on first-year egg production until a pause of approximately 30 days was reached. No attempt has been made to separate the pauses occurring in each bird's record according to whether they were caused by external factors or were

TABLE 19. MEAN FIRST-YEAR EGG PRODUCTION ACCORDING TO NUMBER OF DAYS OF PAUSES IN RHODE ISLAND REDS AT THE U. S. ANIMAL HUSBANDRY EXPERIMENT FARM

Number of Birds	Range in Number of Days of Pauses to March First	Mean First-year Egg Production
407	0– 4	211.24
48	5– 8	197.12
24	9–12	205.86
32	13–16	190.64
26	17–20	190.82
34	21–24	201.84
44	25–28	192.68
42	29–32	179.38
54	33–36	174.30
45	37–40	180.88
42	41–44	164.51
36	45–48	174.83
23	49–52	172.95
21	53–56	165.53
20	57–60	159.80
26	61–64	148.92
24	65–68	164.24

due to inheritance, because no method has been made known whereby the facts can be determined.

From the practical standpoint it would seem that pullets showing pauses in egg production to March first approximating 30 days or more should not be selected for future breeding purposes with the object of improving egg production.

The Importance of Nonbroodiness.—Leghorns, Anconas, and a few other breeds are characterized as being "nonbroody" breeds inasmuch as the occurrence of broodiness is relatively rare. Plymouth Rocks, Rhode Island Reds, Wyandottes, and many other breeds are characterized as being "broody" breeds because in most flocks many of the layers become broody, some of them several times during a season.

That broodiness can be very largely eliminated from a flock that normally shows much broodiness has been demonstrated by Hays and Sanborn (1926*a*), their data being given in Table 20.

The data in Table 20 show that mean first-year egg production for the most part increased to the extent that the relative number of broody birds in the flock and the mean number of broody periods per

Table 20. Mean First-Year Egg Production in Rhode Island Reds in Relation to the Per Cent of the Flock Showing Broodiness and the Mean Number of Broody Periods Per Broody Bird

(Data of Hays and Sanborn, 1926*a*)

Year Hatched	Number of Birds	Per Cent of Flock Broody	Mean Number Broody Periods per Broody Bird	Mean First-year Egg Production
1912	125	89.60	4.4	114
1913	78	91.03	5.4	124
1914	121	85.95	4.3	103
1915	428	89.25	4.3	122
1916	431	86.31	3.5	134
1917	432	48.84	2.7	166
1918	215	61.40	2.9	169
1919	no data	available		
1920	126	46.03	2.9	200
1921	285	44.56	2.7	200
1922	399	28.91	1.9	200
1923	340	27.35	1.9	189

bird decreased from year to year. The results given in Table 20 were accomplished by the selection each year for breeding purposes later those birds that showed no broodiness and those that went broody the fewest times and by selecting breeding males from females that showed the least amount of broodiness.

Among 971 Rhode Island Reds at the U. S. Animal Husbandry Experiment Farm there were 494 birds that showed no broodiness during their first laying year and 477 that showed broodiness, the average number of times they went broody being 2.34. The non-broody birds laid an average of 204.78 eggs per bird and the broody birds an average of 179.65 eggs per bird.

The practical importance of eliminating broodiness from a flock is clearly apparent. The most effective way of accomplishing this is to band every bird every time it goes broody and eliminate such birds from the breeding pen, and in addition to choose male breeders produced by females that have shown no broodiness.

The Importance of Persistency of Production.—The term "persistency" is understood to mean the relative length of time a bird continues to lay prior to the first complete body molt, which usually occurs in the summer or fall subsequent to the completion of the first year's production. Of two pullets that commence laying in the middle of October, one of which completes her first-year record in July and the other in September, the second one is said to have greater persistency of production.

In a group of 2,179 Rhode Island Reds, Hays and Sanborn (1926*c*) observed a correlation of —0.61 ± 0.01 between age in days laying commenced and persistency of production, indicating that birds which commence laying earliest in life are inclined to be among the most persistent layers of the flock. An observation of a similar nature has already been made in the third section of this chapter.

Hays and Sanborn (1930) secured evidence from an analysis of first-year records in Rhode Island Reds tending to show: (1) the higher the rate of egg production to March first relatively the less time required to complete the molt; (2) the most persistent layers required relatively the least time to molt; (3) the greater the number of eggs laid prior to the onset of the molt the shorter the duration of the molt. In other words, the best layers in the flock are usually those which lay over a period of approximately 300 days or more before molting but take relatively little time to complete the molt.

The practical importance of persistency of production is clearly demonstrated in the data in Table 21, where 894 Rhode Island Reds at the U. S. Animal Husbandry Experiment Farm are classified into groups according to the number of eggs laid in August and September, during the last 50 days of the first year of laying. The birds are classified on the basis of 5 egg intervals. The data show that those birds which laid best during the last 50 days were also the best annual layers. The data show, therefore, that persistency of production is a very important factor in securing high annual production.

Since the matter of determining the number of eggs laid per bird during the last 50 days of the first year of laying in a large flock involves much time and labor in examining the records, it was decided to establish a more practical basis for selecting the birds of a flock on the basis of persistency of production. Accordingly, 906 Rhode Island Reds were classified into groups on the basis of the average number of eggs laid during August and September, the birds being grouped on the basis of 5 egg intervals. Some of the early maturing birds may have finished their first-year production prior to August but despite this possibility the data given in Table 21 show that those birds which laid best during August and September were also the birds that laid best during their first year of laying, regardless of when first-year production ceased in the case of each bird. It is apparent, therefore, that egg production during August and September serves as a practical method of determining the most persistent producers.

TABLE 21. MEAN FIRST-YEAR EGG PRODUCTION IN RELATION TO THE MEAN PRODUCTION PER GROUP DURING THE LAST 50 DAYS OF THE FIRST-YEAR PRODUCTION AND DURING AUGUST AND SEPTEMBER IN RHODE ISLAND REDS AT THE U. S. ANIMAL HUSBANDRY EXPERIMENT FARM

Number of Birds	Mean Egg Production Last 50 Days	Mean First-Year Egg Production	Number of Birds	Mean Egg Production August-September	Mean First-Year Egg Production
139	0	149.95	47	0	139.02
108	2.25	163.36	61	2.51	153.48
76	8.07	178.97	56	8.16	166.43
96	13.36	179.89	104	13.15	169.17
112	17.80	191.95	115	18.20	173.59
105	22.98	203.04	114	23.11	187.56
113	27.92	220.70	103	28.05	198.93
103	32.91	234.26	103	33.05	215.55
42	37.57	236.64	109	37.85	221.36
—	—	—	64	42.52	236.66
—	—	—	30	47.53	247.33

From a practical standpoint the poultry breeder might well use the August and September egg-production records for the purpose of selecting the most desirable birds for future breeding purposes.

PROBLEMS

1. What are some of the more important physiological aspects of egg production?

2. In conducting breeding work for the purpose of determining the nature of the inheritance of egg production, what are the more important external factors affecting egg production that should be kept as uniform as possible from year to year?

3. Discuss the significance of available evidence concerning whether or not egg-laying ability in the domestic fowl has been increased during the past 20 years.

4. Discuss the more important factors that should be kept in mind in determining the proportion of pullets that should comprise the laying flock; discuss the decline in egg production that would probably occur in a given flock of pullets.

5. Discuss the relative merits of three theories of the Mendelian inheritance of egg production that have been proposed.

6. From the standpoint of securing maximum egg production, what is approximately the best time to hatch pullets in different parts of the northern and southern hemispheres?

7. In relation to total first-year egg production, of what significance is age in days that laying commences, and at approximately what age should pullets of the various breeds commence laying?

8. Of what relative importance is rate of egg production, and what are some of the most practical ways of determining rate?

9. What is the relationship between age in days that laying commences and persistency of production, and what is one of the most practical ways of selecting layers on the basis of persistency of production?

10. Outline a breeding program that should enable the poultry breeder to improve egg production from year to year.

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CHAPTER IX

THE INHERITANCE OF EGG CHARACTERS

THE inheritance of egg-laying ability has been discussed in Chapter VIII, but there are other things besides the number of eggs produced that every poultryman should take into consideration. The eggs laid should be of good marketable size, of good shape for packing in cartons and cases, uniform in color, of good shell texture to withstand breakage under ordinary methods of marketing, and of good quality of yolk and albumen.

These various egg characters are all of considerable economic importance. For instance, a hen may lay a large number of eggs but most of them may be small, thus commanding a lower price than fewer eggs most of which were of good size. Then again, a hen may lay eggs of good size and shape but they may have poor shell texture so that many of them break when shipped to market. The quality of the yolk and albumen are important, especially from the standpoint of the keeping quality under normal conditions of storage. To whatever extent these various egg characters are inherited, it becomes important for the poultry breeders to give them due consideration in the selection of breeding stock from year to year.

THE INHERITANCE OF EGG SIZE

Egg size and egg weight are synonymous terms as far as new-laid eggs are concerned. The larger the size the heavier the egg. On the other hand, among stale eggs a large egg may be much lighter in weight than a smaller one because of the loss through the porous shell of much of the water from the albumen and yolk. Various investigators, however, have used the terms "size" and "weight" interchangeably in discussing the inheritance of egg size. In a large measure such practice is justified in view of the fact that inheritance studies always involve new-laid eggs, which lose very little water from the time they are laid to the time they are weighed. Moreover, Pearl and Surface (1914) have shown that either weight or bulk may be used as a measure of size. The weight of an egg is the most easily obtained criterion of size so that inheritance studies usually deal in terms of egg weight.

The standard weight of an egg is 2 ounces, and from the standpoint of meeting market requirements, it is obvious that poultrymen should endeavor to maintain flocks the individual members of which lay eggs of approximately standard weight. In practically all studies on the inheritance of egg weight the weights are given in grams because the gram is a smaller unit of weight than the ounce, making it easier to determine the amount of variability of egg weight among eggs laid by a hen or among eggs laid by a group of hens. Weighing eggs in grams permits of more exact determinations of the weight of each egg. A 2-ounce egg weighs 56.7 grams.

Some very interesting records have been reported by Kohmura (1931) for a number of fowls in Manchuria that are noted for the very large egg they lay. Among 25 birds secured by the Manchurian Agricultural Experiment Station, 12 laid eggs averaging 63.5 to 69.0 grams each, 10 laid eggs averaging 70.0 to 79.0 grams each, and 3 laid eggs averaging 80.0 to 86.0 grams each. The next year a pullet laid eggs up to 113.0 grams (practically 4 ounces) in weight and two years later 4 pullets laid eggs averaging over 85.0 grams each for the yearly production of each bird.

Before discussing the results of studies on the inheritance of egg size it is advisable to discuss the various factors that may affect egg size.

Egg Weight in Relation to the Weight of the Different Parts of the Egg.—Obviously, the total weight of an egg is determined by the collective weights of its component parts. Curtis (1911) observed that the albumen contributed 59.26 per cent, yolk 29.14 per cent, and shell 11.18 per cent of the total egg weight. In the annual production records of a group of Barred Plymouth Rocks, Jull (1924*a*) found that the average percentage of total weight represented by albumen was 58.43, yolk 30.99, and shell 10.58. In a group of 707 eggs laid by 67 birds Asmundson (1931*a*) found that the albumen contributed 58.76, yolk 30.01, and shell 10.50 per cent of the total egg weight. It has been determined, however, that the percentage weights of the different parts of the egg and the weight of the egg itself vary during the first-year production of any individual bird.

From studies on the relationship between egg weight and egg shape by Pearl (1909), Curtis (1914*b*), Pearl and Curtis (1914), and more particularly Pearl and Surface (1914), it has been shown that egg weight is more highly correlated with egg breadth than with egg length. This observation has been confirmed by Asmundson (1931*a*), who also found that albumen weight and shell weight are each more highly correlated with egg breadth than with egg length. Asmundson found that, although yolk is somewhat more highly correlated with egg breadth than with egg length, the difference was not significant.

Egg Weight in Relation to Body Weight.—That a relationship exists between body weight and egg weight has been demonstrated by a number of workers. In a flock of White Plymouth Rocks, Hadley and Caldwell (1920) observed that the larger birds tended to lay the heavier eggs, although in another flock there seemed to be no such relationship. Asmundson (1921) found weight of egg to be positively correlated with body weight in White Leghorns. Atwood (1923), also with White Leghorns, observed that there was a significant correlation between the monthly mean body weight and the monthly mean egg weight.

Jull (1924*b*) reported a coefficient of correlation of +0.34 ± 0.09 between maximum body weight and mean egg weight in a group of 40 Barred Plymouth Rock pullets. Atwood (1925) observed that among his White Leghorns the heavier birds laid the larger eggs. Parkhurst (1926), using White Leghorns, corroborated Jull's findings, given previously, concerning the relationship between maximum body weight of the pullet and the mean egg weight of her annual production. Upp and Thompson (1927), with White Leghorns, corroborated Atwood's findings concerning the relationship between mean body weight and mean egg weight. Rhynehart (1929) observed that large birds tended to produce fewer second-grade eggs than smaller birds. For two strains of White Leghorns, Hauschildt (1929) gives correlations of 0.57 ± 0.05 and 0.72 ± 0.05, respectively, between body weight and mean egg weight. In White Leghorns, Barred Plymouth Rocks, Rhode Island Reds, and White Wyandottes entered in the 1923-1924 to 1926-1927 Canadian Egg-Laying Contests it was found that in general the larger the bird the larger the egg it laid.

In a group of 1,388 Rhode Island Reds, Hays (1930) observed that the birds which weighed most when they commenced laying laid the largest eggs up to the first of January, which terminated the period of observations.

Atwood and Clark (1930) found that for Single-Comb White Leghorns in the first, second, and third years of production there was a significant positive correlation between body weight and the mean egg weight of the eggs produced by each bird. Marble (1930) observed a significant positive correlation between body weight and egg weight in six groups of White Leghorns and one group each of Barred Plymouth Rocks and Rhode Island Reds. Marble points out that the mean egg size increases as the body weight increases but at a diminishing rate.

Data regarding the relationship between body weight and egg weight in two strains of White Leghorns bred for 20 and 15 years,

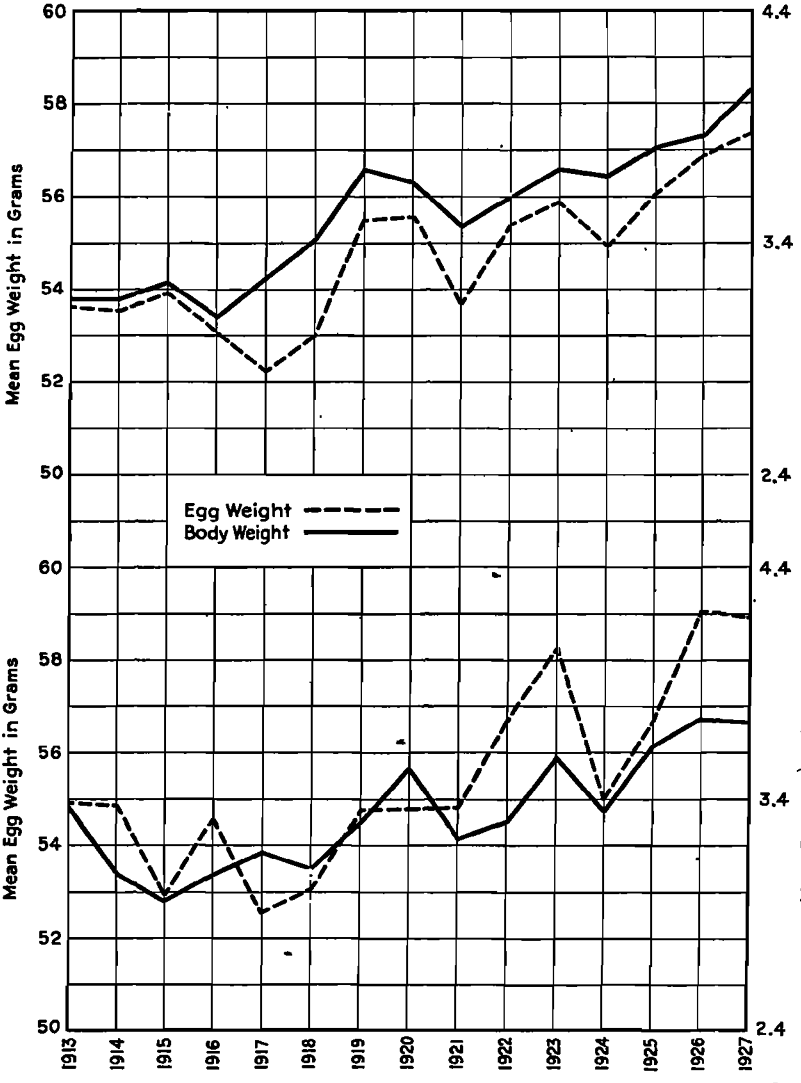

FIG. 46.—Mean annual egg weight changed from year to year in accordance with changes in mean body weight in two strains of White Leghorns. (From data of Hall and Marble, 1930.)

respectively, have been made available by Hall and Marble (1930). It was found that in general annual mean egg weight per bird followed the trend from year to year of mean body weight per bird: the larger the bird the larger the egg, the situation being shown in graphic form in Fig. 46 for the years 1913 to 1927 inclusive.

Graham (1932) has shown that in the 1928 and the 1929 flock of Rhode Island Reds the smallest birds laid the smallest eggs and the largest birds the largest eggs. The data have already been given in Table 16, and the situation is shown graphically in Fig. 47.

Egg Weight in Relation to Nutrition and Other Factors.—Since the annual mean egg weight is affected both by the age in days that laying commences, as shown later, and by the body weight of the birds, it is evident that anything that affects age in days that laying commences or body weight will thus indirectly affect mean egg weight. At the same time, it is possible that nutrition and other factors may affect the weight of eggs without exercising a pronounced effect on either age in days that laying commences or on body weight. The results of several investigators have led them to conclude that nutrition and certain other factors affect the weight of eggs laid, but only in a few cases was consideration given to the possible influence of nutrition or the other factors on age in days that laying commences or on body weight or both.

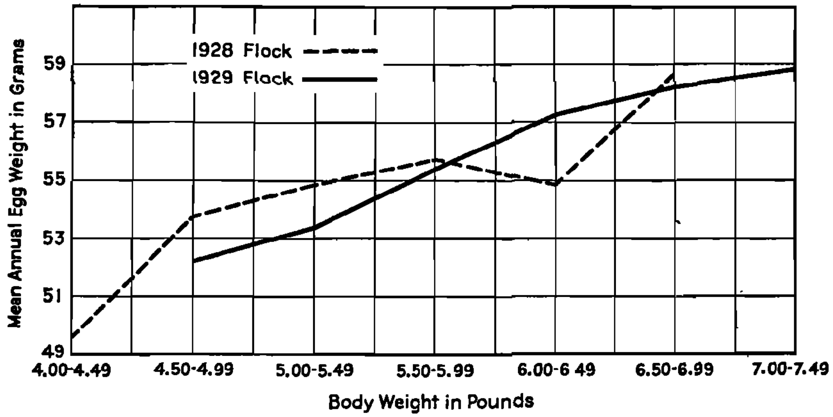

FIG. 47.—In both the 1928 and the 1929 flocks of Rhode Island Reds, the largest birds laid the largest eggs. (From data of Graham, 1932.)

The results of a few experiments tend to show that egg weight is affected, either directly or indirectly, by nutrition. Kistler, Charles, and Knandel (1926) found that birds fed on milk products as a supplement to the ration laid larger eggs than those fed on meat scraps as a supplement, and Röemer (1927) found that birds fed on dried buttermilk as a protein supplement laid larger eggs than birds fed on meat meal as a protein supplement, and that birds fed on fish meal as a protein supplement laid larger eggs than those fed on dried buttermilk. The results secured by Parkhurst (1924, 1927-1928), Kempster (1930), Buckner (1927), Robertson and Basket (1928), and Macdonald and Orr (1930) also tend to show that the kind of diet which birds are given affects the size of eggs they lay although in most cases the body weight of birds on different diets was not taken into consideration.

Egg Weight in Relation to Age in Days that Laying Commences.—Curtis (1914*b*) was probably the first to observe that the size of the first eggs laid in the pullet year of production depends to some extent on the age of the birds and the time of the year that laying commences. Lippincott (1921) with White Leghorns, Atwood (1923) with White Leghorns, and Jull (1924*b*) with Barred Plymouth Rocks, each determined the existence of a very significant correlation between age in days laying commenced and the mean weight of the first ten eggs laid in the pullet year; the earlier that laying commenced the smaller the eggs.

The increase in the mean monthly egg weight expressed as a percentage of the annual mean egg weight is shown in Fig. 48 for four groups of 40 Barred Plymouth Rocks, one group of which commenced laying in September, one in October, one in November, and the other in December. The graph shows clearly that the earlier laying commenced the smaller is the size of the egg in relation to annual mean egg weight up to the month of February, at which time all four groups reached the vernal maximum in mean monthly egg weight.

The observations of Parkhurst (1926), Maw and Maw (1928), Hays (1930), and Schmidt and Zöllner (1930) also tend to show that the earlier in life that laying commences the smaller is the size of the eggs laid at that time. Just what effect this has on annual mean egg weight is discussed later in connection with the problem of the mean egg weight of the first-year production. In the meantime, it may be observed that Marble (1931) has stated that age in days that laying commences is not an important factor in determining mean egg weight of the first-year production. It should be kept in mind, however, that age at commencement of laying has a direct bearing on mean annual production, as pointed out in the previous chapter, and undoubtedly the earlier in life that laying commences the less the average bird weighs, and since body weight has a direct bearing on egg weight, as pointed out previously, age in days that laying commences may be of greater importance in relation to mean annual egg weight than has been generally recognized.

Egg Weight in Relation to Position of Egg in the Clutch.—In the first place, Atwood (1917) and Jull (1924*b*) have shown that the second egg of a two-egg clutch is usually smaller than the first egg. Atwood further found that, in clutches of several eggs, the first egg is usually the heaviest and that there is a progressive decrease in the weight of the egg laid on each successive day. However, the rate of decrease in the weight of the successive eggs in a clutch is less when birds are laying heavily than when they are not laying heavily, according to Atwood (1926).

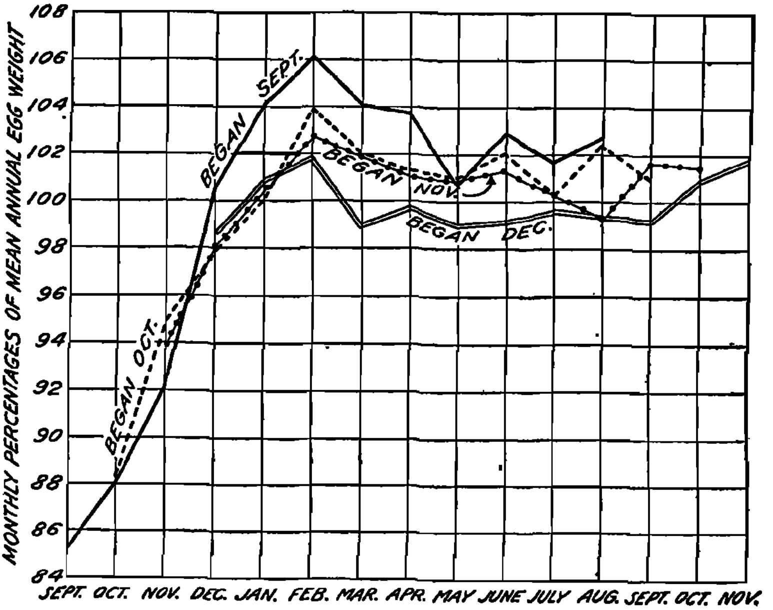

FIG. 48.—Monthly mean egg weights as percentages of the mean weights of the annual production, in Barred Plymouth Rocks, according to the month laying commenced. The earlier in life that laying commenced the smaller were the first eggs laid. Regardless of the month that laying commenced, maximum egg weight was attained in February of the first laying year. (After Jull, 1930.)

Egg Weight in Relation to Rate of Production.—Birds that lay at the highest rate or greatest intensity are frequently birds that lay small-sized eggs. In a group of 1,392 Rhode Island Red pullets, Hays (1930*a*) obtained a negative correlation of —0.32 ± 0.02 between rate of egg production and mean egg weight to the first of January. The value of this correlation indicates that birds that lay at the fastest rate are inclined to be those that lay the smallest eggs, or those that lay the smallest eggs are inclined to lay at the fastest rate.

From a study of the records of 247 Rhode Island Red pullets, Hays (1930*b*) has suggested that linkage exists between genes for high rate and genes for small egg size.

Mean Egg Weight of the First-Year Production.—During the first-year production in a group of White Leghorns, Atwood (1914) found that egg weight varied from month to month and reached the maximum in the early spring. Hadley (1919) developed the thesis that increase in egg weight from the time the pullet commences laying serves as a criterion of numerical production and that it is possible to determine in advance of the conclusion of the first year of production the relative potential laying capacity among individuals in a flock of pullets. In connection with Hadley's thesis, Jull (1925) has pointed out that increase in egg weight can be considered a criterion of numerical production only so far as age in days that laying commences is a criterion of numerical production.

The relationship between the mean egg weight and the number of eggs laid during the first laying year has been studied by Atwood (1923), Jull (1924*b*, 1925), Lohman (1924), Parkhurst (1926, 1927), Upp and Thompson (1927), Thompson (1930), Atwood and Clark (1930*a*), and Dudley (1931), the results of all these investigations showing that the mean egg weight of the annual production is not affected by the number of eggs laid.

On the other hand, Hays (1929) found that heavy winter production, in Rhode Island Reds at the Massachusetts Experiment Station, tended to be accompanied by small egg size. Atwood and Clark (1930*b*) found that in a flock of 200 unselected White Leghorns there was a tendency for the best layers to lay the smallest eggs. A significant negative correlation of —0.22 ± 0.06 between egg production and mean egg size per bird was determined for those birds which laid 170 eggs or more in the first year of production.

Evidence showing that the best layers tend to lay small eggs as compared with birds that do not lay so well is available from a number of sources.

White Leghorns, Rhode Island Reds, and White Wyandottes, in a Scottish laying contest conducted by the Department of Agriculture for Scotland, were divided into two groups according to the mean weight of egg laid. The mean egg size and the mean production for each group were determined by Jull (1930), who found that the highest producing hens laid the smallest eggs. Jull (1930) analyzed the records of 185 White Leghorns in the English National Poultry Council trials and found that there was a tendency for the highest producers to lay the smallest eggs. Jull (1930) also analyzed the records of egg production for 11 months in a group of 40 White Leghorns at the West Virginia Experiment Station and determined a correlation of —0.39 ± 0.12 between mean egg production and mean egg weight per bird. In this group of birds, therefore, the best layers were among those that laid the smallest eggs.

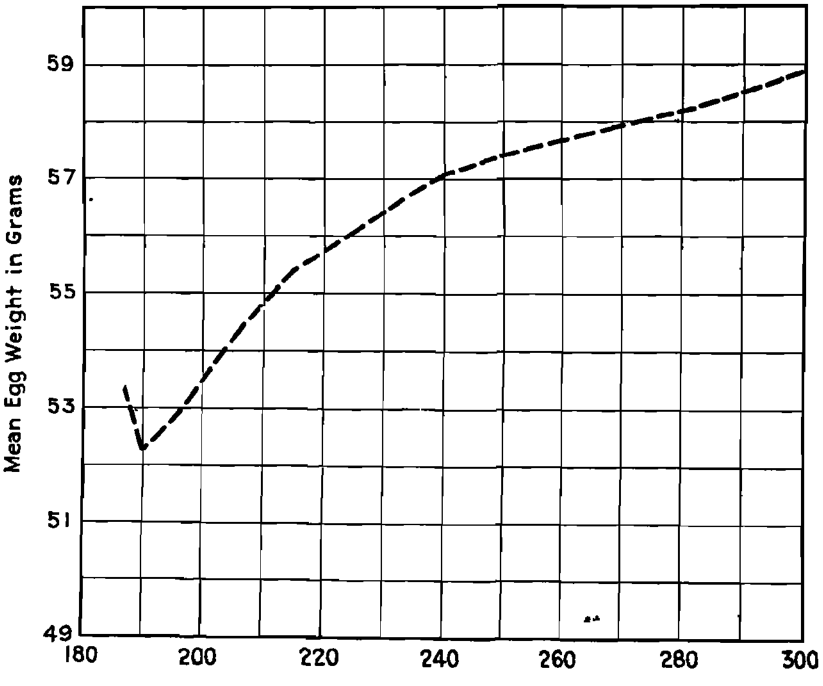

FIG. 49.—In the 1929 flock of Rhode Island Reds it was found that the first year mean egg weight was relatively the lowest among the birds that started laying the earliest in life. (From data of Graham, 1932.)

In a group of 74 White Leghorns hatched in March and April, Maw and Maw (1931) found that the annual mean egg weight was lowest for those birds that started to lay the earliest. They also found that the earlier in life laying commenced the longer was the time required for a bird to lay eggs of standard weight, 56.70 grams. Graham (1932) found that in a flock of 163 Rhode Island Reds hatched in 1929 at the Massachusetts Experiment Station there was a progressive increase in annual mean egg weight as the age at commencement of laying increased. The data are given in Table 16 and are shown in graphic form in Fig. 49. Jull, Quinn, and Godfrey (1932) found that in a group of 51 unselected White Leghorns, whose first-year production ranged from 20 to 283 eggs and whose mean annual egg weight per bird ranged from 49.80 to 61.67 grams, there was a marked tendency for the best layers to lay the smallest eggs.

From the foregoing discussion on the relationship between annual mean egg weight and first-year production it is apparent that the observations of the various investigators are not in entire agreement, since some of them did not find a significant relationship whereas others did. In this connection Marble (1930) has observed that the relationship between mean egg weight and first-year production is non-linear in nature, and that these two factors are correlated to a small degree when the relationship is measured by means of the correlation ratio. Therefore, poultrymen should avoid using as breeders hens which lay small eggs even if they are among the best producers in a flock.

Annual Mean Egg Weight in Successive Years of Production.—It has already been pointed out that during the first-year production in most flocks there is usually an increase in size or weight of eggs laid from the time that laying commences up to the spring of the year, maximum size or weight of egg frequently being attained in February or March; then there is usually a slight relative decline during the late spring and summer months followed by an increase in egg weight at the close of the first year of laying. According to Bennion and Warren (1932), the normal decrease in egg weight that occurs during the summer months is in part due to the summer temperature. According to Hadley and Caldwell (1920), Benjamin (1920), Atwood (1926, 1928), and Atwood and Clark (1930) the mean egg weight of the second-year production is approximately 10 per cent greater than that of the first year and that hens that lay small eggs the first year tend to lay relatively small eggs the second year as compared with hens that lay large eggs the first year. Apparently there is relatively little change in mean egg weight from the second to the third and successive years of production.

Is Egg Weight Inherited in Mendelian Manner?—From what has already been said about the numerous factors affecting the weight of eggs laid, it is quite apparent that the problem of determining the nature of the inheritance of egg weight is an extremely complicated one. In the first place, it has never been determined whether the mean egg weight of the first-year production or the maximum weight of eggs that a bird lays during the first or any other year is the proper basis for determining the nature of the inheritance of egg weight. In the second place, since body weight has been shown to be so closely associated with egg weight, is the problem of the inheritance of egg weight largely a problem of the inheritance of body weight? In the third place, since it has been shown in the preceding chapter that usually the earlier in life that laying commences the greater the number of eggs laid, and since it has been shown in this chapter that the earlier in life that laying commences the smaller is the size of both body and egg at that time and the longer thereafter before either maximum body or egg weight is attained, is the inheritance of egg weight to be controlled for the most part by controlling age in days that laying commences in relation to body weight? These are undoubtedly only a few of the problems involved in any study on the inheritance of egg weight.

Since the commercial egg-weight standard is 24 ounces per dozen or 56.7 grams per egg, it should be the desire of every poultry breeder and commercial flock owner to breed and keep only those birds that lay eggs of approximately these weights. However, if a pullet lays eggs approximating 2 ounces or 56.7 grams each in weight when she commences laying she will most probably lay larger eggs in the spring of the year when eggs are incubated and still larger eggs in the second year. Is this desirable or is it more desirable to have pullets lay eggs approximating standard weight during the hatching season?

The results of the investigations discussed previously in this chapter indicate that if a pullet lays eggs of standard weight during the hatching season then her annual mean egg weight should approximate 2 ounces or 56.7 grams per egg. From a practical standpoint, perhaps the most feasible way for the poultry breeder to attempt to improve the size of eggs laid by his flock is to select eggs for incubation on the basis of whether or not a pullet's eggs approximate standard weight. It should be understood, of course, that practically all the eggs of any one pullet during the breeding season should approximate standard weight or none of them should be incubated.

In a flock of Rhode Island Reds bred for several years for high egg production Hays (1929) found that a pullet must lay eggs averaging 52.0 grams each for the month of November and 55.0 grams each for the month of December in order to lay eggs averaging 56.7 grams each in March. Hays (1930*a*) found, however, that there is wide variability among birds of the same strain in the length of time required to attain standard egg weight. Rate of laying was found to be very important in its influence on rate of increase in egg weight from the time that laying commenced up to the time that the vernal maximum egg weight was attained. Maw and Maw (1931), in a flock of White Leghorns whose mean annual egg weight was 53.73 grams, found that only when the first 10 eggs laid by each pullet averaged 47.50 grams were eggs of standard weight laid before the end of the first year of production.

Small Egg Size Dominant?—Comparatively few experiments have been conducted for the purpose of determining the specific nature of the inheritance of egg weight. A few observations have been made, however, indicating that small egg size is dominant to large egg size. Benjamin (1920) in White Leghorns found small egg size to be dominant to large egg size. Hurst (1921) made the same observation regarding the inheritance of egg size in White Wyandottes and White Leghorns. Kopeć (1924), in crosses between Leghorn males and Polish Greenfoot females, secured results indicating that small egg size is dominant to large egg size.

On the other hand, Waters and Weldin (1929) secured results in White Plymouth Rocks which led them to suggest that large egg size is dominant to small egg size. Breeding was carried on for two years without any selection of the breeding stock on the basis of the size of eggs laid. In the first year the mean weight of the eggs laid was 59.60 grams per bird and in the second year 55.16 grams, although there was considerable variability in regard to the mean annual weight of the eggs laid by each bird. In the first year some birds laid eggs with an annual mean weight of 51.0 to 52.0 grams whereas others laid eggs having an annual mean weight of 69.0 to 70.0 grams. In the second year the annual mean egg weight per bird varied from approximately 45.5 to approximately 63.5 grams.

Beginning with the third year, selection for egg size was practiced, one line being bred for small egg size and another one for large egg size. The females were selected on the basis of their first-year mean egg weight, those whose eggs averaged less than 56.0 grams being placed in the low egg-weight line and those birds whose eggs averaged 56.0 grams and over for the first year's production were placed in the high egg-weight line. The male birds used as breeders were selected on the basis of the annual mean egg weight of their dams, males whose dams had an annual mean egg weight of 56.0 grams or over being used in the high egg-weight line and males whose dams had an annual mean egg weight of less than 56.0 grams being used in the low egg-weight line.

The third year of the project was the first year that selection for egg size was practiced, and in each of the two lines thereafter the selection of the breeding stock to be used was on the 56-gram basis. The small egg-size line was bred for five more years and the large-size line for six more years. The results secured are given in Table 22.

TABLE 22. EFFECT OF SELECTION OF BREEDING STOCK ON THE BASIS OF LOW ANNUAL AND HIGH ANNUAL MEAN EGG WEIGHT, RESPECTIVELY, ON ANNUAL MEAN EGG WEIGHT OF PROGENY IN WHITE PLYMOUTH ROCKS

(Data of Waters and Weldin, 1929)

Year	Low Egg-Weight Line Progeny			High Egg-Weight Line Progeny		
	No. of Birds	Per Cent Low Egg-Weight Birds	Annual Mean Egg-Weight per Bird	No. of Birds	Per Cent High Egg-Weight Birds	Annual Mean Egg-Weight Per Bird
1	46	97.8	49.15 ± 0.14	32	78.2	58.70 ± 0.25
2	18	100.0	49.50 ± 0.25	27	81.5	59.33 ± 0.27
3	15	100.0	46.20 ± 0.30	12	83.3	59.75 ± 0.49
4	55	100.0	47.77 ± 0.17	101	81.2	60.97 ± 0.17
5	22	95.4	48.50 ± 0.25	27	100.0	64.09 ± 0.24
6				16	81.3	59.25 ± 0.48

Waters and Weldin have suggested that the results which they secured indicate that the inheritance of egg weight is due to a single pair of autosomal genes, or if more than one pair of genes is involved they are relatively few in number. Although the results they secured show that the low egg-weight line and the high egg-weight line each tended to produce to a marked extent low egg-weight and high egg-weight birds, respectively, it would be interesting to know the results that would have been secured if their egg-weight lines had been divided up into smaller divisions of egg-weight classes, as for instance, egg-weight lines comprising birds laying eggs weighing from 40 to 44 grams, 45 to 49 grams, 50 to 54 grams, 55 to 59 grams, and 60 to 64 grams. The progeny test should be employed in selecting the birds for the various matings, the body weights of the birds should be secured, data should be recorded regarding age in days to commencement of laying and rate of laying, and relatively large numbers of progeny should be raised each year. Also, in order to determine the number of genes involved in the inheritance of egg weight, F_2 and backcross matings should be made.

Hays' Theory of Egg-Weight Inheritance.—Additional information on the inheritance of egg weight has been submitted by Hays (1929), whose observations are based upon the inheritance of the mean weight of eggs per bird laid from commencement of laying to the first of January of the pullet laying year. Whether such a method of procedure is likely to provide conclusive evidence regarding the nature of the inheritance of egg weight seems rather doubtful because it has already been pointed out that numerous physiological factors affect rate at which egg weight increases up to the attainment of the vernal maximum egg weight. Hays himself (1930) has observed that there is wide variability among birds of the same strain in the length of time required to attain standard weight of eggs.

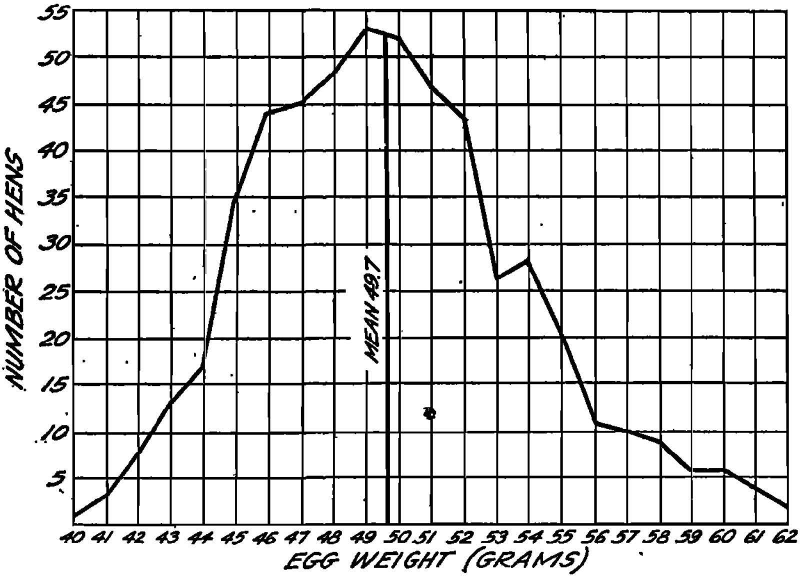

FIG. 50.—Frequency distribution curve showing mean weight of eggs laid by 526 Rhode Island Reds from the date each pullet laid her first egg to January 1. (After Hays, 1929.)

The flock of birds used by Hays as a basis for his egg-weight inheritance studies consisted of 526 Rhode Island Reds, mean egg weight per bird being determined for the eggs laid from commencement of laying to the first of January. The frequency-distribution curve of this flock on the basis of mean egg weight is shown in Fig. 50 and, according to Hays, "suggests that egg weight must depend upon several heritable factors."

The results of these inheritance studies are based upon the records of 5 males mated to 18 females, which produced a total progeny of 224 birds representing families of 7 to 18 birds per family. Upon the basis of the relative number of birds in each family laying eggs of a certain mean weight, Hays has proposed a theory of the inheritance of egg weight involving a pair of autosomal genes, *BB*, dominant for large size of eggs, and a pair of autosomal genes, *AA*, dominant for small egg size, gene *A* being epistatic to *B*. Birds carrying both *AA* and *BB* lay small eggs; birds carrying *AA* and *bb* lay smaller eggs; and birds carrying *aa* and *bb* lay very small eggs. Only those birds of the genetic constitution *aaBB* and *aaBb* lay eggs having a mean weight of 52.0 grams or over from commencement of laying to the first of January, gene *B* having a cumulative effect so that a bird homozygous for gene *B* lays a larger egg than a bird heterozygous for gene *B*. Hays states that his data indicate that there are minor modifiers affecting egg size, and that although such modifiers may be both physiological and hereditary they are of minor significance in relation to gene *B*.

The nine different genotypes proposed by Hays are represented as laying four classes of eggs based on their mean weight per bird from commencement of laying to the first of January as follows:

aabb *Aabb* *AAbb*	47 grams or less	*AABB* *AaBB*	50 to 51 grams
AABb *AaBb*	48 to 49 grams	*aaBb* *aaBB*	52 grams or more

The two middle classes of mean egg weights, 48 to 49 grams and 50 to 51 grams, would appear to be too restricted in weight limits as compared with the other two classes of mean egg weights, particularly in view of the fact that the frequency-distribution curve shown in Fig. 50 indicates that over 30 per cent of the entire flock from which Hays secured his 5 males and 18 females laid eggs having a mean egg weight of 47 grams or less per bird and over 30 per cent of the entire flock laid eggs having a mean egg weight of 52 grams or more per bird. If a range of 2 grams is justified for each of the two middle classes, then it would appear highly probable that the first and last classes should each be arbitrarily broken up into other classes with a range of 2 grams for each class.

Concerning the results which Hays secured in several matings, it may be observed that by his division of the progeny of each mating into the four classes given previously it should be possible to make practically any distribution fit some hypothetical genotype within the range he has given. Moreover, in order to test the validity of the hypothesis developed by Hays, backcross and F_2 matings should be made.

More Work Necessary.—The discussion on the inheritance of egg weight presented thus far indicates that a final solution of such a complicated problem is apparently not near at hand. The work of Waters and Weldin and Hays serves as a valuable contribution to a study of the problem and emphasizes its complex nature. Before a determination can be made of the number of genes involved in the inheritance of egg weight it would seem desirable to take into consideration the various physiological factors affecting egg weight as laying continues. Some of the physiological factors that apparently should be taken into consideration include the following: the amount of yolk material accumulated in the ovary for each egg in relation to body weight and rate of laying; the amount of albumen secreted for each egg in relation to the size of the yolk, body weight, and rate of laying; the rate of increase in egg weight in relation to the rate of increase in body weight up to the time that vernal maximum egg weight is attained; and the annual mean egg weight in relation to the maximum egg weight of each bird.

From the genetic standpoint alone the problem is a very complicated one because it apparently has never been established whether studies on the inheritance of egg weight should be based on the annual mean egg weight or on the vernal maximum egg weight or on the maximum egg weight of a bird during her first laying year regardless of the time of the year that the maximum egg weight is attained. It is even possible that studies on the inheritance of egg weight should be based on second-year egg-weight records since it has been shown that in some flocks the weight of eggs laid during the second year is greater than during the first year.

Furthermore, backcross and F_2 matings should be made, and it would also seem desirable to undertake considerable intensive inbreeding to establish strains in which the variability in egg weight among the birds of each strain is reduced to the minimum and then cross the inbred strains.

The practical poultry breeder can do a great deal, however, toward breeding for good size of egg by eliminating all birds from the breeding pens that lay small eggs. There is a simple way of identifying the birds that lay small eggs. The weighing of all eggs laid by a flock of birds in order to ascertain the mean weight of the first-year production of each bird in the flock represents an enormous amount of work. For poultry breeders interested in determining approximately the mean weight of eggs laid by each bird in their flocks only a relatively few eggs of the total number laid by each bird need be weighed, providing the weighings are distributed throughout the year. Jull (1930) found that the mean weight of the eggs laid by a bird on a given day of the week throughout the year served as a reliable criterion of the mean weight of her annual production. The data are given in Table 23.

Table 23. Mean Egg Weight of Eggs Laid on One Day of Each Week and Mean Egg Weight of Annual Production for Each of 21 White Leghorns

(Data of Jull, 1930)

No. of Bird	No. of Eggs Weighed	Mean Weight of Eggs Laid on One Day Each Week	Mean Weight of Annual Production	Difference in Mean Weights
		Grams	Grams	Grams
5	27	53.08 ± 0.58	52.52 ± 0.28	0.56 ± 0.65
11	29	51.77 ± 0.50	51.33 ± 0.24	0.44 ± 0.55
14	33	51.95 ± 0.56	52.45 ± 0.21	0.50 ± 0.60
16	32	61.45 ± 0.60	61.96 ± 0.28	0.51 ± 0.74
24	23	54.17 ± 0.67	53.71 ± 0.28	0.46 ± 0.73
27	29	50.13 ± 0.32	50.29 ± 0.15	0.16 ± 0.36
35	29	54.31 ± 0.36	54.36 ± 0.16	0.05 ± 0.40
36	20	57.12 ± 0.47	57.45 ± 0.17	0.33 ± 0.50
40	28	50.67 ± 0.38	50.36 ± 0.15	0.31 ± 0.41
41	23	52.96 ± 0.30	53.16 ± 0.16	0.20 ± 0.34
44	40	49.67 ± 0.27	50.02 ± 0.14	0.35 ± 0.30
45	28	52.21 ± 0.46	52.18 ± 0.18	0.03 ± 0.49
51	29	50.18 ± 0.61	49.95 ± 0.22	0.23 ± 0.65
52	27	59.85 ± 0.54	59.14 ± 0.24	0.72 ± 0.60
53	34	50.46 ± 0.48	50.75 ± 0.19	0.29 ± 0.51
54	34	57.48 ± 0.44	58.07 ± 0.20	0.59 ± 0.48
64	28	54.89 ± 0.47	54.36 ± 0.21	0.53 ± 0.51
67	34	52.22 ± 0.46	52.40 ± 0.15	0.18 ± 0.49
71	36	56.86 ± 0.38	56.33 ± 0.15	0.53 ± 0.41
74	38	54.68 ± 0.48	54.63 ± 0.18	0.05 ± 0.52
77	33	50.09 ± 0.35	49.61 ± 0.15	0.48 ± 0.38
		53.63 ± 0.48	53.57 ± 0.49	0.06 ± 0.68

It is probable that in any flock nearly every bird would normally lay a sufficient number of eggs on a given day of the week throughout the year so that the mean weight of those eggs would represent the mean annual egg weight of that bird's production. Dudley (1930-1931), in a group of 198 White Leghorns entered in an English laying contest, found that weighing eggs laid on four consecutive days each month or one day a week served as a good index of mean annual egg weight for each bird.

Another method of determining the approximate mean egg weight of the eggs laid by a bird in the first year of production has been described by Maw and Maw (1931). In a flock of 74 White Leghorns it was found that the mean weight of the first 10 eggs laid by each bird in the fifth month of laying gave a reliable index of her annual mean egg weight.

THE INHERITANCE OF EGG SHAPE

The problem of the inheritance of egg shape has its practical significance because all the eggs marketed from a flock should be of approximately the same shape in order to avoid breakage when shipped in cartons or cases and to present the most attractive appearance to the buying public. Uniformity of shape, therefore, is of considerable practical importance. Investigational work has shown, however, that although most birds in a flock usually lay eggs that are characteristically uniform in shape some hens lay eggs that are quite variable in shape. The poultry breeder should attempt to ascertain those birds which lay eggs lacking in uniformity as well as those birds which produce other birds that lay eggs lacking in uniformity and eliminate them from his flock.

Factors Affecting Egg Shape.—The normal shape of a hen's egg is oval, with one end larger and relatively more blunt than the other end. In order to compare eggs in regard to their shape they are measured and a shape index determined. The method of determining egg shape most commonly employed is the length-breadth index, which is found by multiplying the breadth by 100 and dividing the product by the length. This was the method employed by Pearl and Surface (1914), and Curtis (1914*b*) in their extensive investigations on variability of egg shape. R. and A. Serebrovsky (1926), however, used the measurement of length and two breadth measurements, the latter being taken a certain distance from each end of the egg. Asmundson (1931*a*) used the length measurement and four breadth measurements approximately the same distance apart, thus taking into consideration differences in the diameter near the ends of the eggs.

Factors that apparently operate in producing the characteristic oval shape have been studied by a few investigators whose views differ slightly. Ryder (1893) concluded that the shape of the egg was due to the resistance of the oviduct in front of the egg as it passed down the oviduct and to pressure behind the egg. Cushny (1902) observed that the muscular layer of the uterus was thicker than other regions so that the uterus apparently exercised the greatest influence in producing the shape of the egg. Szielasko (1905) suggested that the uterus gave the egg its definite form, whereas D'Arcy Thompson (1908) felt that the oval shape was due largely to the nature of the pressure exerted by the oviduct, the pressure being greatest behind the middle of the egg owing to the nature and direction of the peristaltic action of the oviduct.

Wickmann (1895), Patterson (1910), and others have claimed that the egg passes down the oviduct with the pointed end forward, whereas Jasse (1886), and others have stated that the egg is laid blunt end foremost. At the same time, it should be pointed out that careful observations on a large number of hens at the U. S. Animal Husbandry Experiment Farm at Beltsville, Maryland, have shown that eggs pass down the oviduct sometimes with the pointed end and sometimes with the blunt end foremost and are laid sometimes with the pointed end foremost and sometimes with the blunt end foremost.

After a careful study of the problem, Pearl (1909) came to the conclusion that although the general shape of the egg may be determined before it reaches the uterus, the particular form of each egg is determined by the muscular activity of the walls of the uterus. Curtis (1914*b*), however, concluded that the muscular activity of the oviduct was primarily responsible for the shape of the egg. R. and A. Serebrovsky (1926) state that not only the muscular activity but also the shape of the oviduct is a factor in determining the shape of the egg.

The problem of the variation in the shape of eggs has been investigated extensively by Asmundson (1931*a*), who performed operations on the oviduct and on the uterus to determine the effect on the shape of the egg. Altering the shape of either the isthmus or the uterus of the oviduct affected the shape of the eggs laid subsequent to the operation but the effect in some cases was not apparent, owing, Asmundson was led to believe, to the muscular activity of the oviduct. Asmundson concluded that there are three factors that determine the general shape of an egg: first, the amount of albumen secreted in the albumen-secreting portion of the oviduct; second, the size of the lumen of the isthmus and the albumen-secreting portion of the oviduct; third, the muscular activity of the walls of the isthmus and the albumen-secreting portion of the oviduct. It was further concluded that the general shape may be more or less altered in the uterus, which, together with the isthmus, gives each egg its particular shape.

Is Egg Shape Inherited in Mendelian Manner?—The inheritance of egg shape has been investigated to a slight extent only. Benjamin (1920) observed that egg shape is inherited, long, narrow eggs apparently being dominant to short, round ones, whereas Kopeć (1924) observed the reverse, but neither investigator made any determinations of the number of genes involved. Whether egg shape is inherited in Mendelian manner remains to be determined by carefully controlled experiments.

THE INHERITANCE OF EGG-SHELL COLOR

Certain breeds lay brown-shelled eggs and other breeds lay white-shelled eggs; it is very desirable for a flock in the first group to produce eggs of a uniform shade of brown, and in the second, all eggs should be free from tints, an objection sometimes encountered in Leghorn, Ancona, and other breeds that normally lay white-shelled eggs. The Araucana breed from South America lays an egg with a blue-tinted shell, but what produces the blue tint apparently has never been investigated.

In brown-shelled eggs the color is due to one type of pigment, the principal representative of which is ooporhyrin, according to Fischer and Kögl (1921, 1923). Although each hen lays eggs the shells of which are approximately the same shade, the degree of pigmentation is influenced by production. In fact, Benjamin (1920) found greater variability in the color of the shell than in the size and shape of eggs laid by the same hen. Benjamin states that "Each year there is a tendency for the eggs produced to gradually become whiter during the first five or six months of production, and then to become more tinted again toward the end of the production season." On the other hand, Kopeć (1927*a*) observed that the intensity of coloring decreased as production increased. The statement by Benjamin may be reconciled with the observation of Kopeć by assuming that in Benjamin's birds there was a decrease in the rate of laying after the first five or six months.

Kopeć also observed that short, round eggs tend to be more deeply pigmented than elongated eggs because the short, round eggs tend to remain for a longer time in the uterus, where the shell is colored. In this connection, Giersberg (1923) concluded that the pigmentation of the shell is completed in the uterus, whereas Asmundson (1931*a*) found that the isthmus portion of the oviduct influences the pigmentation of the shell. It seems highly probable, therefore, that both the isthmus and uterus portions of the oviduct are responsible for the pigmentation of the shell of the egg, most of the pigment being secreted in the uterus.

Genes Producing Egg-Shell Color.—The problem of the inheritance of egg-shell color is important from the standpoint of having a flock representing a brown-shelled breed lay eggs of an uniform brown color, but is still more important from the standpoint of eliminating birds that lay tinted eggs in a flock representing a white-shelled breed.

Hurst (1905), and Benjamin (1920) observed that the F_1 progeny produced by crosses between white-shelled and brown-shelled breeds laid eggs of an intermediate tint.

The most extensive investigation of the inheritance of egg-shell color is that by Punnett and Bailey (1920), a good summary of the results they secured being given by Punnett (1923). The conclusion arrived at was that the difference between breeds that lay white-shelled eggs and breeds that lay brown-shelled eggs is due to one pair of genes of major importance and several pairs of genes of minor importance.

Birds in which the gene of major importance is absent and the multiple genes of minor importance are also absent lay white-shelled eggs. Birds in which the gene of major importance is absent but one or more of the multiple genes of minor importance is present lay lightly tinted eggs, the degree of tint depending upon the number of multiple genes of minor importance present. Birds in which the gene of major importance is present lay dark-tinted-shelled eggs, the degree of tint depending upon the number of multiple genes of minor importance present. Birds in which the gene of major importance is in a homozygous condition lay eggs the shells of which are dark brown in color.

Punnett has also suggested that some strains that normally lay white-shelled eggs carry a gene that inhibits the development of pigmentation in eggs.

Kopeć (1927*b*) secured slightly different results from those of Punnett and Bailey and came to the conclusion that his white-shelled and brown-shelled egg breeds differed in several pairs of genes determining egg-shell color, all pairs apparently being of equal importance.

Apparently the only definite conclusion that can be drawn from the results secured in the studies on the inheritance of egg-shell color is that neither the white-shelled nor the brown-shelled character is dominant and that there are probably several pairs of genes that determine dark-brown pigmentation. From the practical standpoint it is obvious that poultrymen who breed Leghorns or other breeds laying white-shelled eggs should exercise the greatest care in eliminating all tinted-shelled eggs from among those to be incubated; also the birds that lay tinted-shelled eggs should be eliminated from the breeding flocks, and males from hens that lay tinted-shelled eggs should never be used as breeders.

Does Xenia Occur?—The phenomenon known as xenia refers to the supposed change in the shell-color of the eggs laid by a female after being mated to a male representing a breed which lays eggs of a different shell color from that of the breed to which the female belongs. For instance, if a Leghorn female, which normally lays white-shelled eggs, after being mated to a Plymouth Rock male lays tinted-shelled eggs, or if a Rhode Island Red female, normally laying dark brown-shelled eggs, after being mated to a Minorca male lays eggs the shells of which are lightly tinted, the phenomenon of xenia is said to occur. The semen of the male is supposed to affect the normal shell color of the eggs laid by the female.

Among the various reported instances of xenia the more noteworthy seem to be those of Holdefleiss (1911), v. Tschermak (1915), and Kopeć (1922). Holdefleiss claimed that Plymouth Rock females laid eggs with more lightly tinted shells after being mated to Leghorn males. v. Tschermak mated a Langshan male to a White Leghorn female, a Plymouth Rock male to a Brown Leghorn female, and a Cochin male to a White Minorca female, and claimed that there was a darkening of shell color in the eggs laid after each mating was made. Three reciprocal matings were made, and in each case v. Tschermak claimed that the shells of the eggs laid became lighter in color after mating took place. Kopeć observed that after Polish Greenleg females were mated to a Leghorn male they laid eggs the shells of which were lighter in color than their eggs of the previous year.

All these cases and others in which xenia is supposed to have occurred have been examined thoroughly by Kopeć (1926), who has shown that in every instance the results are inconclusive either because of the small number of birds involved or because of the small number of eggs on which the observations were based or because the various investigators failed to take into consideration the natural changes occurring in the pigmentation of the shell in relation to production. Walther (1914) claimed that the observations of Holdefleiss were entirely groundless. Kopeć criticized v. Tschermak's observations on the grounds that no "control" birds were observed, and Kopeć has pointed out that in connection with his own earlier observation of the supposed occurrence of xenia he had overlooked the periodical changes in shell color that usually take place.

The matter was investigated by Kopeć (1926) in reciprocal matings between White Leghorns and Buff Orpingtons, and "control" birds were also kept under observation. In addition, the results were carefully recorded for eggs laid by White Leghorn females into which were injected pieces of Buff Orpington testicles and for eggs laid by Buff Orpington females into which were injected pieces of White Leghorn testicles. Kopeć came to the conclusion that xenia does not occur in the domestic fowl.

ABNORMAL EGGS

In almost every flock abnormal eggs of one kind or another are sometimes produced. For the most part the laying of an abnormal egg is the result of some physiological disturbance, but since it is probably true that none of these abnormal egg characters is inherited they are reviewed here only briefly.

Abnormal eggs are of four major kinds: (1) dwarf eggs; (2) eggs with two or more yolks; (3) eggs within eggs; (4) abnormally shaped eggs.

Dwarf Eggs.—Dwarf eggs probably occur more frequently than all other kinds of abnormal eggs. Dwarf eggs have been studied by Pearl and Curtis (1916), who observed that 35.03 per cent of the dwarf eggs contained no yolks, 55.11 per cent contained a membraneless fragment of yolk, and 9.85 per cent contained a small yolk enclosed in a vitelline membrane. Dwarf eggs differ in respect to size and shape and, frequently, also in internal structure. Only in a few cases did Pearl and Curtis (1916) find that dwarf eggs were produced by hens with abnormal laying organs. Apparently dwarf eggs result from the secretion of albumen, shell membranes, and shell as a result of a stimulus having been exerted upon the oviduct, though in many cases no yolk at all or only a small portion of yolk is present. Asmundson (1931*a*) states that the production of dwarf eggs generally follows the ovulation of yolks that subsequently escape into the body cavity of the bird either intact or after the rupture of the vitelline membrane.

Féré (1898) claimed that the eggs at either end of the litter are smaller than the intermediate ones, but Warner and Kirkpatrick (1916) found that neither small nor large eggs are necessarily laid at the beginning or end of a hen's laying period but are more likely to be laid during the time of heavy production. Apparently the production of dwarf eggs is not an inherited tendency.

Eggs with Two or More Yolks.—The laying of eggs with two yolks contained in one shell is of relatively common occurrence, some birds showing a greater tendency to produce double-yolked eggs than other birds. At the same time, no evidence has ever been submitted to show that this tendency is inherited. The most common cause of double-yolked eggs, according to Curtis (1915*a*), is the fact that a yolk liberated from the ovary one day may be arrested in its progress down the oviduct so that the yolk liberated from the ovary the next day overtakes the first one and both are enclosed in the same shell membrane and shell.

Triple-yolked eggs have also been reported; they apparently owe their origin to the same causes that produce double-yolked eggs.

Eggs Within Eggs.—Cases have been reported from time to time of a complete egg being surrounded by another egg. According to Curtis (1916), sometimes the enclosing egg is normal, although frequently a yolk is not present, and sometimes the enclosed egg is a dwarf egg or a normal one. Asmundson (1931*a*) has described these and other cases of double eggs quite fully, but since their production seems to be due almost entirely to abnormal functioning of the oviduct, without any indications of being inherited, they are not discussed further here.

Abnormally Shaped Eggs.—Occasionally in almost any flock an egg is laid flattened on one side or with a stalk attached or with some other deformity. Such eggs are either the result of a disturbance in the normal activity of the oviduct or are due to yolk or albumen material lying in proximity to a normal egg causing a stimulus which leads to the formation of shell material around the extra yolk or albumen thus giving rise to a stalk attached to the egg.

PROBLEMS

1. Enumerate the more important factors that affect the weight of eggs laid by a given bird during her first laying year.

2. What is the relationship between egg production and egg weight during the first laying year?

3. To what extent might the annual mean egg weight of the first-year production be controlled by methods of feeding and management?

4. (*a*) Give at least two reasons why egg weight seems to be associated with body weight among birds of the same breed.

(*b*) Why is it that birds belonging to different breeds frequently differ significantly in body weight but lay eggs of approximately the same size?

5. What are the more important steps in breeding by which a poultry breeder may increase the average weight of the eggs laid by the birds of his flock?

6. What is the minimum number of eggs that must be weighed and what

portion of the first-year production of a bird should they represent in order that the annual mean egg weight of a bird may be approximated?

7. What is the proper basis for determining the inheritance of egg weight?

8. Of what importance is it to know how egg shape is inherited?

9. How can a breeder of White Leghorns most efficiently develop a flock which will never produce any tinted-shelled eggs?

10. Has the production of abnormal eggs by a breeder's flock any particular significance in his breeding operations?

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CHAPTER X

BREEDING PRACTICE

Except for the relatively few who can afford to indulge their interests in the breeding of poultry regardless of economic returns, the aim of practically every poultry breeder is to make his poultry-breeding operations as profitable as possible. Poultry breeding may be carried on with any of the following objectives in mind: the production of standardbred stock primarily for show purposes; the production of hatching eggs; the production of baby chicks; the production of broilers, roasters, or other classes of market poultry; the production of laying stock; the production of breeding stock for hatchery operators; and commercial egg production. Whatever may be the objective, the incentive is always the same, satisfactory financial returns on the money invested in the breeding operations.

Relative Importance of Egg Production.—In practically all countries, and especially in Canada, Australia, and the United States, the major receipts from all poultry products are obtained from market eggs. In some sections of the United States, for instance, market eggs contribute approximately 75 per cent or more of the total annual poultry receipts.

Breeding practice based on the principles of the inheritance of egg production, therefore, is of great practical significance to poultrymen. At the same time, it should be emphasized that the question of breeding the most suitable type of bird for meat production should not be neglected. The production of poultry meat and eggs should be combined to provide the greatest profits in poultry raising. Since egg production is so relatively important, however, it is well to consider certain practical factors that determine largely the revenue to be made from eggs.

Factors Affecting Economic Returns.—In actual practice there are four primary factors which affect labor income in the production of eggs for market. These four factors are: (1) the quantity of feed consumed, (2) the price of feed from time to time, (3) the number of eggs produced, (4) the prevailing price of eggs at the time of production. Under ordinary conditions the average quantity of feed consumed per bird from month to month is fairly stable. The poultryman has little or no control over the price of feed or the price of eggs. Feed prices vary somewhat from season to season throughout the year but not nearly to the same extent as egg prices. In many respects the poultryman can control egg production per bird, and it is this particular aspect that deserves special mention.

The data in Table 24 show clearly the extent to which the amount of labor income from the flock is governed largely by the average egg production per bird.

TABLE 24. RELATION BETWEEN LABOR INCOME AND AVERAGE EGG PRODUCTION PER BIRD

(Data of Misner, Johnson, and Marble, 1927)

Production Classification	Number of Farms	Hens per Farm	Eggs per Hen	Labor Income	
				Per Farm	Per Bird
Long Island:					
Less than 100 eggs........	8	929	84	$ 273	$0.29
100 to 150 eggs...........	12	1,234	132	2,431	1.97
More than 150 eggs.......	12	1,672	174	3,975	2.38
Other New York Farms:					
Less than 100 eggs........	17	1,036	80	1,255	1.21
100 to 150 eggs...........	77	1,003	129	1,346	1.34
More than 150 eggs.......	27	979	167	2,786	2.85

The correct basis for determining the worth of any hen as a layer should be not only the total number of eggs produced during the year but also the season of production. Ten eggs laid in the fall and early winter are worth approximately twenty laid in the spring and early summer. In the northern hemisphere the average farm hen lays principally from March to June, the season of lowest prices, and, consequently, of relatively lower profits than other times of the year. A study of the trend in the average monthly farm prices in the United States from 1910 to 1924 shows that lowest wholesale egg prices prevail in April, and that there is a slight increase in July and August, with a more perceptible increase beginning in September. The highest price is often reached in October and November. Moreover, if there is good egg production during the fall and winter the average price per dozen for the year is increased. During recent years in the United States the practice of hatching in January and February has been on the increase, since many poultrymen have found that they could have their pullets laying well in the early fall and thus take advantage of the relatively high egg prices prevailing at that time.

Selection Is the Basis of Improvement.—From the discussion in the preceding chapters it is apparent that the problem of developing the most useful and profitable kind of flock of any particular breed is a very complex one because of the number of factors involved. Not only must laying performance, which in itself is affected by a number of physiological factors, be observed over a period of at least a year, but other matters must also be considered, such as the size and standardbred quality of the birds and the size of egg. These considerations are necessarily involved because the breeding stock produced must embody certain minimum qualifications in order to be of the greatest practical usefulness. Future progress in breeding for increased egg production depends largely upon the poultry breeder's ability to control heredity, and heredity can be controlled and directed best only when the poultry breeders acquire sufficient knowledge to enable them to select breeding stock that will transmit to their offspring the most desirable qualities. Selection is the keynote in the program of future development. The refinement of methods of selection, therefore, is a very important problem confronting poultry breeders of today.

More and more is the poultry breeder confronted with the question: How can one best select and breed his birds for the production of offspring possessing the most desirable qualities? A certain male may be of excellent type and color and may be the son of a female that laid 280 eggs, but all his 7 sisters may have laid an average of only 180 eggs each; should such a male be used as a breeder? Another male has a superior ancestry from the standpoint of egg-laying ability, but possesses a standard disqualification; should he be used as a breeder? Still another male has 8 sisters that laid an average of 240 eggs each but the male's dam laid small eggs; should he be used as a breeder? A certain female may have laid 320 eggs averaging 21 ounces to the dozen; should she be used as a breeder? Another female may have laid 260 eggs and 5 of her sisters may have laid an average of 230 eggs each but the female herself has a crooked keel; should she be used as a breeder? Still another female may have laid 250 eggs, but when she was used as a breeder only 50 per cent of her fertile eggs hatched; should she be used again as a breeder? A male and female when mated together may have produced 6 daughters, 3 of which laid an average of over 220 eggs each and 3 an average of only 140 eggs each; should either the sire or dam be used again and should the 3 best-producing daughters be used as breeders? These are only a few of the practical problems that confront the poultry breeder every breeding season.

It is the great variability that exists among the members of a flock regarding such matters as type, size, plumage color, defects and disqualifications, number of eggs laid, size of egg, hatchability of eggs, and kind of progeny produced that makes the problem of selection such an important one. Without intelligent selection of the birds to be used as breeders little progress can be expected. Mass mating is relatively ineffective in increasing the average egg production of the flock beyond an average of about 150 eggs per bird. The average quality of a flock in respect to any character can best be improved by the mating of selected individuals of superior quality.

THE SELECTION OF BREEDING STOCK

Every poultry breeder should always remember that, in chickens, life begins with the egg. From the standpoint of reproducing the flock from year to year the egg is the connecting link between ancestors and progeny. The fertile egg is the product of the union of the male and female reproductive cells, the spermatozoon and the ovum, and the kind of egg that results from the union is determined by the kind of birds that are mated. Progeny of superior quality can be produced only by breeding stock of superior quality.

Every bird used as a breeder should be carefully selected on the basis of the following six points:

1. Standardbred and production quality—the degree to which the bird conforms to the type and size standards of the breed and the color standards of the variety it represents and the extent to which certain physical characters indicate laying condition and laying ability.

2. Constitutional vigor—a most important requirement in all breeding stock.

3. Ancestry—the kind of a sire and dam, grandparents, and great grandparents, particularly from the standpoint of their rating under the six points enumerated here.

4. The kind of brothers and sisters.

5. Reproductive performance—if the bird has been used once as a breeder, what was its record from the standpoint of the fertility and hatchability of its eggs and the viability and growth of its chicks?

6. The kind of progeny produced, particularly from the standpoint of the quality of the sons and the quality, laying performance, and size of egg of the daughters.

In addition to this six-point selection program for all birds used as breeders, the females should also be selected on the basis of a seventh point:

7. Laying performance—the number of eggs laid during the first and later years and the size and quality of eggs laid.

If the males used as breeders each year are carefully selected on the basis of the first six points given above so far as information is available and if the females used as breeders each year are carefully selected on the basis of all seven points it can be said that the poultryman has adopted the safest plan that leads toward progress in developing an egg-laying strain. As a matter of fact, exclusive of factors associated with egg production, the selection of males and females for breeders on the basis of the first six points given above is the best policy for every poultry breeder to follow, whether the object is to produce exhibition stock or market poultry.

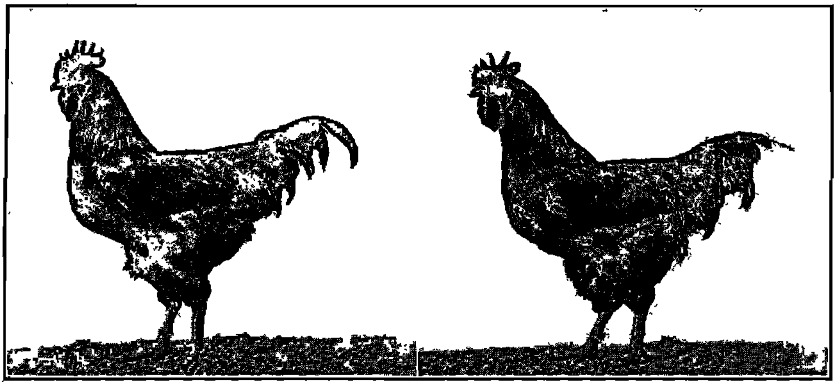

Fig. 51.—Two full-brothers that gave distinctly different results in breeding. Their dam laid 229 eggs and their granddams 219 and 230 eggs each. Each male was mated to females that had laid 225 or more eggs in their first laying year. In the fall of the year the daughters of the two males were selected for the laying house on a family basis, each family having 5 or more full-sisters. Of the 17 selected daughters of the male on the left 4 died during the first laying year and the other 13 laid an average of 159.85 eggs each. Of the 39 selected daughters of the male on the right 3 died during the first laying year and the other 36 laid an average of 205.75 eggs each. The progeny test revealed the difference in the breeding value of these full-brothers. (U. S. D. A.)

Select for Standardbred and Production Quality.—Reasonable care must be taken to maintain standardbred qualities, particularly breed type and plumage coloration, as well as freedom from inherited defects or disqualifications such as side sprigs, stubs on the shanks of breeds with nonfeathered shanks, squirrel tails and wry tails. In Chapter I various standardbred qualities are discussed in detail. The possibility of combining breed type and other standardbred qualities with egg production is present in the case of practically all popular breeds and varieties, although it is apparent that the greater the number of desirable characters being bred for the more complex becomes the breeding program.

There are certain characters that indicate whether or not a hen is in laying condition, and if females are examined sufficiently often the birds that are good producers throughout the year can be identified. The following characters are among the more important ones that indicate when a hen is in laying condition: bright red, smooth, and waxy comb and wattles, a good distance between the pubic bones, a good distance between the ends of the pubic bones and the end of the keel, and a large moist vent.

Among the more important physiological characters that are indicative of continuous egg laying for periods of varying lengths are the smooth texture of the skin, the bleaching of the beak and shanks in breeds and varieties that normally have yellow-colored beaks and shanks, and the lateness and speed of molting.

Skin Texture.—Although no statistical study has apparently been made concerning the texture of the skin over the face and body of birds in its relation to egg-producing ability, nevertheless, it has been apparent for some time that a thick skin of coarse texture is characteristic of poor layers. The so-called "beefy" type of head seems to be due largely to the presence of a thick, coarse skin over the skull and face. The skin over the body parts of a good layer is usually more soft and pliable than that of a poor layer and there is less tendency to accumulate excess fat in the body because the good layer uses it in the production of eggs instead of storing it.

Changes in Pigmentation in Relation to Production.—The yellow pigment in the beak and shanks of breeds that normally have yellow skin color tends to disappear as egg production continues. According to Palmer (1915), the intensity of the pigment is due in part to the presence in some feeds of a certain pigment called "xanthophyl." Yellow corn and green feed contain xanthophyl; but, if rations are fed that do not contain this pigment, the beaks and shanks may be relatively pale, even though the hens may have laid but few eggs.

When normally yellow-skinned breeds are given feeds rich in the pigment, the commencement of laying diverts the pigment received in the feed to the yolks, according to Palmer and Kempster (1919*a*). That continuous production tends to deplete the pigment contained in the beak and shanks was first demonstrated by Blakeslee and Warner (1915) and later by Palmer and Kempster (1919*b*).

The order in which the pigment disappears from different parts of the bird is: from the vent; then from the eye ring, which is formed by the inner edges of the eyelid; then from the earlobes of breeds having normally white earlobes; then from the beak, beginning at the base and extending toward the tip; and finally from the shanks, disappearing first from the front of the shank and later from the rear. Under average conditions a completely bleached beak indicates that the hen has been laying from 4 to 6 weeks whereas completely bleached shanks indicate that the hen has been laying from 15 to 20 weeks. When laying ceases, the pigment reappears in the different parts of the body in the same order in which it disappeared.

The Annual Molt in Relation to Egg Production.—Concerning the phenomenon of molting, of particular interest is the physiological relationship between egg production and the time of year that molting occurs as well as the rate of molting. Whether the factors which determine the time of year that molting normally occurs and the rate of molting are factors which also bring about cessation or decrease of egg production or whether definite factors controlling egg production bring on the molt apparently have not been established. Which is cause and which is effect no one seems to know.

It has been established, however, that females that molt early in their first laying year are usually poor layers, whereas good layers are usually late molters. The time and rate of molt in relation to egg production have been fully discussed by Rice, Hall, and Marble (1930), and their book should be consulted by those who wish to go into details regarding the order in which fowls molt and the length of time required to renew feathers in different sections of the body.

Additional information on the relationship between the duration of the molt and egg production has been supplied by Hays and Sanborn (1930). In a study of Rhode Island Red females hatched during 1917 to 1928, inclusive, Hays and Sanborn observed that there was a significant negative correlation between the number of eggs produced previous to the molt and the duration of the molt, which means that the birds which molted most rapidly were among the best layers. They also found that the most rapid molters were among the best second-year producers. Both intensity and persistency of egg production are correlated with rapidity in molting.

Head Characters in Relation to Egg Production.—The importance of good head shape has been emphasized by different investigators. Steup (1929) points out that the most desirable features include flatness of skull from side to side, width of skull carried well forward, good depth of head in relation to its length, and levelness of the top of the skull from front to rear.

A survey of the literature reveals the fact that very few head measurements have ever been made to determine the significance of head shape or type in relation to egg production. Waters (1927), with 200 Single Comb White Leghorns, found that the correlation between the width of cranium and egg production was —0.19 ± 0.05 and that between depth of head and egg production was 0.10 ± 0.05. Both correlations are of low value, the latter having no significance whereas the former indicates that the narrower the cranium the better the production in the birds that Waters examined, this being contrary to popular opinion.

Fronda and Gamo (1931) compared 11 different head measurements with egg production in 75 Cantonese pullets and 111 Cantonese hens, several of the correlations obtained being contrary to popular opinion.

Jull, Quinn, and Godfrey (1932) in 52 Single Comb White Leghorns and 50 Rhode Island Reds, determined the correlation between gg production and each of the four following head measurements, made on the live birds: (1) from base of upper mandible to top of skull, (2) from base of upper mandible to rear of skull, (3) greatest width over top of skull, and (4) from top of skull to point directly below at base of skull. The correlations obtained indicate that in these two flocks the shape of head had little to do with egg-producing ability.

In order to determine any possible relationship between egg production and each of the three characters, length, breadth, and depth of skull, the heads of 51 Single Comb White Leghorn yearling hens were boiled, the skin and appendages removed, and measurements taken between certain fixed points. The data obtained show that in not a single instance was there any significant correlation between any of the three skull measurements and egg production, total egg weight, and mean egg weight. Apparently, then, in this group of 51 White Leghorns neither length, nor breadth, nor depth of skull bore any relation to egg-laying ability.

The multiple correlation between length, breadth, and depth of skull and egg production was 0.14, which gives a multiple determination coefficient of 0.02, which means that the three skull characters accounted for only 2 per cent of the variability in egg production in the group of 51 birds. This observation shows that the shape of the skull can hardly be used as a reliable guide in the selection of females to be used as breeders.

The simple correlation coefficient between brain weight and egg production was found by Jull, Quinn, and Godfrey (1932) to be —0.03 ± 0.09; between brain weight and total egg weight, —0.001

± 0.094; and between brain weight and mean egg weight, 0.16 ± 0.09. Since none of these three correlation coefficients is significant, it is apparent that total brain capacity bore no relation to egg-laying ability in this group of birds.

In a group of 100 S. C. White Leghorns as well as in a group of 47 Barred Plymouth Rocks, Marble (1932) found that there was no consistent relationship between egg production and six length, two depth, and six width measurements of the skulls.

Body Form in Relation to Egg Production.—Several investigators have made measurements pertaining to body form in its relation to egg production, the measurements being made on live birds. The observations, among the most important of which are those of Asmundson (1921), Sherwood (1922), Hall (1923), Waters (1927), Sherwood and Godbey (1928), and Scholten (1927), show considerable lack of agreement. Jull, Quinn, and Godfrey (1932) have shown, however, that measurements made on live birds cannot safely be used in determining differences in skeletal structure among birds. The same authors have also shown that live bird measurements are of practically no value in selecting birds on the basis of their egg-laying ability.

Careful measurements were made with calipers of the length and width of back and length of keel of 237 White Leghorns that had completed their first year of egg production. No culling had been done during the first year of laying. The birds were divided into three groups as follows: 54 highest producers, 132 intermediate producers, and 51 lowest producers. The mean egg production of each of the groups was as follows: highest producers, 244.91 ± 1.18 eggs; intermediate producers, 200.26 ± 0.94 eggs; lowest producers, 156.43 ± 2.79 eggs.

The length of the back from base of neck to base of pygostyle, the width of back from femur joint to femur joint, and the length of the keel were first measured on the live birds of each group and then the birds were killed and plucked and the same measurements were made on the dressed carcasses. In addition, the same measurements were made of the bones of the 54 highest producers and the 51 lowest producers after the carcasses had been boiled and the flesh removed. The various measurements are given in Table 25.

The data in Table 25 show that the three groups of producers vary only slightly in all three measurements, regardless of whether the measurements were made on the live birds, on the dressed carcasses, or on the bones. The differences in live-bird and dressed-carcass length of back, width of back, and length of keel between the highest and lowest producers are so small as to indicate the impossibility of determining laying ability on the basis of body type.

The differences in live-bird and dressed-carcass measurements between the highest and intermediate producers are practically negligible. The lowest producers were slightly larger than both the highest and intermediate producers, as indicated by the slightly greater length and width of back and length of keel; at the same time, the difference in mean body weight between the two groups was not significant, the mean weight of the highest producers being 1934.25 ± 24.01 grams and that of the lowest producers being 2037.25 ± 34.31 grams.

TABLE 25. MEAN LIVE-BIRD, DRESSED-CARCASS, AND BONE MEASUREMENTS IN THE HIGHEST, INTERMEDIATE, AND LOWEST PRODUCING GROUPS OF A FLOCK OF WHITE LEGHORNS

(Data of Jull, Quinn, and Godfrey, 1932)

Measurements	54 Highest Producers	132 Intermediate Producers	51 Lowest Producers
Live birds	Inches	Inches	Inches
1. Length of back	6.39 ± 0.03	6.38 ± 0.01	6.47 ± 0.03
2. Width of back	3.47 ± 0.02	3.36 ± 0.01	3.50 ± 0.02
3. Length of keel	4.19 ± 0.02	4.18 ± 0.01	4.36 ± 0.02
Dressed carcasses			
1. Length of back	6.28 ± 0.03	6.03 ± 0.01	6.54 ± 0.02
2. Width of back	2.93 ± 0.01	3.02 ± 0.01	3.09 ± 0.02
3. Length of keel	3.85 ± 0.02	3.87 ± 0.01	4.02 ± 0.02
Bones			
1. Length of backbone	5.45 ± 0.02	—	5.45 ± 0.03
2. Width of backbone	2.12 ± 0.01	—	2.23 ± 0.02
3. Length of keel	3.60 ± 0.03	—	3.80 ± 0.02

The data in Table 25 regarding bone measurements of the highest and lowest producers show that the length of backbone in the two groups was the same but that the width of backbone and length of keel were slightly greater in the lowest producers than in the highest producers. Although the differences in width of backbone and length of keel are significant, it is obvious that they are so slight that they could not serve as an index of laying type.

It should be pointed out here, however, that Macht (1930) demonstrated that in a group of 154 White Leghorns at the Bavarian Poultry Institute at Erding, Germany, the birds which proved to be the best layers were, for the most part, those which at 18 weeks of

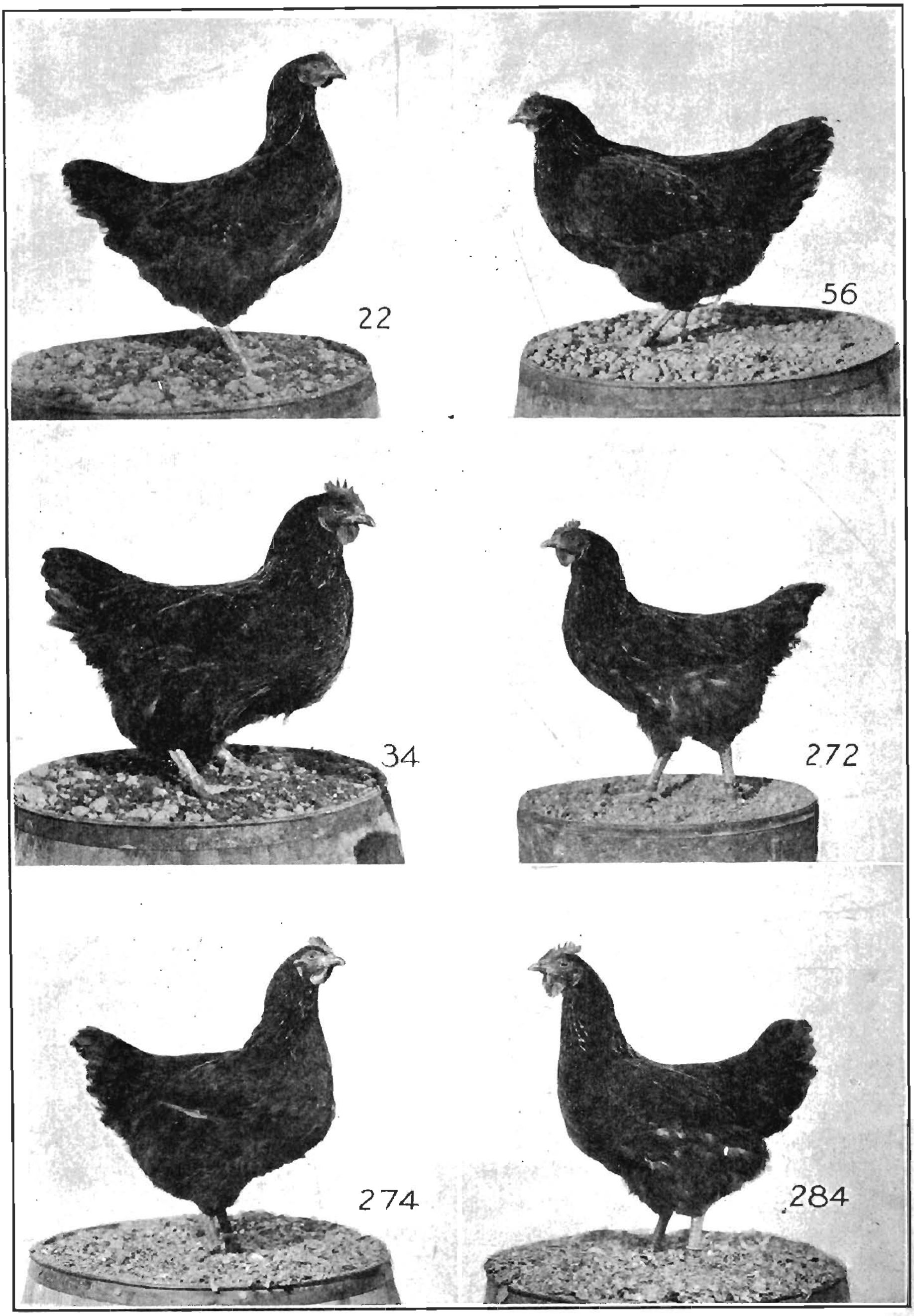

FIG. 52.—In this group of Rhode Island Reds first-year egg production varied from 22 to 284 eggs. It would be difficult, except for differences in breeding, to tell why the bird in the upper left (22 eggs) and the bird in the center right (272 eggs) should differ by 250 eggs. The bird in the upper right (56 eggs) appears to lack vigor. The bird in the center left (34 eggs) inherited the tendency to produce flesh rather than eggs. The two lower birds are of superior breeding. (Photo by U. S. D. A.)

age had the greatest length, width, and depth of body, greatest length of keel, and greatest length and width of head. Observations were also made on the pullets at 11, 15, 22, 26, 30, and 34 weeks of age, but the observations made at 18 weeks were found to be the most significant; in fact, at 26 weeks and later it was found that body shape bore no significant relationship to first-year egg production. Macht's findings tend to support the observations made in Chapter VIII that early-maturing pullets tend to be the best layers and also the observations made in this chapter that among fully matured birds body shape apparently is not related to egg production.

Jull, Quinn, and Godfrey (1932) observed that there was no significant correlation between each of the three bone measurements and egg production in a group of 24 Single Comb White Leghorns and in a group of 51 Single Comb White Leghorns. In the group of 24 birds the multiple correlation coefficient between the three bone measurements and egg production was found to be 0.29, which gives a multiple determination coefficient of 0.08, which means that the three characters measured accounted for approximately 8 per cent of the variability in egg production, leaving approximately 92 per cent of the variability in egg production unaccounted for. In the group of 51 birds the multiple correlation coefficient between the three bone measurements and egg production was found to be 0.44, which gives a multiple correlation determination of 0.19, which means that the three characters measured accounted for approximately 19 per cent of the variability in egg production, leaving approximately 81 per cent of the variability in egg production unaccounted for. The observations made on these two groups of birds show, therefore, that the shape of the body apparently has little influence on egg production.

In the group of 51 birds the multiple correlation coefficient between the three bone measurements and total egg weight per bird was found to be 0.43, and the multiple correlation between the three bone measurements and mean egg weight per bird was found to be 0.42. These correlations are of relatively low value and indicate that neither the total weight of eggs produced by a bird in her first laying year nor the mean egg weight of her first-year production is greatly influenced by the shape of the body of a bird.

An observation made recently regarding the similarity between the skeletal structure of the beef and the dairy cow is of interest in this discussion. Swett, Graves, and Miller (1928) compared the conformation, anatomy, and skeletal structure of a highly specialized Aberdeen Angus with that of a highly specialized Jersey and drew the following conclusions:

> In external form the two cows differed greatly. In weight and size of internal organs, the differences were not sufficiently great to indicate significant differences in function. In skeleton structure the two cows varied somewhat but were generally similar. This would indicate that the evolution of the dairy and beef types, which has been accomplished through breeding and selection, has not materially altered their skeletal structure, but rather that the difference in type is due to extreme fleshing on the one hand and to udder development and absence of fleshing on the other. Aside from the external form, the most marked difference noted between the cows compared was the quantity of secretory tissue in their udders.

Apparently the outstanding difference between beef and dairy cows is in respect to the physiological aspects of flesh production and milk secretion, the physiological characters being transmitted through the agency of genes, which are inherited.

For the domestic fowl the available evidence to date goes to show that flesh production and egg production are apparently inherited largely independently of skeletal structure. Kopeć (1927) and Hutt (1929*a*) have supplied evidence showing that while there are genes responsible for the development of the size of all parts of the body, there are also other genes affecting the development of the size of individual bones. If such is the case then if skeletal structure is definitely associated with egg-laying ability there should be linkage between the genes determining bone size or length and the genes determining egg production. Such, however, has never been demonstrated; in fact, practically all the available evidence indicates that type as determined by skeletal structure is not intimately associated with egg-laying ability.

Body Weight and Egg Production.—The relationship between body weight and egg production has been studied by a few investigators, the simple correlation between the two characters being given in Table 26.

It is to be noted that all the correlation coefficients given in Table 26 are of relatively low value and only the first, the third, and the last have any significance. In these three cases only is the correlation more than three times its probable error. Moreover, among Asmundson's White Leghorns the larger birds tended to be the better layers whereas among Hall's White Leghorns the smaller birds tended to be the better layers.

Apparently size of bird in itself is not a criterion of egg-producing ability. This is borne out by the differences in mean body weight between 52 White Leghorns and 50 Rhode Island Reds reported upon by Jull, Quinn, and Godfrey, mentioned previously. The mean body weight of the White Leghorns was 4.55 ± 0.55 pounds and the mean

TABLE 26. SIMPLE CORRELATION COEFFICIENTS BETWEEN BODY WEIGHT AND FIRST-YEAR EGG PRODUCTION AS DETERMINED BY VARIOUS INVESTIGATORS

Year	Investigator	Breed	Correlation Between Body *Weight and Egg Production*
1921	Asmundson	White Leghorns	+0.23 ± 0.04
1922	Sherwood	" "	+0.01 ± 0.06
1923	Hall	" "	−0.21 ± 0.06
1927	Platt [1]	" "	+0.07 ± 0.03
1927	Platt [2]	" "	−0.06 ± 0.03
1927	Waters	" "	−0.02 ± 0.05
1928	Sherwood and Godbey	" "	+0.18 ± 0.07
1930	Atwood and Clark	" "	+0.11 ± 0.05
1932	Jull, Quinn, and Godfrey	" "	+0.12 ± 0.09
1924	Hervey and Lewis	B. P. Rocks	+0.13 ± 0.07
1924	Jull	" " "	−0.11 ± 0.09
1932	Jull, Quinn, and Godfrey	R. I. Reds	−0.31 ± 0.09

NOTE: [1] and [2] represent two different flocks.

egg production was 175.70 ± 4.15, whereas the mean body weight of the Rhode Island Reds was 6.50 ± 0.09 pounds and the mean egg production was 162.00 ± 4.57. The difference in weight is 1.95 ± 0.10 and is significant, whereas the difference in egg production is 13.70 ± 6.17 and is not significant. It is quite apparent, therefore, that birds of equal egg-laying ability may differ significantly in respect to body weight and also that birds of the same body weight may differ significantly in egg production, depending largely upon their breeding.

Attention is called to the fact that the data in Table 16 show that among the Rhode Island Reds bred at the Massachusetts Experiment Station the best layers weighed from 4.00 to 4.49 pounds in the 1928 flock and from 4.50 to 4.99 pounds in the 1929 flock.

On the whole, the breeding quality of the birds rather than their body weight would seem to be the major factor of importance in determining egg-laying ability, but the poultry breeder should always keep in mind the fact, as pointed out in Chapter IX, that within each breed the smaller the female usually the smaller the egg she lays.

Select Breeding Stock for Constitutional Vigor.—Every poultry breeder appreciates the importance of selecting breeding stock possessing an abundance of constitutional vigor. The basis of selection often differs among poultry breeders because there is little definite information regarding exactly what constitutes vigor. As

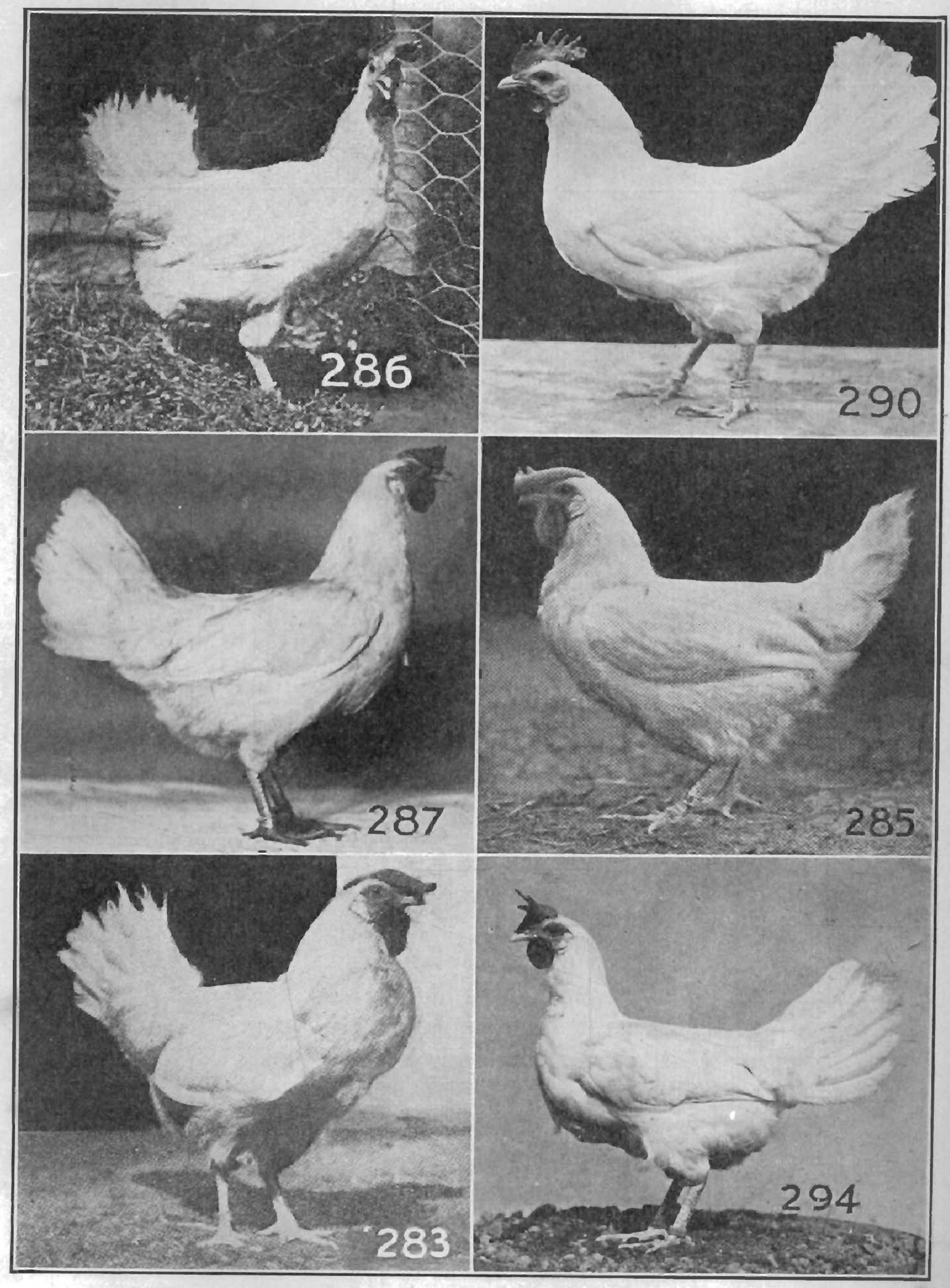

FIG. 53.—Females of the same variety may vary considerably in outward appearances but still lay approximately the same number of eggs. The laying ability of a bird is determined by its breeding.

pointed out in Chapter VI, a bright eye and glossy plumage are indicative of health, and a well-proportioned bird is much more desirable than a long-legged, knock-kneed specimen or one that is obviously weak. Although there is relatively little definite information regarding the extent to which various characters are associated with egg production, the poultry breeder can at least eliminate the obviously unfit.

Select Breeding Stock on the Basis of Ancestry.—A bird's ancestry gives considerable information of value regarding the relative worth of the bird as a prospective breeder. Of two good birds that laid the same number of eggs of approximately the same size, the bird with a good ancestry is to be preferred to the bird with a poor ancestry. The chances that the bird of good ancestry will produce progeny possessing the desirable characters being bred for are greater than those of the bird with poor ancestry; the chances are greater—but there is no guarantee that a good bird of good ancestry will always produce good progeny.

Good ancestry is an important factor in increasing the chances that the bird thus selected will give better results in breeding. But in order that the poultry breeder may make the best selection of his breeding stock he needs to consider more than the characters which the bird itself possesses and its ancestry; he should also consider the kind of brothers and sisters the bird has.

Select on the Basis of the Kind of Brothers and Sisters the Bird Has.—The selection of a bird as a prospective breeder on the basis of the kind of brothers and sisters it has is the next progressive step in the selection of breeding stock. Of two good birds that resemble each other closely the one belonging to a good family is likely to give better results as a breeder than the one belonging to a poor family. Of two good males each with a good ancestry, the one with 5 good brothers should be a better breeder than the other one with 5 poor brothers. Other things being equal, a female that laid 220 eggs and had 7 sisters all of which laid over 200 eggs each should be a better breeder than a female that laid 280 eggs but had 7 sisters none of which laid over 200 eggs. A female with a record of 230 eggs averaging 2 ounces per egg, having 5 sisters each of which laid 200 or more eggs averaging 2 ounces per egg, should make a far better breeder than a female with a record of 260 eggs averaging 1.6 ounces per egg, having 5 sisters each of which laid 220 or more eggs averaging 1.8 ounces each.

As pointed out in Chapter VIII, one of the most effective steps that a poultry breeder can take to breed for increased egg production is to select breeding cockerels according to the laying performance of their full-sisters from the time they commenced laying to the time the cockerels are selected. The cockerels best suited for future breeding purposes should be among those whose full-sisters commenced laying at approximately 150 to approximately 200 days of age, laid at a rate approximating 60 per cent and laid eggs of good size, the importance of which is discussed in Chapter IX. If pullets are used for breeding purposes they should also be selected on the basis of the laying performance of their sisters from the commencement of laying to the time of selection.

The kind of brothers and sisters a bird has is often of greater value than its ancestry in determining a bird's worth as a prospective breeder. Particularly is this the case if the reproductive performance and kind of progeny produced by any of the bird's brothers and sisters that were used as breeders are taken into consideration.

Select on the Basis of Reproductive Performance.—In the selection of breeding stock some consideration should be given to the reproductive performance of the ancestry as well as of the bird itself, if it has been used as a breeder. The reproductive performance of a bird has reference to the relative number of fertile eggs produced, the relative number of fertile eggs that hatched, and the relative number of chicks that lived and grew well.

Fertility apparently is not inherited, but high fertility in the eggs produced by a given mating is desirable in order that as many progeny as possible may be secured. On the other hand, hatchability is inherited, as pointed out in Chapter VI, and in selecting birds for the breeding pen the hatchability of the ancestors of each bird should be taken into consideration. If the bird itself was used as a breeder then the results in hatchability secured from the mating in which the bird was used should be carefully considered before deciding to use the bird a second time. ✓If one female among 12 mated to a male gave poor hatchability as compared with good hatchability of the other 11, there is no good reason for using the hen showing poor hatchability a second time regardless of how good she may be otherwise. A hatchability of 75 per cent of the fertile eggs produced is a good minimum to use as the basis of selecting breeding stock.

The viability and growth of chicks produced by a bird's ancestors are other factors that should be taken into consideration in the selection of breeding stock. A bird representing a family of chicks most of which died or grew very poorly should never be used as a breeder regardless of how good it may be in other respects. So also, if the bird itself upon being bred the first time produces a family of chicks most of which die or grow poorly it would be doubtful wisdom to use the bird again as a breeder.

Select on the Basis of the Kind of Progeny Produced.—The supreme test of the worth of a bird as a breeder is the kind of progeny it produces. When a bird is selected as a breeder for the first time the progeny test cannot be applied, of course, because no progeny has been produced. However, what should be done then is to consider the kind of progeny produced by the bird's ancestors. To some extent this is the same thing as considering the kind of brothers and sisters the bird has, but the kind of progeny produced by the bird's grandparents should also be considered. A bird whose parents and grandparents produced a relatively high proportion of good progeny is much more likely to produce good progeny than a bird whose parents and grandparents produced only a relatively few outstanding individuals.

The progeny test should be applied to the bird itself, providing it meets the requirements concerning standardbred and production quality, constitutional vigor, good ancestry, and has a high proportion of brothers and sisters that possess the desirable qualities being bred for. These various requirements should be met in order to insure that the bird to be tested is a superior individual, for it is only a waste of time to apply the progeny test to a mediocre specimen. To apply the progeny test to a bird, use it as a breeder one year and keep careful records regarding the kind of progeny produced, particularly from the standpoint of the quality of the sons and the quality and laying performance and size of eggs of the daughters. The kind of progeny produced the first year is the only way of determining a bird's real worth as a breeder, and those that produce superior progeny should be used as long as they live.

A practical way of applying the progeny test in the case of male breeders that have been used has been suggested by Hagedoorn (1926). Trap-nesting is not necessary, providing the progeny secured from each male breeder is kept in a separate house. By comparing the average egg production of the progeny of each male the poultry breeder should be able to decide which male to use again if necessary, and he should also be able to decide from which male's progeny to select pullets and cockerels for future breeding purposes. Such a plan of progeny testing should be used by all poultrymen who do not trap-nest their layers. Those who trap-nest their layers should also apply the progeny test to the female breeders used, for it is only by applying the progeny test to both males and females that the greatest progress can be achieved in breeding for increased egg production.

Select Female Breeders on the Basis of Laying Performance.—The selection of females for breeders by their laying performance is a relatively simple matter both for those who trap-nest their layers and those who do not.

For those who trap-nest their layers, the method of selecting females for future breeding purposes based on information given in Chapter VIII should be followed. Briefly, the method suggested includes the following factors:

✓1. Age in days laying commenced, from approximately 150 to 200 days.

✓2. A rate of egg production approximating 60 per cent.

3. Absence or nearly complete absence of broodiness.

4. A production of approximately 30 or more eggs during August and September in the years following that in which the bird was hatched.

5. Size of egg at least 2 ounces each during the breeding season in the case of each pullet, the importance of this factor having been discussed in Chapter IX.

Voitellier (1930) has shown that the best layers in a flock can be identified for the most part if the birds are trapped either one day each week throughout the year, two consecutive days each week throughout the year, or one week during each month of the year. Dudley (1931) has shown that trapping one day each week throughout the year or trapping four consecutive days one month apart throughout the first laying year serves quite well in selecting the best annual layers. According to the observations of Voitellier and Dudley it should be quite possible for a poultryman to select the best breeding females from year to year by trapping his layers one or two days of each week or better still by trapping them for four consecutive days one month apart instead of having to trap-nest the year round.

For those who do not trap-nest their layers, the selection of females for future breeding purposes by their first-year laying performance can be accomplished quite successfully. At the time each pullet commences laying she should be banded with a numbered aluminum or colored celluloid leg band; a very simple way of determining the approximate time a pullet commences to lay is by noting the development of the comb and wattles and width between the pubic bones. Pullets that lay at a high rate can be detected by the degree of the bleaching of the yellow pigment from the beak and shanks; during December or January the layers should be examined and those with the whitest beaks and shanks and in good physical condition should be banded. Every time a bird goes broody she should be banded. Persistent layers could be identified by banding those birds that are laying well during August and September, just before the end of the year; note the condition of the comb, wattles (which should be red and expanded), the width apart and flexibility of the pubic bones, the time of year of molting (especially noting whether molting has taken place before September), and the well bleached beak and shanks.

Such a system of banding is entirely practical and should do a great deal to enable the poultryman who is not trap-nesting to select the best layers for breeding purposes. The banding of the birds should follow a definite method so that at the end of the year the best layers may be identified at a glance. If numbered aluminum bands are used the numbers could be recorded under the four headings—earliness of maturity, rate of production, broodiness, and persistency of production. Numbers recorded under the first two and the last headings indicate desirable birds; numbers recorded under broodiness would indicate undesirable birds.

If colored celluloid bands are used, one color, such as red, should be placed on the left leg of each bird to denote earliness of maturity; another color, such as white, should be placed on the right leg of each bird to denote good rate of production; a black band should be used every time a hen goes broody; and a blue band should be used to identify the persistent layers. Red for an early start, white for bleaching after intensive laying, black in mourning for broodiness, and blue for persistency. At the end of the year the best layers would each have a red, a white, and a blue band.

Laying performance includes more than the mere number of eggs laid, however, because size of egg laid is of great economic importance particularly from the standpoint of selecting breeders. It has been pointed out in Chapter IX that pullets should lay eggs approximating the standard weight of 2 ounces or 56.7 grams per egg during February or March. Pullets laying eggs under standard weight during any part of the last 7 or 8 months of their first laying year should certainly not be used as breeders. The pedigree breeder who trap-nests can very readily select his breeding females on the basis of size of egg laid, but the poultryman who does not trap-nest would have greater difficulty, although by eliminating the smallest birds in his flock each year regardless of the number of eggs they laid he should tend to increase the average size of egg laid by his flock. ✓

The Most Desirable Breeding Age.—As compared with the larger classes of livestock, poultry are relatively short-lived creatures. The discussion in Chapter VIII reveals the fact that egg production declines steadily each year with the advancing age of the female. In the case of males, practical experience has demonstrated that in the great majority of cases their reproductive value declines rather rapidly after the first year, owing largely to the fact that as the male grows older the fertility of the eggs produced by the females to which he is mated usually declines. In other words, a given male usually produces a higher percentage of fertile eggs as a cockerel than as a yearling, and thereafter he is usually of relatively little value. It should be noted, however, that males of the lighter breeds, such as Anconas and Leghorns, usually do not show as great a decline in fertile eggs produced in relation to age as males of the heavier breeds, such as Jersey Black Giants, Light Brahmas, Plymouth Rocks, Rhode Island Reds, and Wyandottes. At the same time, when the progeny test reveals that a particular male is a valuable breeder, he should be used as long as possible. The same applies to a female.

Stewart and Atwood (1909) report that White Leghorn hens two and three years old gave better results than pullets in respect to percentage of eggs hatched, average size of chicks, and percentage of chick mortality. Pearl (1917) observed that in both male and female Barred Plymouth Rocks the reproductive capacity is greatest in the first breeding year as judged by the percentage of chicks alive at the end of the third week after hatching in proportion to the total number of eggs incubated during the breeding season. It should be noted, however, that during the breeding season the pullets laid better than the yearling hens, and, moreover, there is no information as to any differences in the size or vigor of the chicks from the two groups of birds. Kempster (1921) has reported that White Leghorn hens gave 4 per cent better hatchability of eggs set than pullets.

On the other hand, Richardson (1924-1925) has reported that 95 per cent of the commercial poultrymen in New Hampshire use pullets exclusively as breeders. The pullets are hatched during the latter part of February and during March, are early maturing, and after having laid well until the latter part of October usually undergo a partial molt and largely cease production for a period of a few weeks. The rest period apparently enables the pullets to become satisfactory breeders, since the results in hatchability of eggs and the viability of the chicks are reported to be good.

Jull and Quinn (1925) and Upp (1928) show that there is a definite relationship between size of egg and size of chick and, since yearling hens usually lay larger eggs than pullets, chicks from yearling hens are nearly always larger than those from pullets. Hays (1928) has observed from results secured with Rhode Island Reds that yearling hens gave a slightly higher percentage of hatchability than pullets.

One outstanding advantage in the use of yearling hens rather than pullets as breeders is that complete first-year records regarding laying performance and size of eggs laid are available for yearling hens and also for their full- and half-sisters.

Taking all the evidence available into consideration, it seems fairly evident that yearling hens may be expected to produce practically as good results as pullets in respect to hatchability, and that the chicks at hatching time are usually larger. If pullets are used as breeders, they should not be "forced" into excessive egg production prior to the breeding season. Poultry breeders would be well advised to use as breeders those hens which prove to be good layers over a period of years, since it is desirable to develop layers which lay well not only in their first year of production but also in their second, third, and fourth years.

INBREEDING AND ITS EFFECTS

Having taken the proper steps in the selection of the breeding stock the next step is for the poultry breeder to determine which of three different systems of breeding he should follow. The three systems of breeding include: inbreeding, including line breeding; crossbreeding or outbreeding; grading.

Inbreeding is the mating of relatives; and since there are degrees of relationship, such as full-brothers and sisters, aunts and nephews, uncles and nieces, first cousins, and tenth cousins, so there are degrees of inbreeding. There is what is called "close inbreeding," as full-brother × sister mating, and there is inbreeding of tenth cousins, which certainly could not be regarded as close inbreeding.

If a bird's parents are not related, its 4 grandparents are all different and its 8 great-grandparents are also all different. The number of different ancestors in the fourth ancestral generation is 16 and the number is doubled for each generation further removed from the individual, so that in the twenty-fifth ancestral generation there are 33, 554, 432 different ancestors. On the other hand, if a bird's parents are related, the number of ancestors in one or more of the ancestral generations is less than the greatest number possible. East and Jones (1919) say: "Strictly speaking, inbreeding refers only to the way in which individuals are mated together." The mating together of males and females that are full-brothers and full-sisters, the closest form of inbreeding that can be practiced.

From the practical standpoint the results secured in experime on inbreeding and crossbreeding are of interest to the poultry breed because he frequently is in a quandary whether he should use breeding stock within his own flock or purchase breeding stock from a outside source. He is frequently in a quandary whether or not h should crossbreed, especially to produce chicks with sex-linked characters which make it possible to separate the sexes at hatching time He is also frequently in a quandary whether or not he should mat males and females that are related. If such be desirable for th particular purpose in mind, there is still the question as to how closel related the males and females may be in order to secure the mos satisfactory results. Should a sire be mated to his daughters, da to son, brother to sister, or cousin to cousin, in an effort to impro egg production in a flock of birds? These are some of the questio in the minds of poultry breeders with the approach of every breedi season.

Only a few carefully controlled experiments on inbreeding poultry have ever been undertaken, but the results are very interesting. The results secured by various investigators are discussed from the standpoint of the effects of inbreeding on hatchability of eggs, viability of chicks, rate of growth and adult body weight, and egg production

Effects of Inbreeding on Hatchability of Eggs.—Cole an Halpin (1916) inbred Rhode Island Red full-brothers × full-sister for four years and observed a marked decline in vigor to such a extent that in the fourth year hatchability was so low that the exper ment had to be discontinued. Another inbreeding experiment, b Cole and Halpin (1922) produced similar results, according to Cole (1932).

Dunn (1923) reports the results secured in inbreeding six lines o White Leghorns in which the basis of selection each year was the number of full-sisters available for mating on February first of the pullet year. At that time the group was chosen which had the largest number of full-sisters and at least two full-brothers, one for mating and one for reserve. Hatchability decreased as inbreeding was continued whereas in the control lines hatchability did not decrease.

The results of an extensive series of experiments on inbreeding have been reported by Jull (1929*a*). Barred Plymouth Rocks, other varieties of Plymouth Rocks and White Leghorns, approximately 11 females per pen, were each mated to an unrelated cockerel. When the progeny of each pen reached maturity in the fall of the year, 5 fullsters and at least 2 of their full-brothers were selected from the male breeders in each pen that had the largest number of progeny t the time of selection. Two groups each of 3 half-sisters were also chosen from each pen and the related birds were inbred. The results, given in Table 27, show that such close inbreeding resulted in decreased hatchability.

TABLE 27. PER CENT HATCHABILITY AS AFFECTED BY FULL-BROTHER × FULL-SISTER AND HALF-BROTHER × HALF-SISTER MATINGS IN PLYMOUTH ROCKS AND WHITE LEGHORNS

(Data of Jull, 1929*a*)

Pen No.	Kind of Mating	Generation			
		P_1	F_1	F_2	F_3
1	B. P. Rock	72.42	38.62		
2	B. P. Rock	53.11	51.78		
3–4	B. P. Rock	76.20	42.62	44.42	23.17
5	Buff ♂ X White ♀	73.63	27.27		
6	White ♂ X Buff ♀	57.79	52.45		
7	Part. ♂ X S. P. ♀	66.58	63.30		
8	S. P. ♂ X Part. ♀	73.52	62.57		
9–12	White Leghorn	82.54	61.48	51.86	48.59

Jull (1929*b*) found that as the coefficient of inbreeding, determined by the formula developed by Wright (1923), was increased the hatchability was decreased.

The effects on hatchability of different degrees of inbreeding have been given by Dumon (1930), Leghorns being used in his experiment conducted at the Boerenbond Experiment Station in Belgium. Eight cocks related to one another were each mated to the following three different groups of hens: (1) hens not related to the cocks, (2) hens distantly related to the cocks, (3) hens closely related to the cocks. The results secured by Dumon show that in every case except one the per cent hatchability of hens not related to the cocks was higher than that of hens distantly related to the cocks, and that in every case the per cent hatchability of hens distantly related to the cocks was higher than that of hens closely related to the cocks.

The effects on hatchability of three different forms of inbreeding are given by Dunkerly (1930) in experiments carried out by the Northern Sub-Committee of the National Poultry Institute of England. White Wyandottes, Rhode Island Reds, and White Leghorns were used. The three different forms of inbreeding employed were as follows: (1) a cock was mated to daughters whose ancestors were outbred, (2) a cock was mated to daughters derived from a brother × sister mating, (3) a brother × sister mating. The first mating was called father × daughter outbred mating; the second, father × daughter inbred mating. In the father × daughter outbred mating the father was bred to groups of full-sisters, and in all three forms of matings a certain number of pullets that were unrelated to the males were used in each mating, these pullets constituting control lines.

Fig. 54.—The female progeny of a father x daughter inbred White Wyandotte mating and "control" females.* Such close inbreeding resulted, for the most part, in decreased hatchability and egg production. (Photo by W. B. Mercer.)

In the father × daughter outbred mating a direct comparison is possible between the results secured from the sire's daughters and the unrelated pullets to which the sire was mated, one year of inbreeding being compared with the same year of outbreeding. In the father × daughter inbred mating the object was to ascertain the total effect of two years of inbreeding: brother × sister mating followed by sire × daughter mating. In the brother × sister mating the results of this form of inbreeding are compared with outbreeding during the same hatching season. Dunkerly found that the more closely that his birds were inbred the greater was the decrease in hatchability.

On the whole *the results of the various investigations on the effects* of close inbreeding on hatchability are in agreement in demonstrating quite clearly that the immediate effect is a marked decline in hatchability followed by a progressive decline as close inbreeding is continued. The results also show that families differ in respect to the degree of decline in hatchability. It seems certain that a very important factor affecting the viability of the embryo is its genetic constitution. Inbreeding apparently produces embryos having recessive lethal and sublethal genes in a homozygous condition, as a result of which the embryos either die in the early stages of development or fail to hatch, or it tends to increase the homozygous condition of genes which have the effect of lowering the vigor of the embryo so that it cannot emerge from the shell.

Effects of Inbreeding on Viability of Chicks.—Since close inbreeding affects hatchability adversely by increasing embryo mortality, it might be assumed that inbreeding would tend to increase chick mortality. That such need not be the case, however, is apparent from the observations of Dunn (1921-1922) and Jull (1928), who found no correlation between embryo mortality and chick mortality in stock that was not inbred. This does not necessarily mean that certain genes which tend to affect hatchability do not also affect the viability of chicks, but it is very difficult, if not impossible, to compare the effects of the same genes in the developing embryo and in the growing chick because the chick is subjected to environmental influences so different from those under which the embryo develops during incubation. Factors such as the transmission of certain diseases from chick to chick, external and internal parasites, and sudden showers may cause mortality among chicks regardless of their genetic constitution.

The effects of inbreeding on the viability of the chick have been studied by Dunn (1923), Dumon (1930), and Dunkerly (1930), the observations being based on the results secured from the matings mentioned in the discussion on the effects of inbreeding on hatchability. Dunn's and Dumon's results are based on the mortality of chicks up to and including 3 weeks of age; Dunkerly's results are based on the mortality occurring up to 16 weeks. The results secured by Dunn, Dumon, and Dunkerly are in substantial agreement in that they show that close inbreeding has an unfavorable affect on the viability of chicks. Mortality was less in the control lines in practically all cases than in the various lines of inbred birds.

The results secured by Jull (1932) regarding viability of chicks in each of four pens of White Leghorns inbred by brother × sister matings for 3 years in succession show that such close inbreeding as brother × sister matings did not affect the viability of the chicks to any marked extent except in the third year of inbreeding in two of the pens. On the other hand, there was less mortality of chicks in the

F_3 generations in three of the pens than in the original matings. The effects of inbreeding on the viability of chicks depends to a great extent upon the kind of stock used in the original matings and the method of selecting the breeders each year of inbreeding.

On the whole, the results of the various investigations on the effects of inbreeding on viability of chicks show that inbreeding tends to increase chick mortality. This may be due to a general lowering of the vigor or vitality of the inbred chicks as a result of an increase in the homozygosity of deleterious recessive genes, or it may be due to specific causes, such as an increase in the susceptibility to disease.

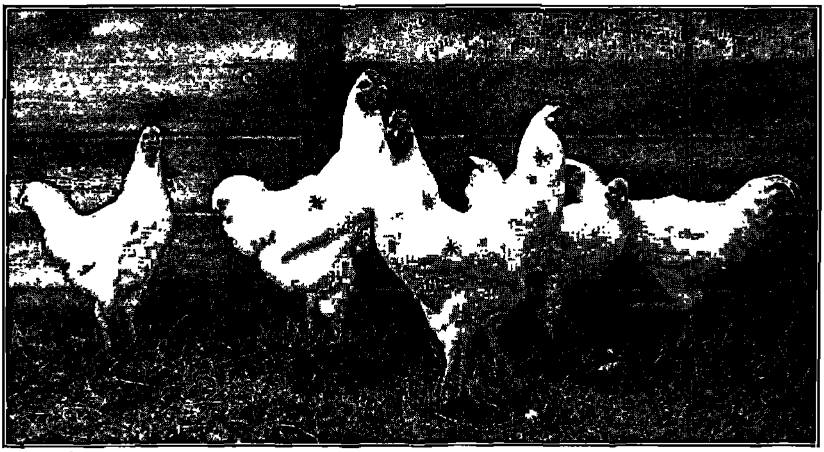

FIG. 55.—The male progeny of a father x daughter inbred white Wyandotte mating and "control" males.* Such close inbreeding retarded the rate of growth. (Photo by W. B. Mercer.)

Effects of Inbreeding on Rate of Growth and Adult Body Weight.—Very little evidence has been made available regarding the effects of inbreeding on either rate of growth or adult body weight. The results which Dunn (1923) secured in his brother × sister matings in White Leghorns indicated that rate of growth in his inbred lines was retarded as compared with rate of growth in his control lines. He states that "inbred birds weigh as much but they take longer to mature." Hays (1929) observed that the body weight of Rhode Island Red pullets when laying commenced was not affected by inbreeding. Dunkerly (1930) found little difference between the average weight of pullets of his inbred and outbred lines in White Wyandottes, Rhode Island Reds, and White Leghorns.

Probably the most accurate basis for determining the effects of inbreeding on adult body weight is a comparison of bone measurements between inbred and outbred birds. Schneider and Dunn (1924) have shown that the bones of the domestic fowl reach their full length relatively early in the life of the fowl, approximately 160 days in outbred White Leghorns. Latimer (1927), also working with White Leghorns, found that leg and wing bones ceased growing at approximately 112 days. Dunn (1928*b*) found much less variability in bone length than in body weight and concluded that bone length is a more reliable index of final body size than body weight, which is affected by egg production, season, state of health, and other factors.

Effects of Inbreeding on Egg Production.—The effects of inbreeding on egg production are of particular importance to poultry breeders because they wish to know whether or not the mating together of closely related males and females from their best layers will tend to produce uniformly high egg producers. The question in the mind of the average poultry breeder is whether or not inbreeding will tend to develop heavy laying as a fixed character in his strain. A partial answer to the question has already been given in the preceding discussion: inbreeding apparently tends to lower the constitutional vigor and rate of growth of chicks so that they would naturally be inclined to commence laying at a later age than noninbred chicks.

The results secured by Dunn (1923), Hays (1924, 1929), and Dunkerly (1930) show that close inbreeding effects a decrease in egg production. Similar results were also secured by Jull (1932), who observed that close inbreeding tends to increase the age in days at which laying commences.

TABLE 28. FIRST-YEAR EGG PRODUCTION AS AFFECTED BY THREE YEARS OF BROTHER × SISTER MATINGS IN WHITE LEGHORNS

(Data of Jull, 1932)

Mating	Pen 1	Pen 2	Pen 3	Pen 4
Outbred ancestors, 1926	168	219	220	213
First-year inbred birds, 1927	143	159	197	152
Second-year inbred birds, 1928	129	119	173	161
Third-year inbred birds, 1929	76	80	139	173

The significant fact brought out in Table 28 is that the first year of brother × sister mating resulted in a marked decrease in egg production and that the second and third years of brother × sister matings resulted in a still further decline in egg production except in the case of Pen 4. The data show that families of birds react differently under similar methods of inbreeding.

The General Effects of Inbreeding.—It has been observed that the general effects of such close inbreeding as father × daughter and brother × sister matings are decreased hatchability of eggs, decreased viability and retarded rate of growth of chicks, and decreased egg production. It has also been observed that the results of inbreeding are not so harmful in some strains and families of birds as in others. As a matter of fact, the final results secured under any form of inbreeding depend to a great extent upon the kind of stock used in the original inbred mating. Moreover, before drawing sweeping conclusions regarding the harmful effects of inbreeding one should keep in mind that the results given in the previous pages were secured from the closest forms of inbreeding that can be practiced. Under less intense forms of inbreeding, such as uncle × niece and first-cousin matings, the results would probably be less harmful and in many cases quite advantageous.

Caution should be exercised before condemning inbreeding on general grounds because inbreeding is not injurious merely by reason of the close relationship of the individuals that are mated. The only injury resulting from inbreeding comes from the inheritance received. The constitution of the inbred birds depends upon the combination of characters that existed in the original stock used as the foundation of the inbred lines. If undesirable characters become manifest in the inbred birds, it is only because these undesirable characters existed in the original stock where they were able to persist for generations under the protection of more favorable characters, many of which are known to be dominant to the unfavorable characters.

A poultry breeder with a flock of inferior individuals should never practice close inbreeding. On the other hand, a poultry breeder with a flock of wellbred birds might wisely mate closely related individuals occasionally. The smaller the size of the flock the less should close inbreeding be practiced, because there would be less chance of making future matings to overcome any inherent weakness present in the inbred progeny. The closer the degree of inbreeding practiced in any flock the more rigid should be the selection of the progeny and the greater the number of individuals necessary from which to select future breeders.

Inbreeding to the extent of mating uncles and nieces, nephews and aunts, and first cousins could undoubtedly be practiced safely over a period of years in any good flock, particularly if the breeding stock is selected on the basis of the various points given in the fore part of this chapter. The mating together of carefully selected, not too closely related birds should lead to an increase in the homozygous condition of the genes for high egg production and at the same time should avoid the harmful effects which so often result from very close inbreeding.

The Advantages of Linebreeding.—Among the various ways in which inbreeding can be carried on is to use one individual repeatedly in the breeding project. Cattle breeders have been known to use a certain bull for several generations, and horse breeders have sometimes done the same thing with an outstanding stallion. The practice of breeding back to a given ancestor has been called linebreeding; in reality it is simply a special method of inbreeding.

A practical method of linebreeding has been presented by Knox (1929). Instead of following the usual method of mating a number of cockerels of average quality to his entire flock of females, one male, called the foundation male, of outstanding value is purchased from a reliable breeder and is mated to some 15 of the best hens selected from the entire flock. This mating is best made in a colony house separate from the large flock. The cockerels secured from this mating are selected carefully and are saved for mating the next year to a selected group of hens in the large flock. The pullets secured from the colony-house mating are put in the large poultry house with the hens selected from the previous year and with the pullets secured from the large flock mating.

During the second year of the linebreeding project the foundation male is again mated in the colony house to the best hens kept over from the previous year; these may include a few two-year old hens from the original colony-house mating and the best yearling hens from the large flock. The selected cockerels and pullets produced by the second-year colony-house mating are put with the larger flock in the fall of the year. The selected cockerels secured from the colony-house mating of the previous year are mated to a selected group of hens in the large flock, which the farmer can keep separated from the rest of the flock during the breeding season. In this way some of the heritable characters of the foundation male become intensified in the progeny of the whole flock. The reason for mating the selected cockerels secured from the colony-house mating the previous year to selected hens only in the large flock is that selected hens should produce better chicks than unselected hens and pullets, and, moreover, the large flock may contain a number of full-sisters and half-sisters of the cockerels. The mating of the cockerels to selected hens avoids the danger of harmful effects resulting from brother × sister matings.

During the third year the same methods are followed, and since the colony-house mating consists mostly of the very best hens selected from the large flock some of these hens should be daughters of the foundation male, providing, of course, that he actually proved to be a good breeder; these daughters would have been produced in the first year of the colony-house mating. During the third year the foundation male would in all probability be mated to a number of his granddaughters, females produced by the mating of the sons of the foundation male to selected hens in the large flock during the second year.

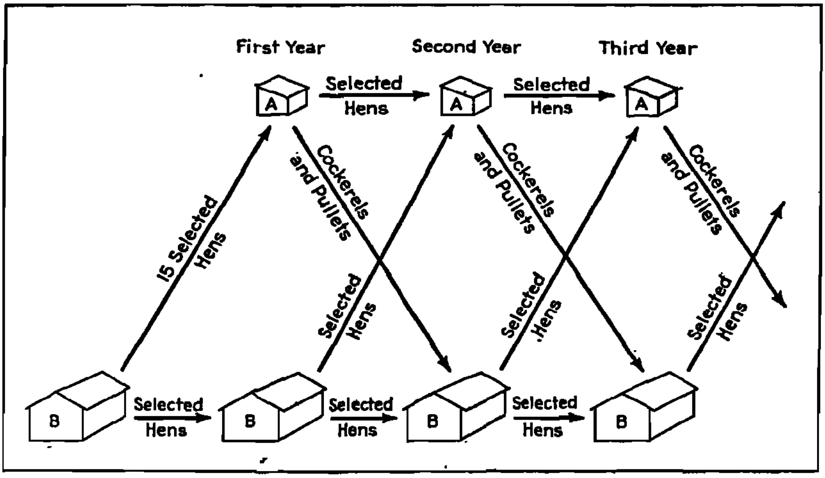

FIG. 56.—A linebreeding scheme that provides for the mating each year of a few of the very best females of the entire flock to a foundation male in a colony-house designated A. Each year the pullets and a few selected cockerels produced by the colony-house mating are placed with the rest of the flock in the laying house designated B. During each breeding season, after the very best females have been selected for the colony-house mating, a second best group should be selected and kept separate from the other hens and from the pullets and should be mated to cockerels secured from the colony-house mating. (After Knox, 1929.)

If the foundation male was used in the colony-house mating during the fourth and later years he would in all probability be mated to related descendants only, unless a few three- or four-year-old hens from the original flock were still on hand.

This linebreeding program has the advantage of requiring the farmer to buy only one good male, for which he should be willing to pay a good price, instead of purchasing several medium-priced males of mediocre value, and the program also has the distinct advantage of obliging the farmer to select his best hens for the purpose of mating them to the foundation male. Another advantage is that the best females of the entire flock are bred back to the foundation male, thus making possible the distribution of the desirable heritable characters possessed by the foundation male to every member of the flock.

Such a definite linebreeding project can be carried on as long as the foundation male lives and is able to produce a high proportion of fertile eggs, providing, of course, that he proves to be a valuable breeder as determined by the egg production of his pullets. Should the foundation male prove to be a poor breeder another one should be secured for the next year.

This plan of linebreeding could be carried on by the commercial poultry breeder, who, however, would probably want to make several colony-house matings each year.

CROSSBREEDING AND ITS EFFECTS

The real purpose of crossbreeding is to provide for the combination of desirable qualities from two distinct lines of stock. At the same time, very little is to be gained by crossing animals that have not been carefully selected. Jones (1925) points out that "Uniform progeny are produced only when the parental races are fixed in their particular type and breed true, and it is only when they are from separate and different lines of descent that decidedly beneficial results from crossing can be expected."

Crossbreeding is sometimes practiced by poultry producers for the production of broilers and roasters. Sex-linked crosses are sometimes used, as pointed out in Chapters IV and VI, for the purpose of separating the sexes at hatching time, the cockerels being marketed as broilers and the pullets kept for egg production. For broiler production, crosses are frequently made between Plymouth Rocks and Rhode Island Reds, Plymouth Rocks and Wyandottes, Leghorns and Wyandottes, as well as other breeds. During recent years the New York City market has shown a preference for broilers with barred feathers, so that many broiler producers in the northeastern part of the United States mate Barred Plymouth Rock males to females of such breeds as White Wyandottes and Rhode Island Reds. The production of roasters often involves such crosses as White Plymouth Rocks and Light Brahmas, a cross practiced for years in the South Shore district of Massachusetts for the production of roasters for the Boston market. Whether crossbreeding for egg-production purposes should be encouraged seems quite doubtful at the present time.

Effects of Crossbreeding on Hatchability.—Pearl and Surface (1910) and Warren (1927) observed an increase in hatchability in the crossing of breeds over that of either parental breed.

Increased hatchability has also been shown to result from the crossing of inbred lines by Dunn (1928), Hays (1929), Dumon (1930), and Jull (1930).

The only plausible explanation to account for the increased hatchability resulting from crossbreeding or crossing closely inbred lines is that complementary genes, including favorable dominant ones, are brought together by the two breeds or two inbred lines. The embryos produced by the two kinds of crosses possess genes introduced by both parents of the cross and are, therefore, heterozygous for more genes, including favorable dominant ones, than either of the parents. Since the embryos produced by the cross are heterozygous for more genes than purebred or inbred embryos are, and since dominant genes are frequently less deleterious than recessive ones, the heterozygous condition of the embryos from crosses gives rise to increased hatchability.

Effects of Crossbreeding on Viability of Chicks.—Comparatively few well-controlled experiments have been conducted to determine the effects of crossbreeding on the viability of chicks. The results secured by Pearl and Surface (1910) and Warren (1927) are not in entire agreement, largely because both purebred and crossbred chicks in the Pearl-Surface experiment showed excessive mortality whereas in the Warren experiment there was less mortality among the crossbred than among the purebred chicks.

Dunn (1928) and Jull (1932) each crossed inbred strains of White Leghorns and observed that the viability of the chicks of each crossed inbred line was greater than in the inbred lines before being crossed.

The greater viability of chicks resulting from crossbreeding, and the crossing of unrelated strains is to be accounted for in the same way that increased hatchability has been accounted for. Crossbred chicks and those secured from crossed inbred lines have a more heterozygous genetic constitution, including dominant genes producing favorable effects, than purebred or inbred chicks.

Effects of Crossbreeding on Rate of Growth and Adult Body Weight.—Since crossbreeding has been shown to be beneficial both in respect to hatchability of eggs and viability of chicks, it might reasonably be expected that the rate of growth of the chicks might also be benefited. That such is actually the case has been observed by Warren (1927, 1930) and by Waters (1931). Both investigators observed that the weight of chicks at hatching time is determined largely by the weight of eggs laid by the dams, crossbred chicks weighing the same as purebred chicks if the eggs from which they hatched were of the same weight. Shortly after hatching time, however, there was an accelerated rate of growth in the crossbred as compared with the purebred chicks; this accelerated rate of growth was maintained for approximately 12 weeks but at maturity the crossbred progeny were usually intermediate in weight between the weights of the purebred progeny.

Effects of Crossbreeding on Egg Production.—Relatively few experiments have been conducted with a view of determining the effects of crossbreeding on egg production. Warren (1927, 1930) crossed Jersey Black Giants with White Leghorns and Rhode Island Reds with White Leghorns and observed that for the most part the crossbred birds laid more eggs than the purebred birds.

The effects of crossing four inbred lines of White Leghorns that had been brother × sister mated for three years in succession on age in days that laying commenced and on first-year egg production have been reported by Jull (1932). In every case except one the crossed inbred pens laid better than the third-year inbred pens.

Crossbreeding could not be expected to increase egg production in high-producing females which are mated to males from low-producing strains, as many poultry breeders have found. Such would be the case irrespective of the amount of increased vigor resulting from crossbreeding.

The General Effects of Crossbreeding.—The most obvious effect of crossbreeding is to increase the heterozygous condition of genes, including dominant ones having favorable effects, the results being manifested in increased hatchability of eggs, increased viability of chicks, and a stimulation in the early growth of the chicks. Crossbred stock may also be more resistant to disease, although this point has not yet been clearly demonstrated.

The increased vigor of the progeny of a crossbred mating over the vigor of either parent is a phenomenon recognized by many plant and animal breeders and is termed hybrid vigor or heterosis. In plant-breeding work the manifestations of heterosis are most noticeable as increases in the size of the various parts of the plant. In animal-breeding work the manifestations of heterosis are most noticeable in the increased vigor of the hybrid progeny and the stimulation of growth during the first few weeks.

From the standpoint of egg production the effects of crossbreeding depend largely upon the nature of the genes affecting egg production carried by the stock that is crossed. The crossing of two groups of birds representing different breeds could not be expected to produce progeny that would lay any better than the parental groups if neither of them carried any of the genes that determine high egg production.

Crossbreeding has its disadvantages as well as its advantages. The progeny produced from certain crosses may possess certain undesirable economic qualities; for instance, when Rhode Island Red males are crossed with Barred Plymouth Rock females the hybrid pullets have black plumage and black or very dark shanks, which are objectionable from the marketing standpoint.

The greatest objection to crossbreeding, however, rests in the fact that the hybrid progeny should rarely if ever be used for breeding purposes because the second generation would in all probability be lacking in uniformity in many characters. There would likely be considerable diversity of plumage color, body type, and other characters that would give the progeny produced by the mating of the hybrids a motley appearance.

Inasmuch as the hybrid progeny resulting from crossbreeding should not be used for breeding purposes, it is obvious that a purebred flock must be maintained of each of the parental breeds used to make the cross. This means that the poultry breeder would have to maintain two purebred flocks and provide room for the hybrid progeny. Maintaining two separate breeding flocks constitutes a distinct handicap for the individual breeder in his breeding operations because fewer progeny could be raised from each purebred flock and there would be less chance for selection than if one purebred flock only was maintained and crossbreeding was not practiced. However, farmers and commercial poultrymen who do not breed their own flocks but rely upon the commercial hatchery as a source of baby chicks each year might find the purchase of crossbred chicks advantageous.

Is Grading Up Advisable?—The term "grading up," is used to denote the mating of common or mongrel females to males of superior quality for the purpose of improving the laying qualities of the mongrel stock. However, the extensive development of the commercial hatchery business, making it a fairly simple problem to replace the entire flock of mongrels with chicks hatched from bred-to-lay stock, detracts somewhat from a long-time grading up program.

METHOD OF MATING TO PRACTICE

Whatever may be the methods used in selecting the breeding stock, the age of the breeders used, or the system of breeding employed, it is obvious that proper methods of mating must be employed or the results in the reproduction of the flock from year to year will not be satisfactory.

Not only should the breeding stock used each year give good results in respect to the fertility and hatchability of the eggs set and the viability of the chicks hatched, but also improvement should result in the quality of the stock produced each year. If progress is not

TABLE 29. DECREASED FERTILITY RESULTING FROM INTERCROSSING CLOSELY INBRED STRAINS OF BARRED PLYMOUTH ROCKS AND WHITE LEGHORNS

(Data of Jull, 1930)

Mating	1928		1929	
	No. of Birds	Per Cent Fertility	No. of Birds	Per Cent Fertility
Inbred Barred Plymouth Rocks	9	84.77 ± 2.10	15	65.03 ± 3.93
Noninbred " " "	72	85.61 ± 1.25	55	83.77 ± 1.45
Inbred White Leghorns	38	90.85 ± 0.97	47	76.29 ± 1.78
Noninbred " "	78	78.57 ± 1.48	89	78.12 ± 1.46

The results given in Table 29 show that in the inbred Barred Plymouth Rocks the percentage of fertility during the third year of inbreeding was 84.77 and that when the inbred strains were intercrossed it was 65.03. In the noninbred Barred Plymouth Rocks for the same two years the per cent of fertility was not significantly different. In the inbred White Leghorns the percentage of fertility during the third year of inbreeding was 90.85 and when the inbred strains were intercrossed it was 76.29. In the noninbred White Leghorns for the same two years the per cent fertility was practically the same. At this time no definite reason can be offered for the significant decreases in fertility resulting from the intercrossing of the inbred strains; the only suggestion that can be offered is that under close inbreeding the reproductive cells of each of the two strains crossed became to some extent physiologically incompatible.

Fertility is not inherited, according to Pearl and Surface (1909) and Hays and Sanborn (1924). The poultry breeder who wants to make sure that maximum fertility will result from a given mating should make up the mating several weeks before the regular breeding season and test the eggs for fertility. This provides sufficient time before the regular breeding season to make any necessary changes.

Good Fertility in Five Days.—It is well for the poultry breeder to know how soon fertility may be expected after the males have been placed with the females. That a fertile egg may be produced shortly after copulation takes place has been demonstrated by the following investigators, the number of hours elapsing from the time of copulation to the laying of the first fertile egg being given after the investigator's name: Gilbert (1905), 39 to 65; Pearl and Surface

(1909), 72; Coste and Gerk (1910), 28; Philips (1918), 23; Erickson (1924), 72; Fronda (1926), 20; and Dunn (1927), 21. It should be noted that the observations of Coste and Gerk, Philips, Fronda and Dunn were based on individual matings, whereas all other observations were based on pen matings. Curtis and Lambert (1929) observed that the onset of fertile production ranged from 24 hours to 7 days, with 57.1 hours as the average.

Waite (1911) from a flock of 20 White Leghorn pullets secured 50 per cent fertile eggs on the third day and 70 per cent fertile eggs on the fourth day after mating. Crew (1926) reports that maximum fertility is reached by the end of the first week after mating. From the practical standpoint, therefore, it may be stated that eggs may be saved for incubation beginning about the fifth day after the males have been placed with the females. More time should be allowed when cock birds are used.

Good Fertility Two Weeks After Matings Discontinued.—The length of time that fertile eggs are produced after the mating pen has been discontinued is a matter of some practical importance, although usually the males are allowed to remain with the females as long as eggs are saved for incubation. Spallanzani (1784) reported that a hen can lay fertile eggs 20 days after being mated, and Crew (1926) secured a fertile egg 32 days after removal of the male, these observations being based on individual matings.

The number of days that the fertility of eggs remained sufficiently high in order to be saved for incubation after the males were removed from the breeding pens has been reported as follows: Gilbert (1904, 1905), 11; Waite (1911), 11; Chapellier (1914), 10 to 18; Elford (1916), 19; Philips (1918), 15; Dunn (1927), 14. Lillie (1919) observed that after the end of the third week the vitality of the spermatozoa is considerably reduced. Curtis and Lambert (1929) observed that the mean duration of fertility was about 11 days, with 21 days as the extreme duration. It would seem, therefore, that reasonably good fertility may be expected for about two weeks after the discontinuance of the breeding pen.

When it is desired to substitute one male for another in the breeding pen and still have definite knowledge of the ancestry of the chicks hatched from both males, fertile eggs secured after the third week after the removal of the first male may be regarded as having been fertilized exclusively by the second male.

Carefully controlled tests have shown that if a male in a pen dies or is removed from the pen, and another male is placed in the pen immediately, the eggs laid by hens mated by both the first and second male are more likely to be fertilized by the spermatozoa of the second male, especially after a few days. Crew (1926) has observed that the influence of the first male is removed by the seventh to the tenth day, the exact time differing in different cases.

Warren and Kilpatrick (1929) mated a Single-Comb White Leghorn male and a Black Minorca male alternately with Black Minorca and Jersey Black Giant females and observed that the spermatozoa of the male making the second mating soon replaced the spermatozoa of the male making the first mating in fertilizing the eggs, and that there was practically no overlapping of the offspring produced by the two males.

SECURING GOOD HATCHABILITY

In the reproduction of the flock the object of the poultry breeder is to secure the greatest possible number of good chicks in proportion to the total number of eggs set. Granted that everything possible has been done to secure good fertility in the eggs produced during the breeding season, the next step is to secure the best possible hatching results. Among the various factors affecting hatching results the most important is the hatchability of the eggs, other factors being conditions of incubation.

The term "hatchability" means the hatching qualities of an egg, the greatest possible number of chicks that could be hatched from a given number of fertile eggs being desired. It is obvious, of course, that conditions of incubation, such as temperature, humidity, and ventilation, affect hatching results, but the discussion in this book is primarily concerned with those factors which determine whether or not a chick can hatch from a fertile egg incubated presumably under ideal conditions of incubation.

Egg Characters and Hatchability.—Several lines of investigational work have been undertaken at different times to ascertain the possible effect of various egg characters on hatchability. Dunn (1922) investigated the relationship between the weight and the hatching quality of White Leghorn eggs and found that, although from among the eggs of an individual fowl those above the mean weight did not hatch as well as those below the mean weight, the deviations were so small that they could not be regarded as an important cause of the variation. Moreover, Jull and Haynes (1925) in a study of Barred Plymouth Rock eggs found no relationship between weight and hatchability. The same authors also found that egg shape, where normal eggs are involved, does not affect hatching quality. These findings corroborate those of Benjamin (1920) and Halbersleben and

Mussehl (1922), who also found that color of eggs was not associated with hatchability.

More recently Hays and Sumbardo (1927) failed to disclose any relationship between hatchability and the following egg characters: length, diameter, fresh weight, specific gravity, the thickness of the shell, and the thickness of the inner and outer shell membranes. Mussehl and Halbersleben (1923) found a slight correlation between specific gravity and hatchability, but it was so low (0.204 ± 0.023) as to lead the authors to believe it had no practical significance. Kaupp (1924) found that eggs with normal shells hatched much better than those with thin or ridged and mottled shells.

These various results go to show, therefore, that for the most part the physical characters of eggs have no significant bearing on hatchability. From the standpoint of poultry-breeding work, however, two of the characters are of considerable importance. The size of eggs used for hatching is very important because the results secured by Benjamin (1920), Halbersleben and Mussehl (1922), Jull and Quinn (1925), and Upp (1928) show that there is a high correlation between the size of a chick and the size of the egg from which it was hatched. Moreover, since egg size is inherited, as pointed out in Chapter IX, it is of considerable economic importance to use for incubation pullet eggs weighing not less than 2 ounces each. Eggs from yearling and older hens should weigh at least 2.2 ounces each.

In the Leghorn and other breeds laying normally white-shelled eggs it is very important to eliminate all tinted-shelled eggs, otherwise it would be practically impossible to eliminate this character from the laying and breeding flocks. All eggs for hatching should be uniform in size, shape, and color and should be sound in shell.

Egg Production and Hatchability.—Some poultrymen are of the opinion that heavy egg production prior to the breeding season tends to reduce hatchability, whereas other poultrymen believe that heavy egg production during the breeding season tends to reduce hatchability. Evidence secured on these two points shows that neither opinion is well founded, except perhaps in the case of late-hatched pullets that have been "forced" into heavy production through heavy feeding and the excessive use of artificial lights.

Lamson and Card (1920), using White Leghorns, observed that the number of eggs laid during the 90 days prior to the hatching season did not affect hatchability. Knox (1927) also obtained no correlation between antecedent egg production and hatchability. Atwood (1927) found that heavy feeding of the breeding hens to induce heavy egg production prior to and during the hatching season did not adversely affect the hatchability of the eggs produced. Jull (1928) found that in Barred Plymouth Rocks, Rhode Island Reds, and Single-Comb White Leghorns, egg production prior to the breeding season did not affect hatchability. Martin and Insko (1930) found the same to be true in the White Leghorns and Barred Plymouth Rocks with which they worked. It is apparent, therefore, that the number of eggs laid prior to the hatching season has no effect on hatchability.

The relationship between current egg production, the number of eggs laid during the hatching season, and hatchability has been but recently investigated. Heuser (1927) observed that eggs from hens laying very heavily did not hatch as well as eggs from hens laying only moderately during the hatching season. Should such a situation exist among all flocks it would be unfortunate, inasmuch as high annual egg production is correlated with high monthly as well as high spring egg production.

Byerly, Titus, and Ellis (1932), from data secured from several pens of Rhode Island Red pullets and cockerels, the cockerels being shifted from pen to pen daily, obtained a positive correlation of 0.16 ± 0.036 between intensity of egg production and hatchability. This low though significant correlation was obtained on the basis of average intensity and average hatchability of pullets in different pens, each of which was on a diet differing in protein level. With the percentage of protein in the diet held constant, the net correlation between hatchability and intensity of production was 0.18 ± 0.036. This correlation indicates that relatively heavy egg production during the breeding season did not reduce hatchability.

Intensity of egg production during March and April when compared with hatchability for the same two months gave a positive correlation of 0.23 ± 0.027. This significant correlation was secured with pullets on different diets. With pullets on the same diet, Byerly, Titus, and Ellis secured a positive correlation of 0.30 ± 0.041. This correlation is significant, and the authors were led to conclude "that hens able to lay eggs at a high rate on a particular diet will, in general, produce a higher percentage of hatchable eggs than those able to lay only at a low rate on the same diet."

Data bearing on this point from flocks of yearling and older Barred Plymouth Rocks, Rhode Island Reds, and Single-Comb White Leghorns have been presented by Jull (1931). There were 27 breeding pens of Barred Plymouth Rocks containing 271 birds, 46 pens of Rhode Island Reds containing 528 birds, and 49 pens of Single-Comb White Leghorns containing 599 birds. For each breed there was approximately the same number of birds per pen and the same number of pens per year for 6 years. It was found that heavy egg production during the breeding season not only is not detrimental but is apparently conducive to high hatchability.

Embryo Malformations and Hatchability.—Although embryo mortality occurs at all times from the first to the twenty-first day of incubation, it has been established that there are two periods during which most of the mortality occurs, the period from the third to the fifth day, and the eighteenth and nineteenth days, the latter period being by far the more important. Undoubtedly some of the embryo mortality is due to faulty conditions in incubation, a discussion of which is out of place in this book. Some of it is probably due to physiological changes occurring in the metabolism of the developing embryo, but in view of the rather meagre knowledge of the effects of these factors it is doubtful if a discussion of them is justified at this time. On the other hand, an examination of many dead embryos at hatching time has revealed the fact that there are certain embryo malformations which apparently prevent the chick from hatching.

Dunn (1923) was apparently the first to observe that some of the fully formed dead embryos at hatching time had peculiar parrot-like beaks and very short legs. Upon closer examination of this kind of embryo by Landauer and Dunn (1926) and by Hutt and Greenwood (1929*a*) it was observed that the lower beak was much shorter than the upper one, so that the latter curved over the former, giving the beak a parrot-like appearance. The skull was found to have a vaulted and rounded shape, and the legs were found to be very short and usually bent. Such embryos are said to exhibit "chondrodystrophy."

That this malformation is of economic importance is shown by the observation of Hutt and Greenwood, who have reported that in three different flocks with which they worked embryo mortality after the eighth day due to chondrodystrophy varied from 0.80 per cent in one flock to 7.96 per cent in another flock. In a fourth flock chondrodystrophy was responsible for embryo mortality equivalent to 6.5 per cent of all eggs set.

Other types of embryo malformations have been described by a number of workers, but since they apparently occur relatively infrequently under normal conditions of incubation they are only mentioned here. For a detailed discussion of these malformations, or monsters, the reader is referred to the review by Hyman (1927) and to the work of Hutt and Greenwood (1929*b*), Hutt (1930), and Byerly (1930). According to Hutt and Greenwood the most common types of malformation, other than chondrodystrophy, include "various degrees of abnormality either in the brain, cranium, or eyes, or in two of these structures, or in all three." The different types of malformations they encountered accounted for at least 3.6 per cent of all the embryo mortality that occurred.

The observations of several investigators have revealed the fact that embryonic development sometimes proceeds in such a way that the embryo is in an abnormal position within the shell at hatching time and frequently cannot emerge from the shell. The normal position of the embryo at hatching time is with the head towards the large end of the egg with the neck bent sufficiently to bring the head to the right side of the body and the beak under the right wing, the tip of the beak pointing toward the air-cell; the legs lie on the ventral side of the embryo with the feet folded so that the toes reach the head.

Sanctuary (1925), Hutt (1929*b*), Byerly (1930), Hale (1930), Smith (1930), and Hutt and Cavers (1931) have described various malpositions and have discussed their influence on hatchability. Since malpositions for the most part appear to be due to conditions other than the genetic constitution of the embryos, various ones are briefly enumerated here and the discussion concerning them is confined to evidence suggesting that one or more may be inherited.

The various malpositions are briefly as follows:

1. The head extends down the median line and is buried between the thighs.
2. The head is in the small end of the egg.
3. The head is in the large end of the egg but is turned to the left instead of to the right, the beak in most cases pointing directly opposite the air-cell.
4. The embryo lies in the normal position but the head is rotated so that the beak points away from the air-cell.
5. The embryo lies in the normal position but both feet are placed on top of the head.
6. The embryo lies in the normal position but the beak is over the right wing instead of under it.

That these malpositions are of considerable economic importance from the standpoint of their adverse affect on hatchability is clearly demonstrated by the observations made by the various investigators cited previously. In 1,490 embryos that died about the eighteenth day of incubation Sanctuary found 51.7 per cent showing some malposition. In 5,050 dead embryos at hatching time examined by Hutt, 55.85 per cent showed some form of malposition. In 305 embryos examined by Byerly 56.4 per cent showed some form of malposition.

Among 1,264 embryos examined by Hale it was found that 35.0 per cent were in such positions within the shell that the chicks were unable to make use of the air-cell. Smith found that among 2,851 embryos 37.85 per cent were in some form of malposition, and he has stated that his results show that malpositions affect hatchability to the extent of at least 5 per cent. Hutt and Cavers (1931) found that, among 24,660 fertile eggs produced by 1,467 fowls, embryo malpositions accounted for 52.1 per cent of the mortality that occurred from the eighteenth to the twenty-first days of incubation and 24.4 per cent of the total embryo mortality.

From the evidence made available by the various investigators it would appear that for the most part malpositions are due to the position of the egg in the incubator, especially during the first day or so, or to other factors in the incubation of the eggs. There are at the present time, however, some indications that one or more of the malpositions may be inherited. Sanctuary pointed out that from the evidence available regarding the dead embryos he examined there was some indication that they were inherited. Smith's findings reported previously were based on embryos produced by birds of known ancestry for ten or more years, and he concluded that there appeared to be a "genetic and possibly a dietary influence on the abnormal condition of dead-in-shell." Byerly (1932) has stated that in his studies on the possible causes of the malposition of head under the left wing (No. 3 listed previously) the evidence suggests that nutrition and factors in the incubation of the eggs are in part responsible for the malposition and that the specific cause is apparently associated with the genetic constitution of the embryo.

Pullorum Disease and Hatchability.—The presence in the embryos of disease of any kind might reasonably be expected to affect hatchability adversely, but the pullorum disease, formerly called bacillary white diarrhea, is the only disease transmitted from dam to offspring through the medium of the egg, at least as far as definite evidence to date is concerned. Poultry breeders should have their breeding stock properly tested in order to eliminate from the breeding pens all birds that carry the disease.

Breeding to Increase Hatchability.—Since hatchability is inherited, as pointed out in Chapter VI, it is obvious that the hatchability of a flock can be increased by the proper selection of the males and females placed in the breeding pens.

The poultry breeder should keep an accurate record of the hatching results secured from each female and each male and should eliminate from future breeding pens all birds that have been shown to carry lethal genes, which cause the death of embryos, and all birds that have been shown to produce abnormalities. The eggs should be gathered from the nests as soon as possible after being laid, held for incubation at a temperature of approximately 50° F., and incubated properly so as to reduce the number of malpositions and malformations to the minimum. The breeders should be tested for the pullorum disease and all carriers of the disease removed from the breeding pens. Too close inbreeding should be avoided.

Females that gave poor hatchability results when used as breeders the first time should not be used again. Hyre and Hall (1932) divided a flock of Single-Comb White Leghorns into three pens according to the hatchability results secured from them the first year they were first used as breeders. The first pen comprised birds that gave low, the second medium, and the third high hatchability the first year. When the pens were bred from the second year, the first pen gave a hatchability of 15.9 per cent, the second pen 55.1 per cent, and the third pen 75.1 per cent, these results being based on 6 or more hatches from each pen.

Since hatchability is inherited, the breeders used each year should be selected from dams that gave approximately 75 per cent hatchability. If the policy is adopted of selecting each year only those birds for breeding purposes whose dams gave high hatchability the poultry breeder should be able to improve the hatchability of his flock quite materially.

SECURING GOOD PROGENY

From the standpoint of the reproduction of the flock from year to year the ultimate object of the poultry breeder is to secure the greatest possible number of cockerels and pullets that possess the various desirable characters developed to the highest possible state of perfection. To the poultry breeder who is desirous of making the greatest progress in his breeding work the reproduction of the flock involves a great deal more than merely replacing a certain number of the old birds annually. The cockerels and pullets raised each year should be better than their ancestors.

Granted, however, that everything possible was done in the proper selection of the breeding stock as outlined in the fore part of this chapter, that the birds were properly mated, and that fertility and hatchability were as good as could be expected, there still remains the problem of rearing the young stock in such a way that it will give the best possible returns. Securing good progeny is the ultimate goal of the successful poultry breeder.

A flock of cockerels and pullets of superior quality can be easily ruined by poor methods of feeding and brooder management, but a flock of cockerels and pullets of inferior quality cannot develop into good progeny even under the best methods of feeding and management. It is obvious that methods of feeding and management cannot be discussed in a book confined to problems of poultry breeding, but it is also obvious that good progeny cannot be secured from poor ancestors.

From the standpoint of breeding operations the poultry breeder can do a great deal to improve the quality of his flock of chicks as they develop from hatching time to maturity. The elimination from the flock of weak chicks, slow-growing, poorly feathered birds, those having plumage color foreign to the breed or variety they represent, and those possessing defects and disqualifications does much toward improving the quality of the flock as a whole.

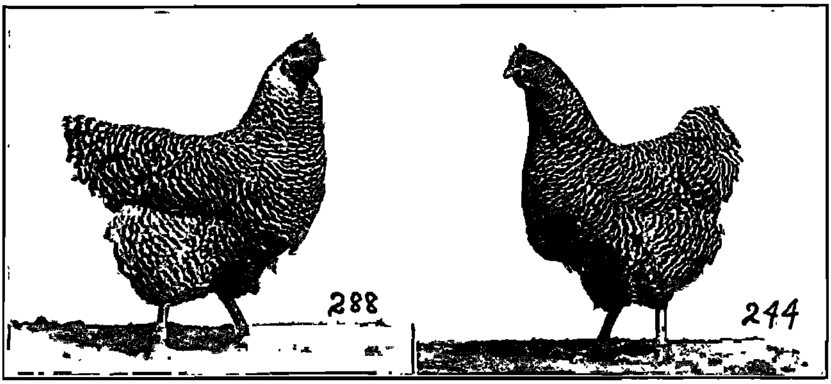

FIG. 57.—Good egg production, as indicated by the records of 288 and 244 eggs, in Barred Plymouth Rocks or any variety of any breed is largely a matter of good breeding, providing the methods of feeding and management are satisfactory. (Photo by U. S. D. A.)

When the chicks are removed from the incubator they should be examined carefully, and all that are obviously weak and deformed should be eliminated from the flock. Chicks with improperly healed vents should also be eliminated. The chicks selected to be put in the brooder should be uniform in size and color, including color of the shanks.

Dunn (1921-1922) and Jull (1928) found that there was apparently no relationship between hatchability of eggs and viability of chicks in the flocks with which they worked. In other words, there were different sets of factors that affected the hatchability of a hen's eggs and the viability of her chicks. It is true that a genetic constitution of the embryo such as to ensure its being hatched might well be expected to ensure the viability of the chick. Thus, as pointed out previously, crossbreeding tends to increase hatchability in eggs and viability in chicks whereas inbreeding tends to decrease both, although in some cases the viability of chicks is not nearly as seriously affected as the hatchability of eggs. At the same time, the fact is appreciated that the test for the viability of chicks is quite different from the test for the hatchability of eggs, the conditions of brooding and rearing being so different from the conditions of incubation.

Throughout the growing season the chicks should be gone over carefully for the purpose of eliminating individuals that are developing poorly and show extremely slow feather growth. Rate of growth is inherited, as pointed out in Chapter VI, so that the best thing for the poultry breeder to do is to compare the development of the chicks of one family with the chicks of another family. He may find that out of a family of 11 brothers and sisters 5 are poorly developed, whereas in another family of 15 brothers and sisters all are well developed, in which case it is highly probable that all the brothers and sisters in the first family should be rejected when the time comes to select cockerels for the breeding pen and pullets for the laying or breeding pen.

In the fall of the year the cockerels that are to be saved for future breeding purposes should be selected on the basis of their vigor, development, freedom from defects and disqualifications, and on the kind of brothers and sisters they have. It is far better to select a good cockerel out of a family of 12 well-developed brothers and sisters of superior quality than to select an outstanding cockerel out of a family of 9 poorly developed brothers and sisters of mediocre quality.

The selection of the pullets for the laying or breeding pen should be carried out on the same principles as suggested for the selection of the cockerels. Select the pullets on a family basis, choosing those from the largest and best families. The subsequent laying performance of the pullets will serve as a very good criterion of the poultry breeder's ability to develop and maintain a flock of birds of superior quality in which the number, size, and quality of eggs laid per bird exceed those of the previous year.

DEVELOPING A HIGH LAYING STRAIN

Since it has been demonstrated quite clearly that egg production is inherited and since it has been shown that there are a number of laying traits associated with the ability to lay a large number of eggs, it should be quite possible for the poultry breeder to develop a practical breeding program for the purpose of improving egg production. The eight most important points of such a program include the selection of birds for future breeding purposes on the basis of:

1. Age in days that laying commences. Sexual maturity.
2. Rate of egg production.
3. Nonbroodiness.
4. Persistency of egg production.
5. Size of egg laid.
6. Size of bird.
7. Breeding males from females possessing desirable characteristics under the six points enumerated above.
8. The results secured from progeny testing.

From the information given in chapter VIII it is apparent that the best layers in a flock are among those that commence laying at approximately 150 to 200 days of age.

Pullets that lay at the rate of 60 per cent from the time they commence laying to March first should lay 200 or more eggs during their first laying year. A production of 75 eggs from the time laying commences to March first should approximate a 60 per cent rate of production. It may also be noted at this time that pullets that lay 30 or more eggs during the first 50 days from the time laying commences, which is equivalent to a 60 per cent or greater rate of production for the first 50 days of laying, should lay 200 or more eggs during the first laying year.

In breeds in which a certain amount of broodiness normally occurs the best layers in a flock are those that show the least amount of broodiness. The poultry breeder should never breed a bird that has shown much broodiness.

Birds that lay approximately 20 or more eggs during the last 50 days of the first-year of laying or approximately 30 or more eggs each during the months of August and September should lay 200 or more eggs during their first year of production.

The relative size of egg laid by pullets is a matter of great economic importance, the factors affecting size of egg laid having been discussed in Chapter IX.

The breeding birds should have good size of body, as pointed out in Chapter IX.

Males that are to be used as breeders should be chosen from females possessing the most desirable characteristics from the standpoint of age in days that laying commences, rate of production, relative lack of broodiness, persistency of production, and size of egg.

The discussion up to the present concerning the selection of breeding stock implies trap-nesting the layers throughout their first year of laying and carrying on pedigree breeding work. That the poultryman who does not trap-nest his layers and does not do pedigree breeding work can accomplish much in the selection of the most desirable breeders is made clear previously. It should also be mentioned here that Hagedoorn (1926) has described a method of testing the breeding value of male breeders without the use of trap nests. The progeny of each male breeder is placed in a separate house and the relative breeding worth of all male breeders used is determined by comparing the mean egg production of the daughters of one male with the daughters of each of the other males. Such a system should be worth a great deal to the poultryman who is not able to trap-nest his layers, although it does not enable the poultryman to select the best breeding females.

Finally, in order to make the greatest progress in improving egg production from year to year, the breeding program should include progeny testing. This simply means that the poultry breeder should analyze very carefully the results he secures from his various matings each year and make future matings accordingly. It is obvious that in order to carry on progeny testing it is necessary to trap-nest the female breeders, each of which is mated to one male only, and just before the chicks hatch the eggs of each hen must be placed in a separate hatching basket or bag in order that the ancestry of each chick hatched may be definitely established. Such a procedure is called pedigree breeding, the details of which are discussed in the last chapter.

It is by virtue of pedigree breeding that the poultry breeder is able to trace the ancestry of the pullets and cockerels that are hatched each year. The laying performance of full-sisters may be compared, and also the breeding performance of various males and females. The progeny of one mating may be compared with the progeny of another mating. By progeny testing the poultryman is able to tell which females mated to a certain male produce a majority of good progeny and which females mated to the same male produce a majority of poor progeny. The females producing the majority of poor progeny should not be used in future matings.

One of the most effective ways of applying the progeny test is to base the selection of the breeding cockerels each year on the laying performance of their full-sisters from the time they are placed in the laying pen up to December or January. Other things being equal, a cockerel the majority of whose full-sisters commenced laying at approximately 170 to 190 days of age and laid at a good rate to December or January, their eggs being of good size, should make a better breeder than another cockerel the majority of whose full-sisters commenced laying at approximately 230 to 250 days of age and laid at a poor rate to December or January, their eggs being small in size.

The laying performance of the pullets to December or January will provide a great deal of useful information regarding the breeding worth of their dams, sires, and brothers as well as their own breeding worth. If every bird that has been proved to be an undesirable breeder is discarded from future matings the poultry breeder would more readily attain his goal. In addition, however, he should apply the progeny test in every conceivable way that will enable him to select the best breeders each year, for it is only thus that the greatest progress can be achieved in improving egg production from year to year.

PROBLEMS

1. Discuss the relative importance of the following 6 points in the development of a flock for the purpose of providing the largest possible revenue from the sale of baby chicks, breeding stock, market poultry and market eggs: (*a*) constitutional vigor, (*b*) plumage color, (*c*) freedom from standard disqualifications, (*d*) egg production, (*e*) size of eggs, (*f*) color of egg shell.

2. Which of the two following practices is the more logical one for a poultry breeder to follow: (*a*) first breeding for high egg production, disregarding all other matters, then breed for egg size, then breed to eliminate any standard disqualifications that may be common in the strain, then breed for good head characters in the breeders, and finally breed for perfection in plumage coloration; (*b*) breed for perfection in all five characters simultaneously?

3. What is the most important point to be kept in mind if inbreeding is to be practiced?

4. In selecting male breeders tell how to select for (*a*) constitutional vigor, (*b*) good fertility and hatchability prior to the regular breeding season, (*c*) ability to produce good progeny.

5. From a flock of 375 birds that have just completed their first-year production, 75 are to be selected for future breeding purposes. Discuss the relative importance of the following 6 points in selecting the 75 best birds: (*a*) age at commencement of laying, (*b*) rate of egg production, (*c*) persistency of production, (*d*) size of egg laid during the first six months of laying, (*e*) size of bird, (*f*) the laying performance of each bird's full-sisters.

6. (*a*) What steps should hatchery operators take to insure good fertility in the flocks supplying eggs to their hatcheries?

   (*b*) A hatchery operator secures eggs from 15 different flocks, and, although all the flocks are given the same management, including the same kind of ration, and although the eggs from all the flocks are incubated under identical conditions, the hatchery operator finds that the eggs from 3 flocks hatch poorly and the eggs from 2 other flocks hatch very poorly. What should the hatchery operator do to improve the hatchability of the eggs from these 5 flocks?

7. Since egg production is relatively the most important branch of poultry production, outline a plan whereby commercial hatchery operators may be of the greatest possible service in improving egg production in farm and commercial flocks throughout the country.

8. Since most farmers are not in a position to carry on pedigree breeding work and since the average farm flock is composed of relatively poor producers, explain how the average farmer can best improve the laying qualities of his flock.

9. What are the most important effects that have been observed in crossbreeding poultry?

10. Explain what is meant by progeny testing, and tell why a pedigree poultry breeder should practice progeny testing regardless of whether he is breeding poultry primarily for show purposes or for egg production.

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CHAPTER XI

POULTRY-BREEDING IMPROVEMENT PLANS

In spite of the possibilities for improving egg production through the intelligent selection and mating of breeding stock, the fact remains that the average egg production per bird of the laying stocks of all countries is extremely low. In every country too many poor producers are reared every year and also too many poor producers are bred from. Many farmers, commercial poultrymen, and poultry breeders fail to realize that mediocrity tends to reproduce itself, and that egg production can be increased only through the most careful selection of the breeding stock from year to year.

The discussion in the preceding chapters of this book has shown clearly that egg production is inherited and that it can be increased considerably if systematic selection of the breeding stock is practiced. Even under the best of circumstances, however, progress in developing a "bred-to-lay" flock may be relatively slow because of the number of factors involved. In the first place the inheritance of egg production has been shown to be a fairly complex problem, involving, as it does, such things as age in days that laying commences, rate of laying, freedom from broodiness, and persistency of production toward the close of the first laying year. In the second place, the number of eggs produced is not the only criterion of a wellbred flock, for size and quality of egg should also be given every consideration. In the third place, the quality of the birds themselves is very important.

EGG-LAYING CONTESTS

The results secured in egg-laying contests held in various parts of the world demonstrate the possibilities of improving the average egg production of all the flocks of a country. Apparently the first organized laying contests were held in England, for Brown (1930-1931) states that the first "laying trials" were held in that country in 1897. Later, contests were organized in Australia, Ireland, the United States, Canada, Poland, Union of South Africa, and in other countries. Apparently the primary object in organizing egg-laying contests was to determine the laying ability of the birds entered in the contests and to stimulate increased interest among poultrymen in breeding for increased egg production. Since it is impossible to enumerate the results of even a majority of the contests, typical results secured from three representative ones are given here.

The results obtained in the first ten years of the Hawkesbury egg-laying competitions conducted by the Hawkesbury Agricultural College in New South Wales, Australia, and the results obtained in the first ten years of egg-laying contests conducted by the Canadian Government are given in Table 30.

TABLE 30. MEAN EGG PRODUCTION PER BIRD IN THE FIRST TEN HAWKESBURY EGG-LAYING COMPETITIONS, AUSTRALIA, AND IN THE FIRST TEN CANADIAN EGG-LAYING CONTESTS

Hawkesbury, Australia			Canada		
Year	Number of Birds	Mean Egg Production per Bird	Year	Number of Birds	Mean Egg Production per Bird
1902–1903	228	130	1919–1920	1,610	123
1903–1904	420	163	1920–1921	2,480	135
1904–1905	600	152	1921–1922	2,590	146
1905–1906	600	166	1922–1923	3,000	165
1906–1907	600	171	1923–1924	3,710	170
1907–1908	360	173	1924–1925	4,100	172
1908–1909	300	180	1925–1926	4,220	179
1909–1910	360	181	1926–1927	4,210	173
1910–1911	240	168	1927–1928	4,230	175
1911–1912	300	184	1928–1929	4,370	177

The data in Table 30 show that in both the Australian and Canadian contests rather steady progress was achieved during the first five years but that during the last five years the average egg production per bird remained somewhat stationary. It should be pointed out, however, that in the Canadian contest of 1926-1927 the point system of scoring eggs according to size was adopted, all eggs weighing less than at the rate of 20 ounces per dozen being eliminated in the determination of the average egg production per bird. The fact should be kept in mind that the results of the Australian contests are for the years 1902 to 1912 inclusive and the results of the Canadian contests are for the years 1919 to 1929 inclusive.

The results secured in the first nine international egg-laying contests held at the Storrs Agricultural Experiment Station, Connecticut, from 1911 to 1920, inclusive, have been compiled by Dunn, for Wyandottes (1924*a*), Rhode Island Reds (1924*b*), Plymouth Rocks (1924*c*), and White Leghorns (1927). The results are given in Table 31.

TABLE 31. MEAN EGG PRODUCTION PER BIRD IN THE FIRST NINE INTERNATIONAL EGG-LAYING CONTESTS AT STORRS, UNITED STATES

(Data by Dunn, 1924*a*, 1924*b*, 1924*c*, and 1927)

Year	White Wyandottes		Rhode Island Reds		Plymouth Rocks		White Leghorns	
	No. of Birds	Mean Egg Production per Bird	No. of Birds	Mean Egg Production per Bird	No. of Birds	Mean Egg Production per Bird	No. of Birds	Mean Egg Production per Bird
1911–12......	64	155*	56	155	54	150	136	156
1912–13......	67	154	62	151	15	150	204	171
1913–14......	80	148	128	134	35	147	309	151
1914–15......	91	160	169	154	57	151	375	154
1915–16......	151	169	183	161	93	160	366	159
1916–17......	155	158	188	157	82	171	450	161
1917–18......	123	169	120	153	100	175	415	157
1918–19......	80	147	91	146	120	160	433	152
1919–20......	83	162	126	164	90	174	443	164

* For the sake of saving space, the decimal point has been left off.

The results given in Table 31 demonstrate that in all four varieties the mean egg production per bird in 1919-1929 was greater than in 1911-1912 but that progress from year to year was not steady. That such results should have been secured is readily understood when it is realized that the majority of the birds in the different annual contests were supplied by different breeders and that there were changes from year to year in the personnel caring for the birds.

The results secured in the Australian and Canadian contests as well as in the contests conducted in the United States and other countries demonstrate the wide gap that exists between the mean egg production per bird of all flocks of the country and the mean egg production per bird of the birds in the contests, the latter probably being approximately twice that of the former.

Official Records.—The officially conducted contests held in the various countries have rendered a very distinct service to the poultry industry of each country. The contests conducted by national and state governments, agricultural colleges, and experiment stations have been regarded as officially conducted, and the records secured at these contests have been accepted as official. The publication of these official records as they were secured from year to year had a great deal to do with exploding the claims of certain unscrupulous private breeders that they had secured phenomenal records, some of them going so far in their absurd advertisements as to state that they possessed "250-egg strains" and even "300-egg strains," the like of which has never been known to exist.

Moreover, private breeders who were securing good records and making honest claims in their advertisements were vindicated in the eyes of the public when the birds which they entered in the official contests produced as good records as they claimed for their "home" birds.

Egg Weight Considered.—The contests had not been in operation long before it was recognized that in many cases the best producers were birds that laid small eggs. The natural tendency for relatively small egg size to be associated with relatively high egg production has been emphasized in Chapter IX. In order that poultry breeders should be encouraged to give proper consideration to size of egg, the authorities in charge of several of the different egg-laying contests instituted schemes for giving credit on the basis of size as well as number of eggs laid.

Different countries have adopted different schemes of giving credit to contest birds for the size of egg produced in relation to the number laid. Three schemes that apparently have the widest application are those adopted in connection with the laying trials in England and the contests in Canada and the United States.

Egg Weight in English Trials.—The problem of making the records obtained in English laying trials more generally useful to poultry breeders and others has engaged the attention of the National Poultry Council for many years. The first practical step in this direction was the convening of a conference of representatives of laying trials on April 5, 1923, for the purpose of discussing the possibility of introducing a uniform system of grading and scoring. Although agreement could not then be attained on the question of scoring, the conference agreed upon a uniform basis of grading eggs for test purposes into first grade and second grade, which has subsequently been adopted in all the recognized tests.

Out of this conference arose also a scheme under which all tests which comply with standards of equipment and management laid down by the National Poultry Council receive the official recognition of the Council. At present there are thirty-one such "Recognized Tests," viz.: Harper Adams, Lancashire Federation, Lancashire Utility Poultry Society, National, Northern Utility Poultry Society, St. Dunstan's, Yorkshire Federation, East Lancashire, and Southern Laying Test (Southern Counties Poultry Society, Ltd.), and twenty-three county laying trials.

A further step was taken in 1927 by the Council in the issue of an "Official Annual Register of Laying Trials Records." By resolution of the Council the Register is restricted to entries in recognized laying trials and to birds which attain the following minimum standards of production, except in the case of birds entered in the county laying trials, particulars of which are given subsequently.

(*a*) For White Leghorns, White Wyandottes, Black Leghorns, Rhode Island Reds, Buff Plymouth Rocks, and Anconas:
200 First-Grade Eggs
(*b*) For other breeds:
180 First-Grade Eggs.

The scheme of egg-grading approved by the National Poultry Council and adopted by all the recognized trials is as follows:

PULLETS

	Minimum Weights	
Period of Trials	First Grade ounces	Second Grade ounces
First 4 weeks	1 7/8	1 5/8
5th to 8th week (inclusive)	1 15/16	1 11/16
9th week to end of trials	2	1 3/4

The method of scoring eggs laid by birds entered in the county laying trials is as follows:

Lunar Month	Period	Scoring Points for Each Egg		
		Special Grade	First Grade	Second Grade
First four weeks	17 days in October 11 " " November	11	10	8
Second "	19 " " November 9 " " December	13	12	9
Third "	22 " " December 6 " " January	11	10	7
Fourth "	25 " " January 3 " " February	9	8	5
Fifth * "	25 " " February 3 " " March	8	7	4

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* In leap years the dates of the 5th and subsequent periods will need alteration.

Lunar Month	Period	Scoring Points for Each Egg		
		Special Grade	First Grade	Second Grade
Sixth four weeks	28 days in March	6	5	3
Seventh "	28 " " April	6	5	3
Eighth "	2 " " April 26 " " May	6	5	3
Ninth "	5 " " May 23 " " June	6	5	3
Tenth "	7 " " June 21 " " July	7	6	4
Eleventh "	10 " " July 18 " " August	7	6	4
Twelfth "	13 " " August 15 " " September	8	7	5

SPECIAL GRADE.

Eggs of normal shape and shell weighing:
- 2 ounces and over during the first 4 weeks.
- $2\frac{1}{16}$ ounces and over during the second 4 weeks.
- 2⅛ ounces and over during the third and succeeding 4 weeks.

FIRST GRADE.

Eggs of normal shape and shell weighing:
- 1⅞ ounces and over, but under 2 ounces during first period of 4 weeks.
- $1\frac{11}{16}$ ounces and over, but under $2\frac{1}{16}$ ounces during second period of 4 weeks.
- 2 ounces and over, but under 2⅛ ounces during the third and succeeding periods of 4 weeks.

SECOND GRADE.

All double-yolked eggs and all eggs of normal shape and shell weighing:
- 1⅝ ounces and over, but under 1⅞ ounces during first 4 weeks.
- $1\frac{11}{16}$ ounces and over, but under $1\frac{15}{16}$ ounces during second 4 weeks.
- 1¾ ounces and over, but under 2 ounces during third and succeeding 4 weeks.

No limit is fixed as to the number of second-grade eggs allowed to score.

No points will be given for:
- (*a*) Eggs weighing less than the weights indicated above for second grade.
- (*b*) Soft-shelled eggs.
- (*c*) Eggs of such abnormal shape or possessing such imperfect shells as to be obviously unfit for incubation.

In these trials the best pen of birds in each section is determined by the total number of points gained. In the event of a tie the pen obtaining the greatest number of points during the first three monthly periods takes precedence.

In reckoning the number of points scored by each pen, the number of points actually scored by any birds which have died during the period are added to the total score of the remaining birds in the pen. Pen averages are calculated by dividing the total pen score (including the scores of birds which have died) by 6.

Uniform certificates are issued in conjunction with the Ministry of Agriculture at all county trials. The qualification for a Certificate of Special Merit is that a bird must score 1,650 points and have laid a minimum of 200 special and first-grade eggs. Only birds which secure this certificate at county trials, in counties which are affiliated with the National Poultry Council, are eligible for inclusion in the N. P. C. Register. The N. P. C.'s copper Certificates of Merit are awarded to birds scoring 1,500 points or over and laying a minimum of 170 special and first-grade eggs during the period of the test.

Egg Weight in Canadian Contests.—A method of scoring eggs by points was adopted for the Canadian contests beginning with the contest year of 1926-1927. A weekly egg chart is placed in each pen and eggs are recorded as taken from the trap-nest by the contest attendant. All eggs are marked by the attendant with pen and bird numbers. Eggs are gathered in the evening and delivered to the recording room. The following morning the contest clerk marks each egg up in the official contest register. At the end of each week these two records are summed up and compared so that there is a cross check on all the work. All eggs under 20 ounces per dozen are disallowed. Birds laying eggs with shell color not characteristic of the breed are disqualified and replaced.

The method of weighing eggs varies to some extent with the season. Weighings are taken daily at first, later twice weekly.

All eggs are scored by points on the following basis:

Under 20 ounces per dozen	Disqualified
20 ounces per dozen	0.6
21 ounces per dozen	0.7
22 ounces per dozen	0.8
23 ounces per dozen	0.9
24 ounces per dozen	1.0
25 ounces per dozen	1.1
26 ounces per dozen	1.2
Over 26 ounces per dozen	1.2

Egg Weight in Contests in the United States.—In connection with the numerous officially conducted contests held in the United States the following scale of points for size of egg was adopted for the contests beginning in the fall of 1929:

Under 18 ounces per dozen	Disqualified
18 ounces per dozen	0.70
19 ounces per dozen	0.75
20 ounces per dozen	0.80
21 ounces per dozen	0.85
22 ounces per dozen	0.90
23 ounces per dozen	0.95
24 ounces per dozen	1.00
25 ounces per dozen	1.05
26 ounces per dozen and over	1.10

That the adoption of schemes for scoring records of egg production at the various contests is amply justified is shown by the benefits which have already resulted to the poultry industry. The greatest benefit has been that practically all poultry breeders are giving much more consideration to egg weight in relation to production than formerly.

Limitations of the Contests.—Although the egg-laying contests that have been conducted in various parts of the world have served a very useful purpose in stimulating interest in breeding for increased egg production, it is probably true that in a large measure they are now of relatively little value except when they constitute a part of record of performance work, which is discussed later. Egg-laying contests merely serve to identify a few of some of the best layers which a poultry breeder is able to produce; contests do not give any indication whatsoever of the average egg production of the poultry breeder's entire flock. Many poultry breeders mate their best layers every year to males from some of their best layers but fail to make much progress in increasing the average egg production of their flocks. The fact that a hen laid 250 or more eggs in a laying contest does not in itself indicate that the hen is a good breeder or will produce daughters that will lay well.

What the poultry breeder should want to know is how the egg production of a certain hen compares with the egg production of all her full-sisters and half-sisters when all are fed the same rations and kept under the same environmental conditions. Egg records made at laying contests, however, can rarely be compared with egg records made on the breeder's own premises because rations and environmental conditions are usually quite different.

Then again, egg production at laying contests is computed on an arbitrary basis, since the contest begins on an arbitrary date. Such an important matter as age in days that laying commences is not taken into consideration in birds that are entered in the contests. It is because of these and other limitations that egg-laying contests are of relatively little value to a poultry breeder who develops a well-rounded-out breeding program on his own premises.

RECORD OF PERFORMANCE AND OTHER BREEDING IMPROVEMENT PLANS

The egg-laying contests served as the foundation for the development of what is now known in various countries as record of performance work carried on by the private breeders on their home premises. So long as record of performance work was limited to the records made at officially conducted egg-laying contests, but relatively little progress was possible in developing the breeding industry upon a sound basis, for the simple reason that the number of birds concerned would always be greatly inadequate to the needs of the industry. Moreover, in connection with the contest records, no definite steps had been taken for the official recognition of the hatching eggs, baby chicks, and breeding stock produced by contest birds. This is precisely what record of performance work, as now developed, provides for, and since it is possible to include many times as many birds as could be accommodated in the officially conducted contests, it is obvious that the value of record of performance work conducted on a national basis would increase manyfold in service to the industry.

The development of record of performance work on the poultry breeders' own premises has led to the adoption of other lines of poultry-breeding improvement plans, one of the most notable of which is the use of record of performance males in flocks supplying eggs to commercial hatcheries. Such a plan is destined to have a most desirable influence on the quality of the flocks of the country because so many farmers and commercial poultrymen now rely upon the commercial hatchery as a source of their baby chicks required each year.

In the United States, England, Canada, and Holland, definite steps have been taken in the adoption of well-rounded-out plans of poultry breeding on a national basis, and since these plans are typical of those adopted in other countries, some of the more fundamental aspects of the plans in operation in the four countries mentioned are given here.

The discussion which follows is organized on the basis of presenting the program of breeding-improvement work of each of the four countries separately in order that readers may become acquainted with the complete program in each country.

POULTRY-BREEDING IMPROVEMENT PLANS IN THE UNITED STATES

In the United States two major lines of poultry-breeding improvement work are being carried on, the first being the record of performance work and the second the hatchery flock improvement work. Both lines have been developed in several states, and in other states one or the other line has been developed.

Record of Performance Work.—In the United States the record of performance work is sponsored by the United States Record of Performance Federation, an organization of private breeders. In several states the work is supervised by an official state agency. Complete details governing the activities of the Federation are contained in the constitution and by-laws of the organization, but in order that readers may become acquainted with the conditions under which records of egg production and the breeding of birds are recognized, the more important features of the work are given here.

In order to qualify as an Approved R.O.P. female a pullet must lay 200 or more eggs averaging 24 ounces or more per dozen in 365 days from the date of laying the first egg. No female is eligible for an R.O.P. Certificate which during or at the end of the record year shall have developed any standard disqualifications or whose eggs are not reasonably uniform in size, shape, color, of good shell texture, and, in case of white egg varieties, free from tint.

An Approved R.O.P. male is one individually pedigreed from an R.O.P. individual mating. His dam must have laid at least 225 eggs and qualified according to the American Standard of Perfection requirements for the breed and variety. In order to become an approved R.O.P. male, each male chick at time of hatching must be banded with an approved sealed R.O.P. wing band and later in the season, after having been passed by an R.O.P. inspector, must be banded with an approved leg band.

An R.O.P. Individual Mating is one that is headed by a single approved R.O.P. male individually pedigreed from an approved R.O.P. female, that has laid at least 225 eggs in 365 consecutive days, and an approved R.O.P. individually pedigreed male.

The hens in this mating must consist of Approved R.O.P. females which are trap-nested during the entire breeding season. The egg from each hen is marked with the hen's leg band number and date. When pedigreeing, a hatching record must also be properly recorded.

An R.O.P. Pen Mating consists of Approved R.O.P. individually pedigreed males that are full-brothers mated to Approved R.O.P. females. The hatching eggs and chicks from an R.O.P. pen mating must be designated as such to properly distinguish them from eggs and chicks from an R.O.P. Individual Mating.

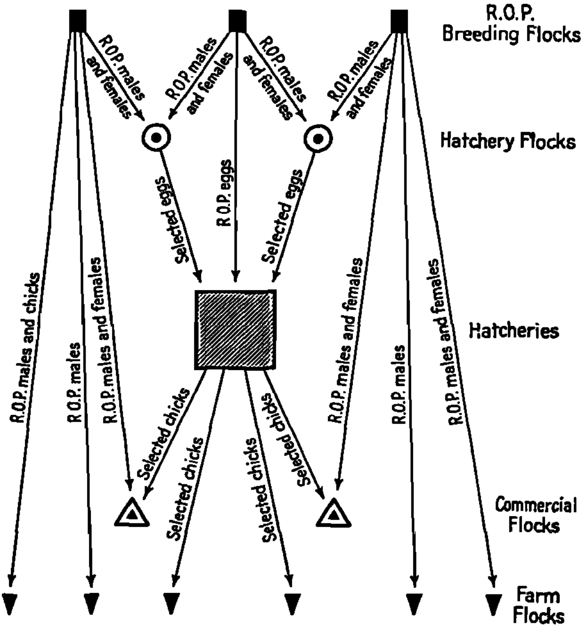

FIG. 58.—A general scheme for the improvement of the laying qualities of the farm and commercial flocks of the country. The R. O. P. flocks, comprised of standard-bred birds progeny-tested for egg production, serve as the basis of all improvement work through the distribution of R. O. P. males and females to hatchery flocks and R. O. P. males, females, and chicks to farm and commercial flocks. By the use of R. O. P. males and females, the hatchery flocks are enabled to produce hatching eggs of high quality for the hatcheries, from which are distributed carefully selected chicks to the farm and commercial flocks. The great majority of hatchery flock owners could well afford to purchase R. O. P. males and the great majority of farmers and commercial poultrymen could well afford to purchase chicks of superior quality from the hatcheries.

An R.O.P. egg is one produced by an Approved R.O.P. female that has been mated to an Approved individually pedigreed R.O.P. male and is marked with the hens' leg band number when the hen is trapnested.

R.O.P. Individually pedigreed chicks must be hatched in pedigree baskets or other approved individual receptacles, each hen's eggs being placed together in separate compartments. When removed from the pedigree tray, each chick must be banded with an individual pedigree wing band denoting its breeding and preferably marked with the dam's Approved R.O.P. leg band number. An R.O.P. chick must be hatched from an R.O.P. egg and wing-banded by an R.O.P. breeder.

Hatchery Breeding Flock Improvement.—In several states definite steps have been taken to improve the breeding quality of the baby chicks produced by the commercial hatchery. Such work is very widespread in its influence because, there are in the United States several thousand hatcheries from which are distributed annually throughout all parts of the country many millions of baby chicks. The use of Record of Performance males in hatchery breeding flocks is one of the most effective ways of improving the egg-laying quality of the flocks of the country.

Although the details of hatchery breeding flock improvement work as carried on in different states vary somewhat, the essential features are much the same and are given here.

All females are selected for constitutional vigor and are rigidly selected for egg production at least once each year. Standardbred and production qualities are required to a reasonably high degree, the American Standard of Perfection and the method of production judging, prescribed by the state college of agriculture or state university, or other properly constituted state agency, serving as the basis for the selection of males and females. The male birds must be from Record of Performance matings, special attention being given to constitutional vigor and standard qualities.

The hatchery breeding flocks are inspected by an official state inspector at least once during the breeding season.

All birds passed by the inspector are banded with state sealed and numbered leg bands. Only one variety may be kept on the farm, unless, where more than one variety is kept, ample provision has been made to keep these varieties and their eggs separate. No birds except those with official state sealed and numbered leg bands are allowed in the breeding flock, and no male birds are allowed in any other flocks that may be kept on the same farm.

The eggs incubated in the hatchery must come only from flocks that have been approved and must weigh at least 1⅞ ounces each, and must average 23 ounces to the dozen, and must be sold only in original packages.

All chicks sold by the hatchery operator must be hatched only from eggs secured from approved flocks and hatcheries that have been approved, and must be sold in original packages only. Chicks sold for re-sale lose their identity.

The hatcheries must be kept in strictly sanitary condition at all times, and incubators must be thoroughly disinfected after each hatch. Each hatchery must be inspected by an official state inspector at least once during the hatching season. The hatchery management must keep accurate records concerning the number of eggs received from each flock, name and address of each purchaser, the number, breed and variety, and date of shipment of all chicks. These records must be open for official inspection at all times. Eggs received and chicks hatched must be subject to inspection at all times.

Pullorum Disease Eradication Recognized.—In several states official recognition is given to those flocks that have passed two consecutive negative agglutination tests for the pullorum disease, such tests being at intervals of not less than six months nor more than one year apart, such flocks being required to pass one negative agglutination test yearly thereafter. Individual birds purchased must come from flocks that have passed two negative agglutination tests not less than six months nor more than one year apart or the individual birds must have passed two negative agglutination tests at least twelve weeks apart.

POULTRY-BREEDING IMPROVEMENT PLANS IN ENGLAND

During recent years in England poultry-breeding improvement plans have taken definite shape in the form of five major lines of work. According to Mr. Percy Francis, Poultry Commissioner in the Ministry of Agriculture, the five lines of work include the investigations conducted at the Northern Breeding Station, the county laying trials, the cockerel breeding scheme, the Lancashire breeding scheme, and the accredited poultry breeding scheme.

The work of the Northern Breeding Station is analogous to that carried on by some of the state agricultural experiment stations in the United States and therefore needs no further discussion at this time.

County Laying Trials.—The more important aspects of this important line of work are presented here, the method of scoring the eggs already having been given. The primary object is to demonstrate the importance of well-bred stock in profitable egg production.

The trials run for a period of 48 weeks, a section for heavy breeds and a section for light breeds being provided. Each entry comprises 6 birds bred by the competitor on his own farm. The trials are operated under the management of the County Committee.

Approved Cockerel Breeding Scheme.—In order to obtain greater value from the county egg-laying trials, a scheme known as

"The Approved Cockerel Breeding Scheme" has been instituted whereby birds which have attained a certain standard of egg production and are otherwise considered suitable for breeding stock are kept under official observation at the conclusion of the trials.

The introduction of a standard upon which to issue Certificates of Special Merit at all county egg-laying trials enables a uniform standard to be set, so far as egg production is concerned. In order to qualify for a Certificate of Merit, a bird must have laid not less than 200 special and first-grade eggs and must have gained a minimum of 1,650 points, based on weight of eggs as explained previously.

The approved cockerel breeding scheme is under the control of the County Poultry Sub-Committee. The scheme is open only to purebred birds which have gained a Certificate of Special Merit and eligible birds that are approved by the Sub-Committee are leg-banded and, after passing the agglutination test for the pullorum disease, are tattooed.

The birds are then sent to a breeding centre where they are mated to cockerels that are selected and approved by the Sub-Committee. A careful record is kept of all eggs laid and those used for incubation must weigh 2⅛ ounces each or more. The chicks hatched are reared at the breeding center for 3 months, after which those approved by the Sub-Committee are returned to their owners.

The owners are required to permit inspection of their farms, stock, and records at any reasonable time by members of the Sub-Committee or by an official of the Ministry of Agriculture. All cockerels which pass final inspection are marked with an indelible mark by the Sub-Committee and all cockerels which fail to pass the final inspection have their wing bands removed. All approved cockerels are offered for sale at a public auction, the owner being permitted to place a reserve price on any bird he may wish to retain.

Lancashire Breeding Scheme.—The Lancashire Utility Poultry Society sponsors the Lancashire breeding scheme, which has been described by Barron (1930). Females entered in the various English laying trials which are recognized by the National Poultry Council are used as breeding stock providing they qualify for registry in the "Official Annual Register of Laying Trial Records" as explained previously.

Females that qualify are banded with copper leg bands on the right leg, the band being riveted to prevent removal, and are sent from the laying trial to the breeding station where they are mated to cockerels furnished by the owners of the females. Both males and females are required to be free from bacillary diarrhea or the pullorum disease.

Pedigree breeding is carried on at the station, the chicks hatched from each mating being toe-punched and wing-banded. The chicks are reared up to ten to twelve weeks of age, when they are selected very carefully, all but the best being eliminated. The best of them are banded with riveted and sealed wing bands which are numbered and stamped "National Poultry Council." Each chicken is also tattooed on the underside of one wing, a different tattoo mark being used each season. The good chicks are then sent to their owners.

A so-called stud book is published each season giving full details of all chicks shipped from the breeding station, and those who buy chicks from the owners may secure, from the secretary of the Lancashire Utility Poultry Society, information regarding the breeding of the chicks purchased.

Accredited Poultry-Breeding Stations.—The stations are under the control of the County Poultry Committee. The main object of these stations is to provide poultry keepers and those intending to start poultry keeping in the county with reliable information for obtaining healthy stock, free from the pullorum disease, of good type, and of authentic pedigree as regards egg production and egg size.

Only those farms are considered for accreditation on which all the hens, pullets, cocks, and cockerels are subjected to the agglutination test for the pullorum disease in accordance with certain regulations. The breeding stock used is approved by the County Poultry Instructor. The accredited flock owner is required to keep careful records of eggs laid, the number of chicks hatched, the number of eggs and chicks sold, and to provide his flock with the best possible conditions of management.

POULTRY-BREEDING IMPROVEMENT PLANS IN CANADA

The major lines of poultry-breeding improvement work in Canada include registration, record of performance, the progeny testing of breeding males, a distribution policy for record of performance cockerels, and a hatchery flock improvement plan.

Registration.—The registration of poultry in Canada is sponsored by the Canadian National Poultry Record Association, which is an organization of private breeders except that the secretary is an employee of the Dominion Government. The Association is affiliated with the Canadian National Livestock Records, a government organization responsible for issuing registration certificates for all classes of purebred livestock in Canada.

Registration is limited to birds meeting certain requirements in Canadian egg-laying contests and to the progeny of registered birds. All birds in the laying contests not otherwise disqualified, whose eggs average 24 ounces to the dozen after the first 4 weeks' laying and which in the contest year lay 200 eggs or more, are registered in the Canadian National Poultry Record Association. Females kept on the breeders' premises that have been approved as pullets by an official of the Dominion Department of Agriculture and later qualify on the same basis as laying contest females are eligible for registration providing they are the progeny of registered sires and dams. Male birds over 6 and under 12 months of age that have passed inspection are eligible for registration, providing their sires, dams, maternal grand dams, and maternal great grand dams are registered.

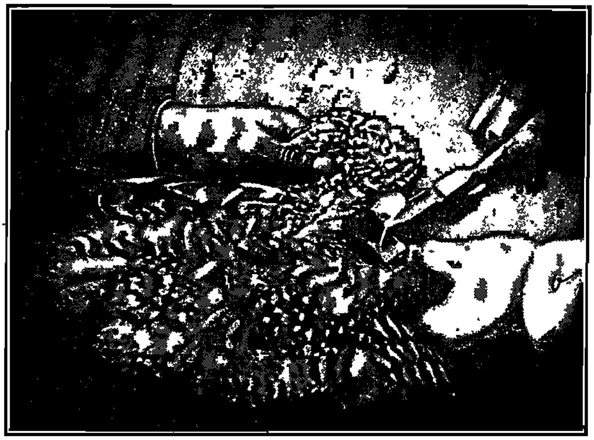

FIG. 59.—Stamping the tattoo marks on the wing of a "registered" female. (Photo by Can. Nat. Poul. Rec. Assn.)

Record of Performance.—In Canada the record of performance work is carried on by the Dominion Government, certificates of production being issued to all birds that lay 200 or more eggs on the breeder's own premises and otherwise meet certain requirements. Record of Performance advanced certificates are issued to birds laying 225 or more eggs from the date of first egg laid. In both cases, starting two months after each bird's record commences at least half the number of eggs laid during official inspections must weigh 2 ounces each or over.

The R.O.P. breeders are requested to keep available for the information of inspectors appointed by the Dominion Government and others a detailed statement showing number of eggs laid, number of eggs put in incubators and under hens, number of infertile, number of dead germs, number failed to hatch, number chicks hatched, number chicks banded; further, that such eggs as do not hatch be held, if so directed, for the information of the inspector. The final inspection of the cockerels raised is made after they are 6 months of age, the inspector being required to band all approved R.O.P. cockerels.

Progeny-Tested Breeding Males.—A plan of progeny testing breeding males has been worked out in conjunction with the Record of Performance work. Males eligible for certificates are required to possess evidence of outstanding vigor and physical perfection, and to be free of standard disqualifications, and shall have been registered or approved by an inspector as suitable to head a Registered or R.O.P. mating of females that have been certified under policies of the Dominion Department of Agriculture.

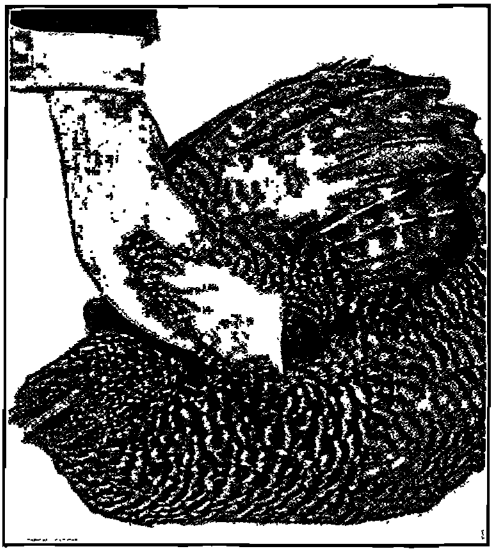

FIG. 60.—The wing of a "registered" female, feathers removed, bearing the tattoo marks and a wing band. (Photo by Can. Nat. Poul. Rec. Assn.)

Certificates for progeny-tested males may be issued for all males based on the production of daughters, it being required that 50 per cent of all eligible daughters, meaning all healthy, normal matured birds, from at least four mothers, with a minimum of at least four daughters each, and 50 per cent of all daughters eligible from all mothers mated in one year shall qualify for certification under Departmental policies.

Cockerel Distribution Policy.—The purpose of this policy is to more effectively link the products of the pedigree breeders of Canada with the Approved Flock Associations whose flocks are used as the sources of supplies for eggs for hatcheries. The Approved Flock Associations are organized under federal or provincial auspices.

Only cockerels over 6 and under 12 months of age at time of shipment bred from matings approved under the Federal Departmental Policies are selected for distribution under this policy. Each cockerel selected must meet the requirements of the Minister of Agriculture, as interpreted through a Departmental Inspector, respecting production qualifications, size, type, vigor, and freedom from disqualifications. The Federal Department bears one-third of the purchase price of the cockerels selected and the cost of the transportation of the birds in carlots from the carlot loading point to points of unloading.

Hatchery Approval Policy.—The primary object of the hatchery approval policy is to improve the quality of chicks produced by commercial hatcheries. The Federal Department furnishes qualified inspectors for the hatchery flocks and designates the inspectors for the hatcheries.

Sanitary conditions on farms where hatchery flocks are kept must be satisfactory to the inspector before the hatchery flock is approved. Every bird in an approved flock must be passed upon and banded by the inspector.

Sanitary conditions at hatcheries must be approved by the hatchery inspector. Only eggs from approved hatchery flocks may be incubated and they must weigh at least 24 ounces to the dozen in tray lots and no eggs may be set that weigh less than 23 ounces to the dozen. Only selected chicks may be sold as approved chicks.

Hatchery operators must keep open for the examination of the hatchery inspector the following records: (*a*) egg purchases; (*b*) chick purchases; (*c*) chick sales; (*d*) custom hatching; (*e*) advertising. Hatchery records must be kept on forms approved by the Hatchery Approval Associations and the Department. In addition proofs in triplicate of catalogues, circulars, advertisements, and other publicity material used by an approved hatcheryman or his agent must be mailed promptly to the hatchery inspector for approval together with a list of publications in which the advertisements will appear.

A POULTRY-BREEDING IMPROVEMENT PLAN IN HOLLAND

One of the most important kinds of poultry-breeding improvement work in Holland has been described by Hagedoorn (1927). An officially conducted breeding center is maintained for the purpose of determining the laying ability of a representative group of pullets from the flocks of poultry breeders who enter the work. After each poultry breeder has mated his breeding pens, the official inspector visits his farm and releases all hens from the trap nests and then collects 50 eggs at random as they are laid and these 50 eggs are taken to the official breeding center where the chicks hatched are reared to maturity.

In the fall of the year 7 pullets secured from the 50 eggs of each breeder are selected and kept at the breeding center for one year. No trap-nesting is done but the average number of eggs laid by each group of 7 pullets is regarded as a good index of the laying ability of the large flock from which each group of 7 birds was secured.

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CHAPTER XII

THE PURPOSE AND METHOD OF PEDIGREE BREEDING

IF THE discussion in the preceding chapters of this book has done nothing more than to demonstrate to poultry breeders the necessity of conducting their breeding work on the basis of the results secured in the progeny test it will perhaps have been worth while. The fruits of Mendelism and the existing knowledge governing the inheritance of egg production and other characters are the result of progeny testing.

When Bateson and Punnett mated Black Rose-Comb with White Rose-Comb Bantams and observed that all the first-generation birds were black and that when these were bred among themselves they produced progeny in the proportion of 3 blacks to 1 white, a valuable lesson was learned. The results secured demonstrated the facts that in this particular cross black is dominant to white, and that the characters are produced in the second generation in a definite mathematical proportion. If records of the matings and careful descriptions of the birds in each of the generations had not been made the results could not have been interpreted accurately. What Bateson and Punnett really did was to conduct a progeny test, for the kind of progeny secured gave a true picture of the genetic constitution of the parents.

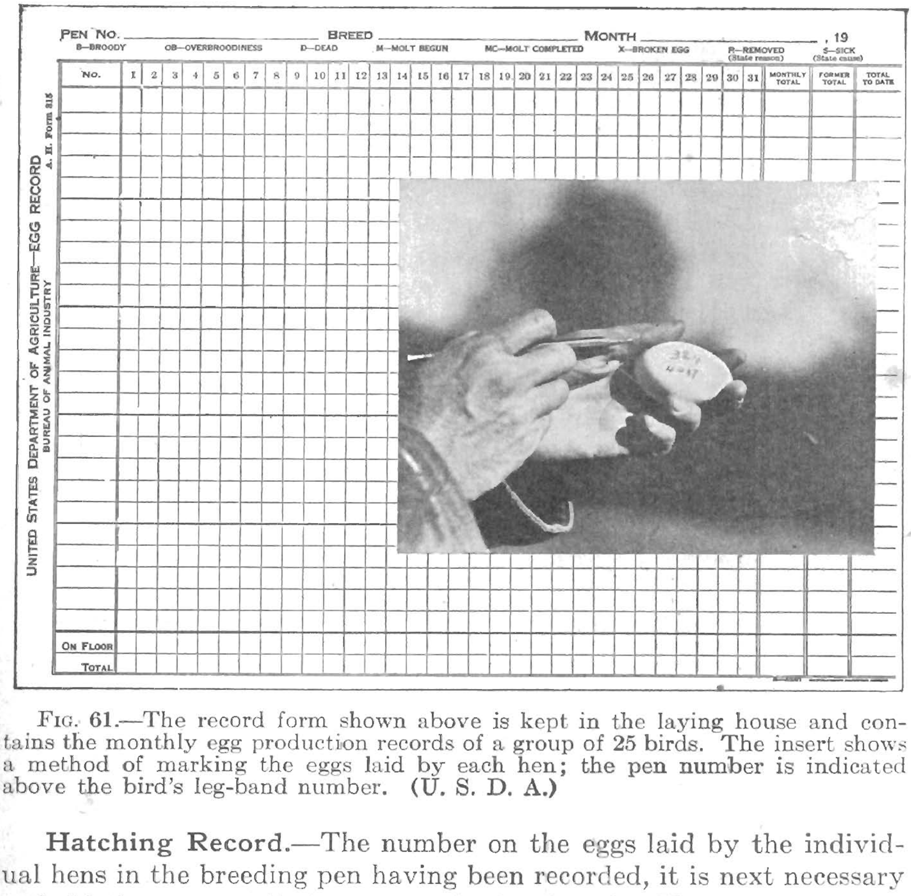
The modern poultry breeder should do precisely the same thing, whether he is breeding for increased egg production, perfection in plumage pattern, or any other character, for the worth of any animal as a breeder is determined by the kind of progeny produced. Pedigrees in themselves are of little value, but pedigree breeding based on the kind of progeny resulting from a given mating is of the greatest value.

By pedigree breeding is meant the mating of birds with pedigrees and keeping account of the parentage of the chicks produced so that their pedigrees are a matter of record. The purpose of pedigree breeding is to make the various matings in such a way that the resulting progeny will be an improvement over the parents or at least over the progeny produced the preceding year. Pedigree breeding will result in progress, however, only when the poultry breeder uses sound judgment in the selection of his breeding stock after he has made use of all the information available in the records which are kept. Records are of little value to a poultry breeder who does not *know* his birds. Conversely, a poultry breeder who keeps no records can hardly be expected to make much progress in developing a strain of birds for any particular purpose.

The results secured from year to year can be determined accurately only by the use of records of various kinds. Records must be adapted for the purpose of describing the number and kind of progeny produced and for comparing progeny with parents. Records should also be kept giving necessary information regarding the brothers and sisters of a given bird. The various records which a pedigree breeder should keep are discussed subsequently, and for the most part they are as necessary for the progressive breeder of poultry for exhibition purposes as for the poultry breeder who is interested primarily in breeding for increased egg production.

The real object in maintaining breeding records is to be able to identify the progeny of all parents in order to see what kind of progeny each pair of birds produces. For this purpose a set of records must be maintained which will permit of tracing each egg from the time it is laid to the time it hatches and tracing each chick up to maturity and later if it is used as a breeder. The record forms used should contain an adequate description of the parent and of the progeny, particular note being made of any undesirable characters which any of the birds may possess. This is necessary because a progressive breeding plan involves the elimination of the undesirable in addition to breeding from the best. The fundamental feature of a system of pedigree records is that any given pedigree or part of a pedigree may be entered or consulted after entry with the least possible expenditure of time and labor and the greatest possible accuracy. The system should be adapted to reducing the possibility of error to the minimum, and it should be simple enough to be operated rapidly.

Egg-Production Record.—The first step in carrying out a scheme of progeny testing is to record on each egg the number of the hen that laid it. To be able to do this, trap-nesting is necessary, and, of course, the hens must have numbered leg bands, preferably sealed. As each hen is released from the trap nest, the pen number and the number on the hen's leg band is recorded on the egg and the egg is recorded on the Egg Record form, shown in Fig. 61, which is suspended on the wall near the trap nests. The egg record form is 8 by 9½ inches and provides for the recording of the monthly production of 25 hens. The various notations at the top of the form should be noted, inasmuch as it is only when as complete information as possible is kept concerning the behavior of each hen that the poultry breeder knows all that he should know concerning his birds.



UNITED STATES DEPARTMENT OF AGRICULTURE—EGG RECORD
BUREAU OF ANIMAL INDUSTRY
A. H. Form 315

PEN NO. ____________ BREED ____________ MONTH ____________, 19

B—BROODY OB—OVERBROODINESS D—DEAD M—MOLT BEGUN MC—MOLT COMPLETED X—BROKEN EGG R—REMOVED (State reason) S—SICK (State cause)

NO.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	MONTHLY TOTAL	FORMER TOTAL	TOTAL TO DATE
ON FLOOR																																		
TOTAL																																		

FIG. 61.—The record form shown above is kept in the laying house and contains the monthly egg production records of a group of 25 birds. The insert shows a method of marking the eggs laid by each hen; the pen number is indicated above the bird's leg-band number. (U. S. D. A.)

Hatching Record.—The number on the eggs laid by the individual hens in the breeding pen having been recorded, it is next necessary to hold the eggs until they are to be incubated. The eggs should be incubated as soon as possible after being laid, but much time will be saved if the eggs of a week's production from each hen are incubated together. An egg table fitted with drawers, such as shown in Fig. 62, is very suitable for holding eggs for incubation. The depressions running across the top facilitate in the sorting of the eggs laid by the different hens. Each hen's eggs are grouped together and, as the incubator is filled, the entries are made on the Hatching

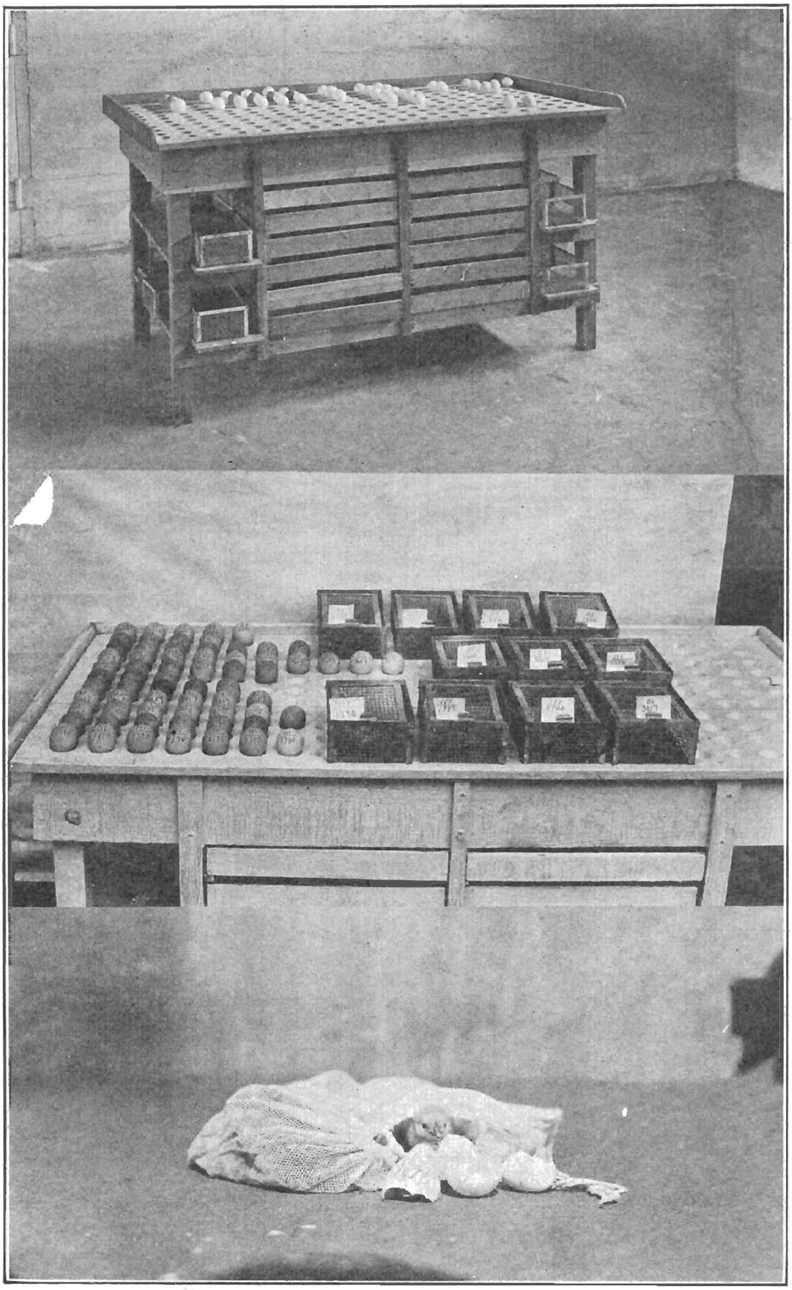
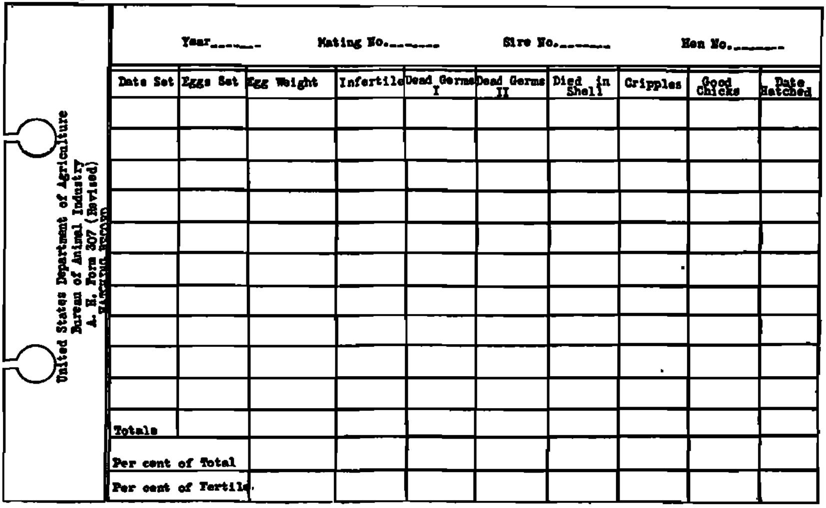


FIG. 62.—At the top, a table for storing and sorting hatching eggs. In the center, showing how the eggs are sorted by number and then the eggs of each hen are placed in separate hatching baskets, which are carefully numbered and securely fastened. At the bottom, a hatching sack has been used to keep one hen's eggs and chicks hatching from them separate from those of other hens. (Photo by U. S. D. A.)

Record form shown in Fig. 63. This form will do for each hen for about 18 weeks, which is longer than the normal hatching season. The form is 6 by 9½ inches.

On the eighteenth day of incubation the eggs remaining in the incubator are all placed on the sorting table and each hen's eggs are grouped together for placing in the hatching bag or basket, shown in Fig. 62. Suitable hatching bags for holding five or six eggs may be made of strong cheesecloth or scrim, or a wire basket with a securely fitted top may be used. It is very important that every precaution be taken to keep each hen's eggs and the chicks hatched from them separate from the others. The hatching bag or basket should be carefully numbered and securely fastened.



United States Department of Agriculture
Bureau of Animal Industry
A. H. Form 307 (Revised)
HATCHING RECORD

Year______ Mating No.______ Sire No.______ Hen No.______

Date Set	Eggs Set	Egg Weight	Infertile	Dead Germs I	Dead Germs II	Died in Shell	Cripples	Good Chicks	Date Hatched
Totals									
Per cent of Total									
Per cent of Fertile									

FIG. 63.—The Hatching Record gives the results in fertility and hatchability of all eggs set each hatching season from each female breeder. (U. S. D. A.)

Chick Banding Record.—After the chicks are hatched it is necessary to give each chick a numbered leg band or a numbered wing band, as shown in Fig. 64. The bands should be numbered serially from 1 up to the number desired. If leg bands are used they will have to be changed from the legs and inserted in the wings when the chicks are three of four weeks old, or the chick leg bands may be changed for sealed wing bands. The advantages in wing banding the chicks at hatching time are that it is at once permanent and the danger is avoided of causing lameness before the leg bands are

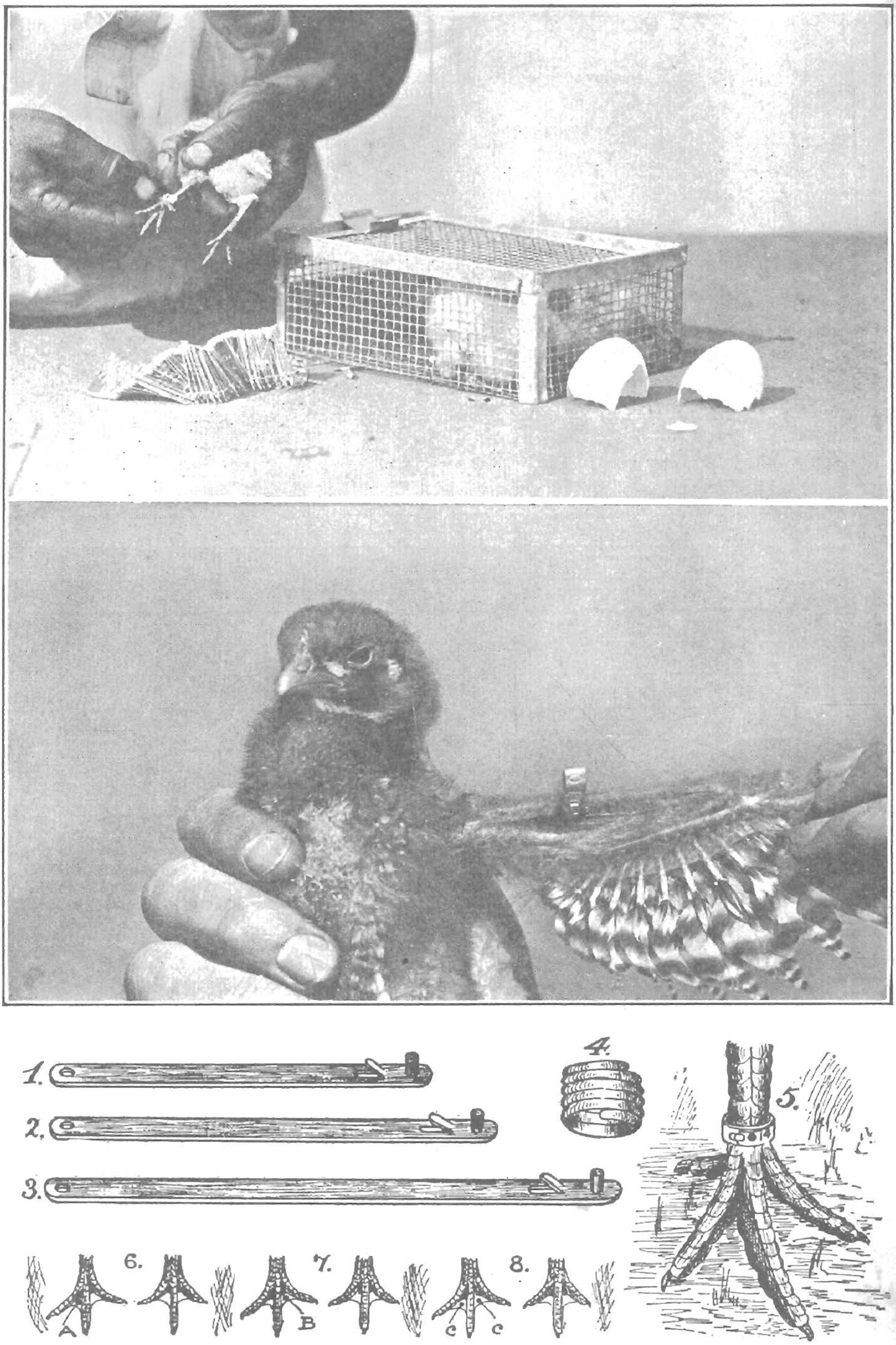
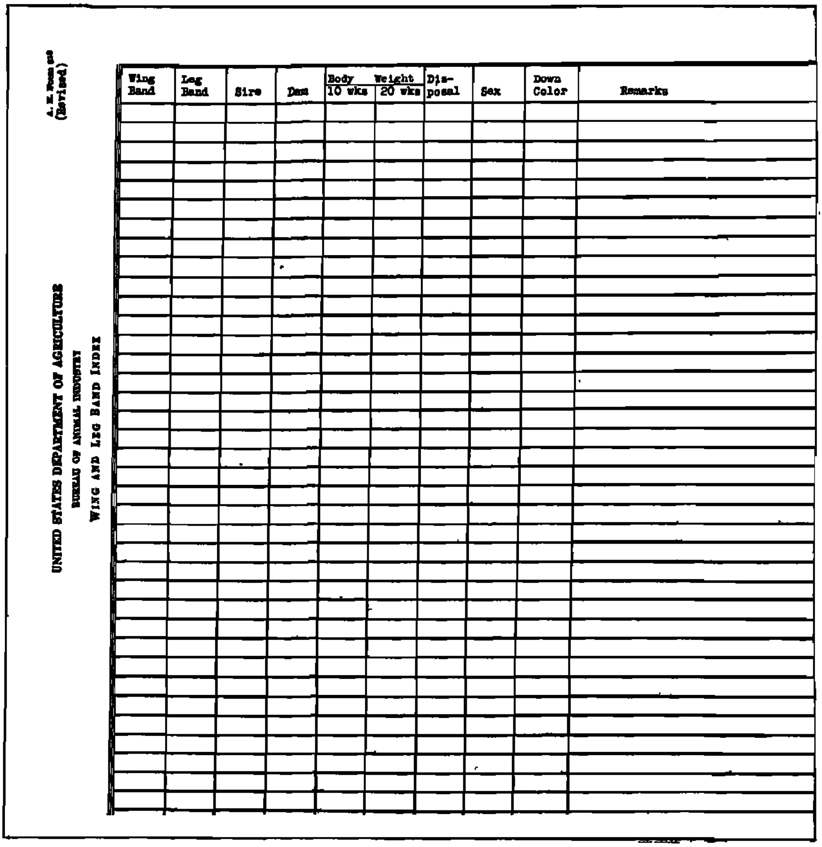


FIG. 64.—At the top, leg banding the chicks. In the center, wing-band in place. At the bottom, wing and leg bands of various kinds; also various ways of toe-punching. (U. S. D. A.)

enlarged or removed. For very valuable chicks a band may be inserted in each wing.

As the chicks are banded, the band numbers are entered in the "Wing Band" column of the Wing and Leg Band Index form shown in Fig. 65. The reason for putting the band number of the chick in the "Wing Band" column, even if the chicks are first banded on the leg, is that when the chicks are three or four weeks of age the leg bands are transferred to the wings. The band placed on each chick



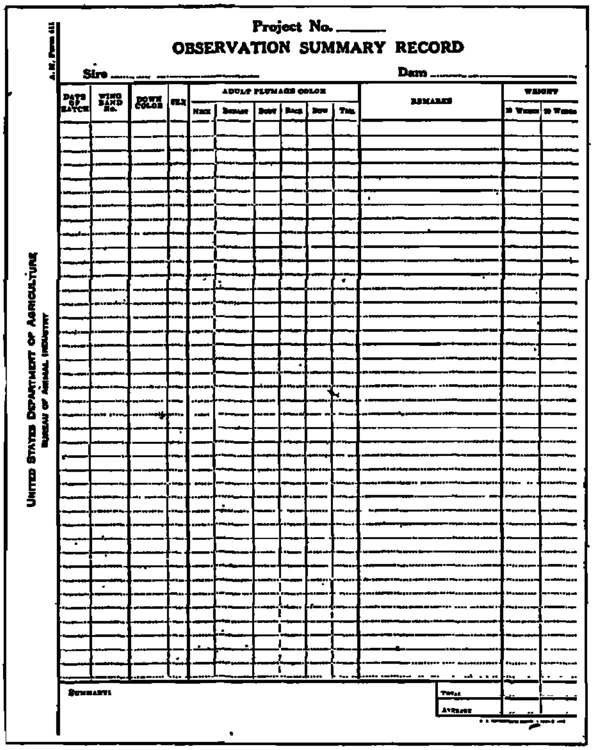
A. H. Form 88
(Revised)

UNITED STATES DEPARTMENT OF AGRICULTURE
BUREAU OF ANIMAL INDUSTRY
WING AND LEG BAND INDEX

Wing Band	Leg Band	Sire	Dam	Body Weight		Disposal	Sex	Down Color	Remarks
				10 wks	20 wks				

FIG. 65.—The Wing and Leg Band Index for recording the band number of all chicks hatched. At hatching time, the band number that is placed on each chick is recorded in the first column from the left. The second column from the left is reserved for recording the leg-band numbers of pullets placed in the laying house and cockerels saved for breeding purposes. Columns are provided for recording the sire and dam of each chick, the weight of each chick at 10 and 20 weeks of age, date of disposal, sex, down color, and remarks. (U. S. D. A.)

at hatching time is really the wing band by which the bird will be permanently identified for the rest of its life. The wing and leg band index form provides for the entry of 37 chick band numbers. It is understood, of course, that each sheet of this form will contain the chicks from a number of hens taken off. from one hatch. The ancestry of each chick is indicated by the dam and sire numbers inserted in their appropriate columns. The purpose of the wing and leg band index form is to provide for the ready entry of the band numbers of the chicks and their parents at hatching time and to permit of entering the date of death of any chick during the growing period and also to record the sex and any other information that may be desired concerning each chick.



United States Department of Agriculture
Bureau of Animal Industry

Project No. ______
OBSERVATION SUMMARY RECORD

Sire ______ Dam ______

Date of Hatch	Wing Band No.	Down Color	Sex	Adult Plumage Color						Remarks	Weight	
				Neck	Breast	Body	Back	Bow	Tail		[illegible] Weeks	[illegible] Weeks

Summary

Total

Average

FIG. 66.—The Observation Summary Record form is used for recording various items of information concerning the progeny of each mating. A poultryman could use some of the columns for items of information other than those given in the form. (U. S. D. A.)

The second column, entitled "Leg Band," in the form shown in

Fig. 65, is for the purpose of entering the leg-band numbers of the cockerels and pullets in the fall of the year when certain cockerels are saved for breeding purposes and the pullets are selected for the laying pens. All birds saved have a cross-reference number on this sheet, a wing-band number and a leg-band number, so that if either a wing or leg band is lost the identity of the bird can be established.

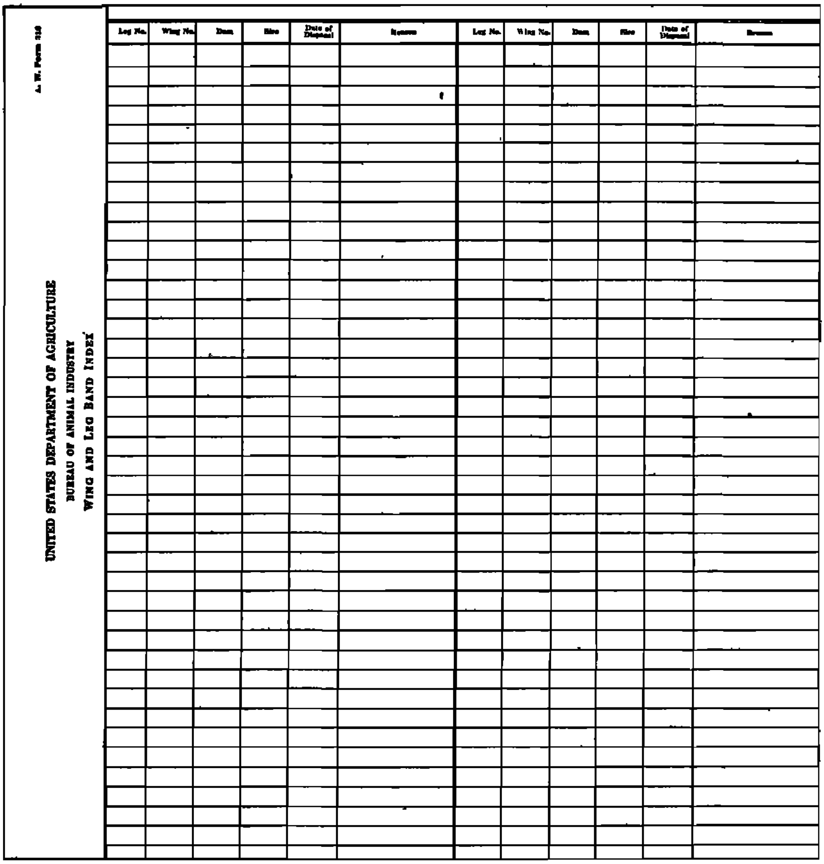
Observation Summary Record.—After the hatching season is over it is desirable to have the records of the progeny of each mating assembled in one form so that there will be readily available the total number, kind, and quantity of chicks produced by each dam. This makes it possible to determine the worth of a dam as a breeder when mated to a particular sire and the progeny of one dam may be compared with the progeny of other dams mated to the same sire as well as with the progeny of dams mated to other sires.

The wing-band numbers of all chicks hatched from each dam are entered in the Observation Summary Record form, shown in Fig. 66. The details of this form could be modified to suit the individual breeder's needs, for if he were breeding a solid-colored variety he might want to make observations other than those indicated in the form pertaining to adult plumage color.

Leg Banding Record.—In the fall of the year, as the young stock approaches maturity, the pullets that are to be placed in the laying houses and the cockerels that are to be used as breeders are banded with leg bands. The bands should be put on the left leg of the pullets so that the numbers on the band are upside down when the bird is standing; this makes it easier to read the numbers when the pullets are released from the trap nest. The bands should be placed above the spur on cockerels. The leg-band numbers of all pullets are entered in serial order in the "Leg No." column of the Leg and Wing Band Index form, size 11 by 11 inches, as shown in Fig. 67, except that in this case the color of the form is different from that used for recording the chick band numbers. The forms shown in Figs. 65 and 67 constitute an excellent cross-reference for both wing-band and leg-band numbers, the cross-reference system being very useful in identifying any bird which may have lost either its wing or leg band. A double check is provided for tracing the pedigree of any bird at any time.

Female Summary Record.—The front of the Female Summary Record form, shown in Fig. 68, provides for the entry of various items of major importance in determining the reproductive ability of the female and her breeding worth from the standpoint of egg production. The form is 6 by 9½ inches.

The top of the form provides for the entry of important information concerning the hen herself and her sisters. The female breeder that has a large number of good sisters that started to lay early in life, had good average egg production and laid eggs of good size has a better chance of being a good breeder than the female breeder with very few or no sisters with similar records.



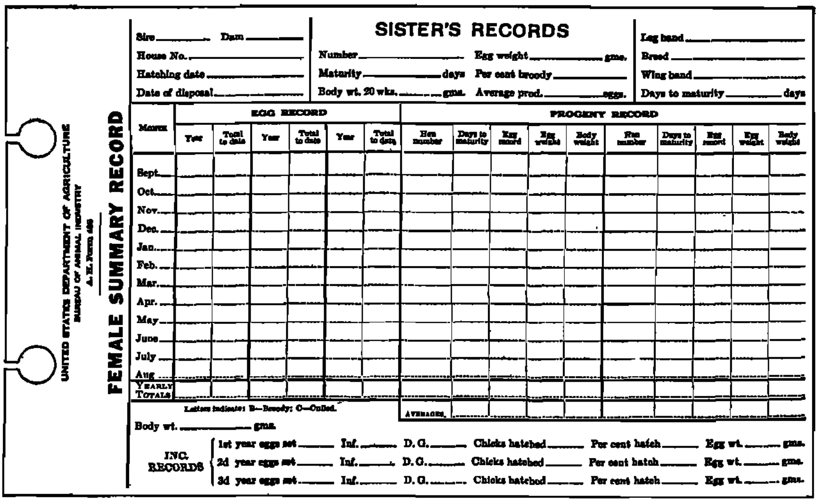
A. H. Form 310

UNITED STATES DEPARTMENT OF AGRICULTURE
BUREAU OF ANIMAL INDUSTRY
WING AND LEG BAND INDEX

Leg No.	Wing No.	Dam	Sire	Date of Disposal	Remarks	Leg No.	Wing No.	Dam	Sire	Date of Disposal	Remarks

FIG. 67.—The Wing and Leg Band Index form is used for recording the wing-band and leg-band numbers of pullets kept. The dam and sire of each pullet is given. The form shown here and the form shown in Fig. 65 make useful cross-reference forms since in this form the leg-band numbers are in serial order whereas in the form shown in Fig. 65 the wing-band numbers are in serial order. (U. S. D. A.)

The bottom portion of the form provides space for the entry of the hatching results for three years.



UNITED STATES DEPARTMENT OF AGRICULTURE
BUREAU OF ANIMAL INDUSTRY

FEMALE SUMMARY RECORD

Sire ________ Dam ________
House No. ________
Hatching date ________
Date of disposal ________

SISTER'S RECORDS

Number ________ Egg weight ________ gms.
Maturity ________ days Per cent broody ________
Body wt. 20 wks. ________ gms. Average prod. ________ eggs.

Leg band ________
Breed ________
Wing band ________
Days to maturity ________ days

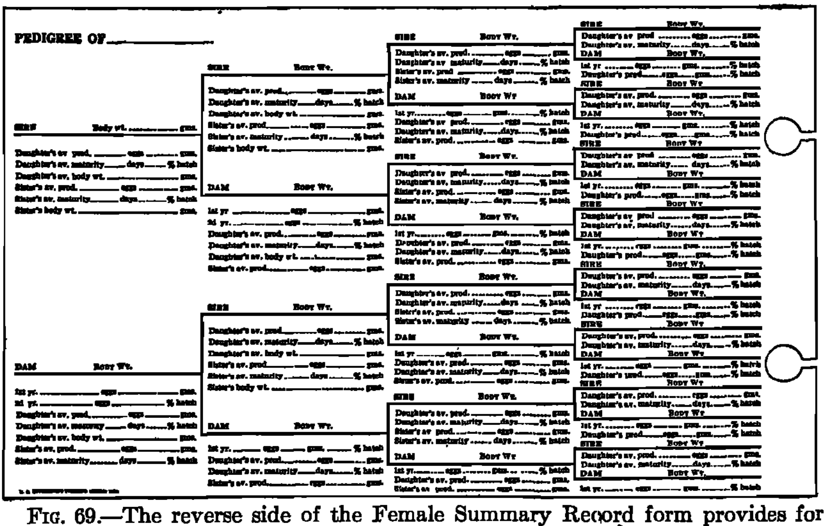
Month	EGG RECORD						PROGENY RECORD									
	Year	Total to date	Year	Total to date	Year	Total to date	Hen number	Days to maturity	Egg record	Egg weight	Body weight	Hen number	Days to maturity	Egg record	Egg weight	Body weight
Sept.																
Oct.																
Nov.																
Dec.																
Jan.																
Feb.																
Mar.																
Apr.																
May																
June																
July																
Aug.																
Yearly Totals																
							Averages									

Letters indicate: B—Broody; C—Culled.

Body wt. ________ gms.

INC. RECORDS
1st year eggs set ______ Inf. ______ D. G. ______ Chicks hatched ______ Per cent hatch ______ Egg wt. ______ gms.
2d year eggs set ______ Inf. ______ D. G. ______ Chicks hatched ______ Per cent hatch ______ Egg wt. ______ gms.
3d year eggs set ______ Inf. ______ D. G. ______ Chicks hatched ______ Per cent hatch ______ Egg wt. ______ gms.

Fig. 68.—The Female Summary Record form on the front side, shown above, provides for the entry of a great deal of information of value in connection with the female herself, her sisters, and her progeny. The reverse side of this form is shown in Fig. 69. (U. S. D. A.)



PEDIGREE OF ________

SIRE Body wt. ________ gms.
Daughter's av. prod. ______ eggs ______ gms.
Daughter's av. maturity ______ days ______ % hatch
Daughter's av. body wt. ______ gms.
Sister's av. prod. ______ eggs ______ gms.
Sister's av. maturity ______ days ______ % hatch
Sister's body wt. ______ gms.

Fig. 69.—The reverse side of the Female Summary Record form provides for the entry of a great deal of information of value concerning the female's ancestors. (U. S. D. A.)

The main portion of the form provides space for recording the hen's egg production by months for three years and also egg-production data of her progeny. It is thus possible to compare the performance of the progeny with that of the dam. Moreover, the egg-production data of the progeny of one dam may be readily compared with those of the progeny of another dam.

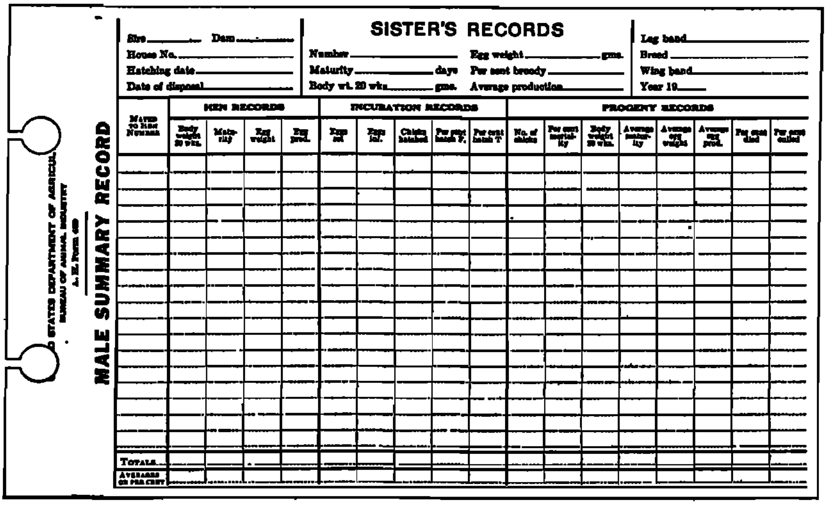
The reverse side of the Female Summary Record form gives a fairly complete pedigree of the hen, as shown in Fig. 69. It is to be noted that not only is the body weight of the female's sire given but also very valuable information concerning the egg production, egg weight, hatchability, and body weight of both the sire's daughters and his sisters. It is obvious that a sire with many good sisters and good daughters has a better chance of being a good breeder than a sire with few or no good sisters and daughters. Similar information is recorded regarding the daughters and sisters of the sire's sire and the dam's sire.

The pedigree of the female also gives considerable data of value regarding her dam, including the number of eggs laid by the dam during the first and second years, the mean weight of the eggs laid the first year, the hatchability of the eggs incubated, and data pertaining to the dam's daughters and sisters. The same kind of information is recorded for the sire's dam and the dam's dam.

Information of value is recorded pertaining to the female's great-grandparents and her great-great-grandparents, so that the pedigree taken as a whole should be of considerable value in estimating the worth of the female as a breeder. Her real worth as a breeder is determined, however, by the kind of progeny she produces, as indicated by the information recorded on the face side of the Female Summary Record shown in Fig. 68.

Male Summary Record.—From the standpoint of the results secured in breeding work the male is "half the flock." Therefore, the greatest possible care should be exercised in the selection of males for breeding purposes. When the results of the progeny test reveal that a particular male is a good breeder he should be used as long as possible. The male that has a large number of good sisters stands a better chance of being a good breeder than a male with few or no good sisters. Also the male with a good ancestry stands a much better chance of being a good breeder than a male with poor ancestry. The more complete the information regarding the sisters and ancestors of a group of males the better is one able to choose the best breeders from among them.

The front of the Male Summary Record form, shown in Fig. 70, provides for the entry of records regarding the male's sisters, the egg-production and egg-weight records of the hens to which he is mated, the incubation records of each hen to which he is mated, and data of value regarding the progeny of each hen to which he is mated. The results secured from one hen may be compared with the results secured from the other hens to which the male is mated. The results secured from one male are readily compared with the results secured from other males. The male that proves to be a good breeder should be used as a breeder as long as he lives and is able to mate. Moreover, his progeny should be used for breeding purposes in preference to the progeny of a male that proves himself to be a poor breeder.



MALE SUMMARY RECORD

SISTER'S RECORDS

Sire ________ Dam ________
House No. ________
Hatching date ________
Date of disposal ________

Number ________
Maturity ________ days
Body wt. 20 wks. ________ gms.
Egg weight ________ gms.
Per cent broody ________
Average production ________

Leg band ________
Breed ________
Wing band ________
Year 19____

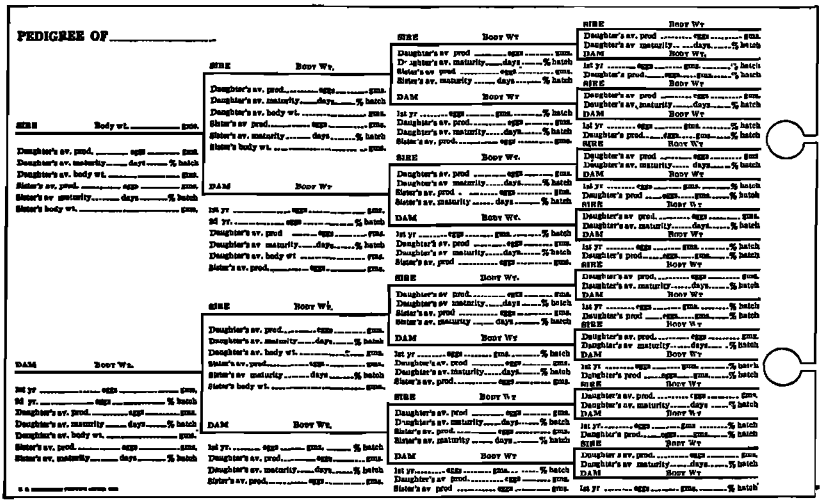
Mated to hen number	HEN RECORDS				INCUBATION RECORDS					PROGENY RECORDS							
	Body weight 20 wks.	Maturity	Egg weight	Egg prod.	Eggs set	Eggs inf.	Chicks hatched	Per cent hatch F.	Per cent hatch T	No. of chicks	Per cent mortality	Body weight 20 wks.	Average maturity	Average egg weight	Average egg prod.	Per cent died	Per cent culled
Totals																	
Averages or per cent																	

FIG. 70.—The Male Summary Record form on the front side, shown above, provides for the entry of a great deal of information of value in connection with the male himself, his sisters, and his progeny. The reverse side of this form is shown in Fig. 71. (U. S. D. A.)

The reverse side of the Male Summary Record form gives a fairly complete pedigree of the male, as shown in Fig. 71. The pedigree of the male contains the same information regarding the sisters and daughters of his various ancestors as provided for in the pedigree of the female. Perhaps the most valuable items of information recorded in the pedigree are the data pertaining to the daughters of the male's sire, the male's dam, and the male's grandparents. Just as the quality of the progeny produced by the male himself is the best index of his breeding work so the records of the daughters of the various ancestors constitute the best means of estimating in advance the results that will probably be secured by choosing a certain male for the breeding pen.

Suppose that the pedigrees of seven males are available for comparison. Particular attention should be paid to the records of the daughters of each of the ancestors of each of the seven males, and first choice should be given to the male whose ancestors' daughters have the best records.

Intelligent Use of Records.—Pedigree breeding for a particular purpose involves a great deal more than merely writing down the pedigrees of a lot of birds and then choosing the breeders on the basis of the records without examining the birds themselves. Pedigree breeding also involves a great deal more than selecting birds according to their appearance and hoping that the results of a certain mating will prove satisfactory. In order to make the surest progress in pedigree breeding work the birds should be examined carefully and only those birds should be saved for breeding purposes that are constitutionally fit, are of good breed type, and are free from standard disqualifications and serious defects. The birds that are selected on this basis should then be gone over carefully with the records in hand, and selections for various matings should be made based on what the records, especially the pedigrees, reveal. The poultry breeder should realize that it is better to breed from 10 carefully selected birds than



PEDIGREE OF ......

SIRE Body wt. ...... gms.
Daughter's av. prod. ...... eggs ...... gms.
Daughter's av. maturity ...... days ...... % hatch
Daughter's av. body wt. ...... gms.
Sister's av. prod. ...... eggs ...... gms.
Sister's av maturity ...... days ...... % hatch
Sister's body wt. ...... gms.

DAM Body Wt.
1st yr ...... eggs ...... gms.
2d yr. ...... eggs ...... % hatch
Daughter's av. prod. ...... eggs ...... gms.
Daughter's av. maturity ...... days ...... % hatch
Daughter's av. body wt. ...... gms.
Sister's av. prod. ...... eggs ...... gms.
Sister's av. maturity ...... days ...... % hatch

SIRE Body Wt.
Daughter's av. prod. ...... eggs ...... gms.
Daughter's av. maturity ...... days ...... % hatch
Daughter's av. body wt. ...... gms.
Sister's av prod. ...... eggs ...... gms.
Sister's av. maturity ...... days ...... % hatch
Sister's body wt. ...... gms.
DAM Body Wt
1st yr ...... eggs ...... gms.
2d yr. ...... eggs ...... % hatch
Daughter's av. prod ...... eggs ...... gms.
Daughter's av maturity ...... days ...... % hatch
Daughter's av. body wt ...... gms.
Sister's av. prod. ...... eggs ...... gms.

SIRE Body Wt.
Daughter's av. prod. ...... eggs ...... gms.
Daughter's av. maturity ...... days ...... % hatch
Daughter's av. body wt. ...... gms.
Sister's av. prod. ...... eggs ...... gms.
Sister's av maturity ...... days ...... % hatch
Sister's body wt. ...... gms.
DAM Body Wt.
1st yr. ...... eggs ...... gms. ...... % hatch
Daughter's av. prod. ...... eggs ...... gms.
Daughter's av. maturity ...... days ...... % hatch
Sister's av. prod. ...... eggs ...... gms.

SIRE Body Wt
Daughter's av prod ...... eggs ...... gms.
Daughter's av. maturity ...... days ...... % hatch
Sister's av prod ...... eggs ...... gms.
Sister's av. maturity ...... days ...... % hatch
DAM Body Wt
1st yr ...... eggs ...... gms. ...... % hatch
Daughter's av. prod. ...... eggs ...... gms.
Daughter's av. maturity ...... days ...... % hatch
Sister's av. prod. ...... eggs ...... gms.

SIRE Body Wt.
Daughter's av. prod ...... eggs ...... gms.
Daughter's av maturity ...... days ...... % hatch
Sister's av. prod ...... eggs ...... gms.
Sister's av. maturity ...... days ...... % hatch
DAM Body Wt.
1st yr ...... eggs ...... gms. ...... % hatch
Daughter's av. prod ...... eggs ...... gms.
Daughter's av maturity ...... days ...... % hatch
Sister's av. prod ...... eggs ...... gms.

SIRE Body Wt.
Daughter's av prod. ...... eggs ...... gms.
Daughter's av maturity ...... days ...... % hatch
Sister's av. prod ...... eggs ...... gms.
Sister's av. maturity ...... days ...... % hatch
DAM Body Wt
1st yr ...... eggs ...... gms. ...... % hatch
Daughter's av. prod ...... eggs ...... gms.
Daughter's av. maturity ...... days ...... % hatch
Sister's av. prod. ...... eggs ...... gms.

SIRE Body Wt
Daughter's av. prod ...... eggs ...... gms.
Daughter's av. maturity ...... days ...... % hatch
Sister's av. prod. ...... eggs ...... gms.
Sister's av. maturity ...... days ...... % hatch
DAM Body Wt
1st yr ...... eggs ...... gms. ...... % hatch
Daughter's av prod. ...... eggs ...... gms.
Sister's av prod ...... eggs ...... gms.

SIRE Body Wt
Daughter's av. prod ...... eggs ...... gms.
Daughter's av maturity ...... days ...... % hatch
DAM Body Wt.
1st yr ...... eggs ...... gms. ...... % hatch
Daughter's prod. ...... eggs ...... gms. ...... % hatch

SIRE Body Wt
Daughter's av prod ...... eggs ...... gms.
Daughter's av. maturity ...... days ...... % hatch
DAM Body Wt
1st yr ...... eggs ...... gms. ...... % hatch
Daughter's prod. ...... eggs ...... gms. ...... % hatch

SIRE Body Wt
Daughter's av prod ...... eggs ...... gms
Daughter's av. maturity ...... days ...... % hatch
DAM Body Wt
1st yr ...... eggs ...... gms. ...... % hatch
Daughter's prod ...... eggs ...... gms. ...... % hatch

SIRE Body Wt
Daughter's av prod. ...... eggs ...... gms.
Daughter's av. maturity ...... days ...... % hatch
DAM Body Wt
1st yr ...... eggs ...... gms. ...... % hatch
Daughter's prod. ...... eggs ...... gms. ...... % hatch

SIRE Body Wt
Daughter's av prod. ...... eggs ...... gms.
Daughter's av. maturity ...... days ...... % hatch
DAM Body Wt
1st yr ...... eggs ...... gms. ...... % hatch
Daughter's prod. ...... eggs ...... gms. ...... % hatch

SIRE Body Wt
Daughter's av. prod. ...... eggs ...... gms.
Daughter's av maturity ...... days ...... % hatch
DAM Body Wt
1st yr ...... eggs ...... gms. ...... % hatch
Daughter's prod ...... eggs ...... gms. ...... % hatch

SIRE Body Wt
Daughter's av. prod. ...... eggs ...... gms.
Daughter's av. maturity ...... days ...... % hatch
DAM Body Wt
1st yr. ...... eggs ...... gms ...... % hatch
Daughter's prod. ...... eggs ...... gms. ...... % hatch

SIRE Body Wt
Daughter's av. prod. ...... eggs ...... gms.
Daughter's av maturity ...... days ...... % hatch
DAM Body Wt
1st yr ...... eggs ...... gms. ...... % hatch

FIG. 71.—The reverse side of the Male Summary Record form provides for the entry of a great deal of information of value concerning the male's ancestors. (U. S. D. A.)

from 50 poorly selected birds. The development of a breeding program based on progeny testing is the surest way of making progress.

Pedigree breeding work is expensive, time consuming, and requires much painstaking effort, and unless the records are accurate perhaps more harm than good will result. Only a relatively few poultrymen are properly qualified to undertake pedigree breeding work, and they are the ones who should be encouraged to provide quality breeding stock for the farmers, commercial poultrymen, and hatchery operators who have thousands of flocks under their control for the production of eggs for the commercial hatcheries from which so many millions of chicks are distributed annually.

The true test of a competent poultry breeder is the quality of stock resulting from the matings he makes from year to year. In order to qualify as a competent poultry breeder the poultryman must *know* his birds, he must be able to judge and select them according to their intrinsic value as breeders, he must be able to mate the selected birds wisely, he must follow a system in the development of his breeding program, and he must love his work. These are among some of the most important qualifications that give lifelong satisfaction to one engaged in the art of breeding along scientific lines for the purpose of producing more beautiful and profitable birds for the benefit of mankind.

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