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Hatchability of Chicken Eggs as Influenced by Environment and Heredity, The

Walter Landauer

University of Connecticut - Storrs

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The Hatchability of Chicken Eggs as Influenced by Environment and Heredity

Walter Landauer

Monograph 1
UNIVERSITY OF CONNECTICUT - AGRICULTURAL EXPERIMENT STATION
STORRS, CONNECTICUT
The Hatchability of Chicken Eggs as Influenced by Environment and Heredity

Walter Landauer
Department of Genetics

APR 1961
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J'ai quelquefois entendu demander: *Dans quel but toutes ces recherches, et quelle utilité doit-on en retirer?* Il me suffirait de répondre: *pour S A V O I R, pour arriver sur ces réalités, besoin de l'esprit humain, qu'avait si bien exprimé cette pensée du prince des poètes, Rerum cognoscere causas.*

Etienne Geoffroy-Saint-Hilaire, 1825

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*Fides enim certa non provenit ex auditu.*

Frederick II of Hohenstaufen

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As yet, the quantity of human knowledge bears no proportion to the quantity of human ignorance.

Benjamin Franklin, 1756

---

It does not pay to tether one's thoughts to the post of usefulness with too short a rope.

John Dewey
THE HATCHABILITY OF CHICKEN EGGS
AS INFLUENCED BY
ENVIRONMENT AND HEREDITY

Walter Landauer

The problem of hatchability has great economic importance but also outstanding scientific interest. The poultryman wishes to know how to secure a high percentage of chicks from the eggs which he puts into his incubator; the biologist would like to determine the causes of death during development of the chicken embryo.

The art of artificial incubation is of relatively recent date in the West, and much progress has been made in clarifying a variety of circumstances which may contribute to the failure of fertile eggs to yield hatched chicks. The evidence bearing on this question will be reviewed in the following pages. Detailed coverage, the reviewing of controversial issues, and the exposition of methodological weaknesses of approach to specific problems were among the author’s aims. This made it at times unavoidable to devote to some problems and publications more space than they merit intrinsically.

Surprisingly little is known concerning the efficiency of natural incubation in fowl. The most extensive observations on this problem have been made by Tretyakov (1937), who also reviewed other interesting Russian literature on the subject. Tretyakov obtained from sitting hens an average hatchability of 89 percent of all fertile eggs \(N = 219\). This strengthens the general belief that the best results with artificial incubation today compare favorably with those produced by natural methods. For earlier observations the reader is referred to publications by Graham (1908) and Dryden (1908). According to Penionzhkovich (1945) metabolic differences exist between eggs developing under either natural or artificial incubation conditions.

Experimentation by man with artificial incubation was far anticipated by birds themselves. In the order of gallinaceous birds, to which our domestic fowl belong, we find that one whole family, the Megapodidae, uses methods of artificial incubation ranging from very primitive provisions to rather complex procedures (Ashby, 1922, 1929; Stresemann, 1927-1934; Meyer and Stresemann, 1928; Mayr, 1930; Meyer, 1930a and b; Barrett and Crandall, 1931; Groebbels, 1937; Friih, 1959). Only a brief survey of the pertinent facts can be given here.

Eulippos walliceti, living in the Moluccas Islands, simply digs its eggs 35 to 60 cm. deep into the sand of the ocean beach and lets the sun provide the heat for incubation. Megacephalum maleo, an inhabitant of Celebes, buries its eggs in soil that is warmed by neighboring hot springs (Sarasin; quoted from Portmann, 1936). Megapodius hneskeri deposits
its eggs in crevices in the slopes of active volcanoes (Powell, 1884). *Megapodius eremita* of the Bismarck Archipelago makes holes in loose soil, 60 to 100 cm. deep, lays the eggs on the bottom of these holes and covers them with the excavated soil mixed with vegetable matter. *Megapodius forsteni*, inhabiting the South Moluccas, piles up large heaps of humus and buries its eggs in them when the fermentation processes occurring inside the heaps have resulted in the proper temperature.

Finally, *Leipoa ocellata* of Southern Australia begins preparations for incubation by digging holes in sandy soil and filling them with vegetable matter such as fallen leaves, twigs, bark, and so on. After fermentation has proceeded for several months, the center of these chambers becomes quite hot. The birds do not lay their eggs in the mounds until the temperature has again declined to about 29-36° C. (84-97° F.). About six to nine days before the first egg is laid, the birds dig a hole into the center of the chamber. After the egg has been laid, they cover it with fermenting plant material which, however, they mix at the same time with sand. This process is repeated until all of the eggs have been laid. During the period of incubation the birds open the mounds on clear, hot days almost down to the eggs, and close them again before evening. It may be assumed that the sand thus heated by the sun retains its warmth for considerable periods. Some allowance in the size of the mounds seems to be made by *Leipoa* according to the temperature of the surroundings at the time of construction.

Frith (1955) found that *Leipoa* varies its incubation practices according to changing seasonal conditions. In spring and early summer, when the air temperatures are relatively low, the birds rely chiefly on heat of fermentation. During the early part of spring loss of heat to the surrounding air appears to be sufficient to keep the temperature of incubation in the mounds at the proper level. Later on, with rising ambient temperatures, the birds forestall an excessive development of heat inside the mounds by removing, daily at dawn, and down to the level of the eggs, the soil that covers them, replacing it at once with new soil. In mid-summer this practice is discontinued; fermentation no longer contributes much to keeping the mound properly warm, but the outside temperatures have become sufficiently high to insure proper incubation conditions. In autumn, the processes of fermentation having run their course, the Leipoas open their mounds at noon in order to let the eggs be warmed by the mid-day sun. This soon becomes inadequate to maintain incubation, and thus the hatching season comes to an end. It is assumed that the *Megapodiidae* test the temperature by inserting their beak into the mound.

In the case of *Melipoa* the only external source of energy for incubation is the radiation of the sun. The necessary degree of humidity is presumably provided by the nearness of the ocean, and the sand in which the eggs are imbedded allows gaseous exchanges to take place.
The situation is similarly simple in the case of *Megacephalum malleo* and of *Megapodus huekeri*. But much more complex incubating arrangements are made by the other two *Megapodus* species and by *Leipoa*. Here, the temperature prevailing at the level of the eggs seems to suffice for starting development, while the humus serves as a good insulator for preserving the heat which is generated by the embryos themselves. The mixing with sand of the fermenting material, practiced by *Leipoa*, probably facilitates the gaseous exchanges of the eggs.

In *Alectura lathami*, an Australian mound-building genus, Fleay (1937) observed that the cocks open the top of the mound before rain begins to fall and close it over afterwards. This may be a general practice among mound-building birds and presumably increases the rate of fermentation in the interior of the mound while, at the same time, regulating the degree of humidity. Some doubt still remains, however, with regard to the role which fermentation of organic material plays as a source of heat (Groebbels, 1937).

One surprising fact about these “natural” methods of artificial incubation is the relatively low temperature at which development takes place. For *Alectura lathami*, Fleay (1937) recorded incubation temperatures of 85-90° F. (29-32° C.); fluctuations between 90 and 95° F. were observed by Frith (1959) in *Leipoa ocellata*, but he reports that many birds of this species aim at exactly 92° F. As an obvious adaption to this situation, we find that the eggs are very large (up to 17 percent of the laying female’s body weight!) and that they contain relatively much yolk (185-220 percent of the albumen, as compared with about 62 percent in domestic fowl), thereby providing increased fuel value. Moreover, development in these species is very slow, requiring in different forms from 45 to as many as 84 days. One would like to know something about the efficiency of these different methods of artificial incubation evolved by the *Megapodiidae*, but information on hatchability appears to be lacking. A further remarkable feature about this group is the fact that its members are singular among birds in depositing their eggs in a vertical position, large end up.

There is a possibility that the eggs of the *Megapodiidae* have special heat-retaining or even heat-generating properties. The existence of mechanisms of this kind has been demonstrated for the European Ruddy Duck (*Erismatura leucocephala*). The eggs of this parasitic duck, after a few days of incubation, can proceed to hatching with little or no supply of external heat; they can also withstand exposure to abnormally high temperatures. As is true for *Megapodiidae*, the eggs of *Erismatura leucocephala* are unusually large in size (Friedmann, 1932).

Outside the group of gallinaceous birds few examples are known of similar behavior. The African ostrich (*Struthio camelus*), in the warmest parts of its area of distribution, apparently buries its eggs in sand and lets them be incubated by the heat of the sun. This excited much curious speculation, as illustrated by the following legend attributed to the gar-
den of the Grand Master of the Knights Hospitallers on the island of Rhodes: "In 1496 an old ostrich and two young were kept with their wings clipped in a walled enclosure here. They laid their eggs in sand and hatched them by simply looking at them; they fed on iron and steel" (Torr, 1887). What might be called a sitting instinct in reverse has been reported for the Egyptian plover (Pluvianus aegyptius). These birds also deposit their eggs in hot sand, but, during the warmest part of the day, they sit over the spots where their eggs are buried, presumably in order to protect them from too much heat (Stresemann, 1927-1934). Similar behavior has been reported for certain Passerine birds of South-West Africa (e.g., Terpsiphone viridis); still other species of that region provide their nests with roof-like structures, thereby protecting the eggs against full exposure to the sun (Hoesch and Niethammer, 1940).

Another interesting instance in which birds do not themselves incubate their eggs is provided by the cuckoos. In this case the eggs are laid into the nests of other birds, and it is left to the foster parents to take care of them. Frequently they are not accepted, but what interests us here is the fact that even for those which are accepted, hatchability is relatively low (70 percent or less). It seems likely that the foster parents often provide incubation conditions below the optimum for cuckoo eggs, thereby reducing hatchability. There is also evidence, however, for the interesting conclusion that cuckoo embryos possess special mechanisms which enable them to survive adverse conditions (cooling) for prolonged periods (Groebbels and Möbert, 1930). Furthermore, the development of cuckoo embryos probably proceeds at a more rapid rate than that of the embryos of the host species (Ingram, 1907-1908). An adaptive shortening of the incubation period seems to occur also among parasitic cowbirds (Friedmann, 1927) and is probably a general feature of this type of parasitism (Stresemann, 1927-1934).

In the practice of hatching chicks artificially the two major factors responsible for poor results used to be, and perhaps still are, faulty management of the incubators and improper feeding of the laying stock. In each of these areas many different factors contribute to survival and hatching of the embryos, some being crucial while others have only minor importance. But even where these sources of failure have been eliminated, many other causes of embryonic death have come to light. Numerous hereditary factors are known to play a role in hatchability; particular methods of breeding have been found to decrease the hatching quality of eggs; it has been learned that various physiological conditions of the laying hens have an effect on viability of the embryo. It is altogether probable that only a beginning has been made in unraveling the enormously complex train of events to the end result of which we refer with the one word, "hatchability." This simplification of language has probably led to the common fallacy of assuming that we are dealing with a simple problem, genetically or otherwise. The processes of development
are, in fact, so complex that one can appreciate the simile used in primitive religions, such as among Polynesians or as related in the Kalewala of the Finns, that the world had hatched from a bird’s egg (Reinach, 1935).

The first step towards an understanding of hatchability problems was the exclusion of fertility as a complicating factor. To determine the result of hatching according to the total number of eggs put into an incubator may yield information concerning the cost of each chick, but unless we know the role which lack of fertility played in producing poor hatches, it is hopeless to attempt an analysis of the situation. It is for this reason that the word hatchability has come to be restricted to the percentage of fertile eggs which hatch, and it is only with this problem that we are concerned here. It must be noted, however, that death of the zygote in the earliest stages of segmentation, viz. prior to incubation, cannot be differentiated from infertility by means of a candling lamp (Munro and Kosin, 1945; Kosin, 1945, 1948; Gow, 1950; Križenecký, SajnéT, Olle and Musil, 1955), and that, therefore, this earliest mortality may often remain undiscovered unless special studies are made. The fact that some of the germs that perish during the earliest stages of segmentation may have started development parthenogenetically (i.e., without fertilization) creates an additional difficulty in appraising their significance. There is evidence that the incidence of such parthenogenetic first steps of development varies with the genetic constitution of stocks and that in some stocks it may be a relatively common feature (Poole and Olsen, 1958; Kosin, 1958 b).

In the evaluation of various agencies affecting hatchability great caution must be (and often has not been) exercised in regard to the intrinsic uniformity, or lack thereof, within the stock used for experimentation. Titus (1953) has provided an excellent demonstration of the importance of such considerations and his publication should be consulted by all interested students of these problems. On the basis of extensive tests Titus concluded that “before one makes a comparison of the egg production and hatchability of groups of birds that have not been pre-tested and selected for uniformity, he should have information about the variation that may be encountered.” In untested and unselected stock with an average hatchability of 83 percent, Titus found that the coefficient of variation of relative hatchability amounted to about 20 percent. In another sample the variance might be an appreciably different one. The reliability of group differences (or the number of birds required in each group in order to secure valid results) will vary with the size of the coefficient. Hence the necessity of taking this coefficient into account.

In order to make the data of different authors comparable, standard errors of statistical constants are given throughout this publication. Wherever probable errors appeared in the original papers, they have been converted to standard errors.
Historical

Our Western knowledge of artificial incubation is a belated, though methodologically independent, sequence to practices which have been used in China and Egypt since ancient times.

We cannot be sure when means of artificial incubation were first invented in China, but we know that incubation was practiced at least as early as the Ch'in period (246-207 B.C.). For this we have the testimony of Yang Hsin of Mao-ling whose publication ("Pin-feng Kuang-i" or "Report on the Customs of the Province of Shensi") appeared about 1740 and was reprinted, together with other articles, about 1900. The principle features of the method, as given by Yang Hsin, were as follows:

The incubators were set up in draft-free sheds which were kept at an even temperature. Two k'angs or hatching ovens were built in such a shed. These k'angs were ovens constructed from mud, adobe or stones. They consisted of a lower rectangular part in which the fire was kept and an upper circular part, hollowed out on top, into which the eggs were placed. (Figs. 1 and 2). The ovens were brought to the proper temperature either by putting pre-heated pieces of dry manure or (in summer) hot rice husks into the fire box, or by starting in it a slow fire with cakes of dry manure or with rice husks. The bottom of the incubating part was covered with a layer of soft, broken wheat straw, 3 to 5 inches deep. Over this was a layer, 2 or 3 inches deep, of warmed rice (or other cereal) husks, and then followed alternate layers of eggs and husks until from eight to ten thousand eggs were in the incubator. The top layer of husks was covered with rice or wheat straw. If, after two or three days, the eggs became too cool, they were moved to the incubating part of the second k'ang, the position of the eggs, from top to bottom, being reversed. This moving of the eggs from one k'ang to the other was repeated six or seven times, but finally the eggs were divided evenly between the two ovens. As soon as there were signs of hatching, the eggs were spread out on the floor of the incubator room in a single layer and were covered with warm husks. Within the following two days hatching was completed. This method was employed for duck and chicken eggs. The usage of modifications of this system on a much larger scale was witnessed by Dabry (1865).

Next we have a report by Juan González de Mendoza, first published in 1585. His description of the hatching of eggs is based on a travel account by Martín de Herrada who, accompanied by Geronimo Marín had, in the year 1575, spent two months in the Chinese province of Fukien. This interesting story is worth quoting at some length (González, 1588).

"The great number of people that is in this countrie, and not permitting any idle people to liue therein, is the occasion that it doth stirre vp the wits of poore men (being constrained
Diagram of a Chinese k'ang (incubating oven) of the Ch'in period. Near the floor line was an opening to introduce the fuel; the smoke escaped through a flue at the back (From Pin-feng Kuang-i).

thereunto by necessitie, the inuenter of manye thinges) to secke new inuentions to get their lining, to relieve and supply their necessitie. So that many of this kingdome, seeinge the whole countrie so thourghly inhabited and tilled, that there is not one foote without an owner, they do take them vnto the riuers (which are verie great), and there they do make their dwellings in ships and barkes (as is aforesaid), where they have their whole families vnder borde to defende them from the sunne
and rayne, and inclinations of the heauen. There they doe vs the occupation that they do knowe, or that which they did inherite of their father, and many misteries to liue by, verie strange: whereof the most principall is to bring vp in some of their barks so great quantitie of ducks, that they sustaine a great part of the countrey therewith; and the vsed thereof is as followeth."

"They haue cages made of canes so bigge as the upper most holde of the barks, in the which may be foure thousand ducks at once. They haue in certaine places of these cages made nestes, where these ducks do almost every day laye egges, the which they take; and if it be in the sommer, they doo put them in buffes doong, or in the doong of those ducks, which is verie warme, where they leaye them so many dayes as experience hath taught them that they will come forth. Then they doo take them out of the doong, and do breake them one by one, and take a little duckling, the which they do with so great cunning that almost none of them doth perish, which is yt which causeth great admiration vnto some that go to see it: although they bee but few, for that it is an auncient custome vsed for long time in that countrie. And for to haue the fruition of this benefite all the yeare, in the winter they must use an artifciall helpe: to giue a little warmenes vnto the doong for the bringing forth of their egges, they do use then an other invention as ingenious as the first, and that is this: they take a great number of canes tied one by another, whereon they do lay the doong, then vppon that they doo lay their egges, and do cover them verie well with the same: this being done, they put vnder the canes straw, or some other like thing, and set it on fire, but in such sort that it dooth not burne, but keepeth a naturall heat all the time, till they thinke
that they are ready to be taken out. Then doo they take and breake them, as aforesaide, so that their pultrie dooth increase in such number as though they were antes."

"This manner of lining is greatly used in all that countrie, and verie profitable, for that it is a victuall most used amongst them, and is esteemed as a thing of great sustentation and of small price, by reason that at al times there is breeding of them and of small cost."

Very different statements concerning incubation procedures in China were made by Osbeck (1756) and Ekeberg (1768). Osbeck wrote as follows:

"They lay an iron plate on a brick hearth; on this they place a box full of sand half a foot high, in which the eggs are put in rows: the box they cover with a sieve, over which they hang a mat. To heat them, they make use of the coals of a certain sort of wood, which burn slowly and uniformly; at first they give them but little warmth, and increase it gradually; and it becomes a strong heat by the time the eggs are hatched."

The Abbé Grosier (1785) related that prodigious numbers of ducks were being raised in the province of Kwantung and that the eggs were hatched either in ovens or in manure.

In 1847 Fortune visited the Chinese island of Chu-san and gave the following description of the incubation of duck eggs as practiced there.

"The hatching-house was built at the side of the cottage, and was a kind of long shed, with mud walls, and thickly thatched with straw. Along the ends and down one side of the building are a number of round straw baskets, well plastered with mud, to prevent them from taking fire. In the bottom of each basket there is a tile placed, or rather the tile forms the bottom of the basket; upon this the fire acts, — a small fire place being below each basket. Upon the top of the basket there is a straw cover, which fits closely, and which is kept shut whilst the process is going on. In the centre of the shed are a number of large shelves placed one above another, upon which the eggs are laid at a certain stage of the process."

"When the eggs are brought, they are put into the baskets, the fire is lighted below them, and an uniform heat kept up, ranging, as nearly as I could ascertain by some observations which I made with a thermometer, from 95° to 102°, but the Chinamen regulate the heat by their own feelings, and therefore it will of course vary considerably. In four or five days after the eggs have been subject to this temperature, they are taken carefully out, one by one, to a door, in which a number of holes have been bored nearly the size of the eggs; they are then held against
these holes, and the Chinamen look through them, and are able to tell whether they are good or not. If good, they are taken back, and replaced in their former quarters; if bad, they are of course excluded. In nine or ten days after this, that is, about fourteen days from the commencement, the eggs are taken from the baskets, and spread out on the shelves. Here no fire-heat is applied, but they are covered over with cotton, and a kind of blanket, under which they remain about fourteen days more, when the young ducks burst their shells, and the shed teems with life. These shelves are large, and capable of holding many thousands of eggs; and when the hatching takes place, the sight is not a little curious. The natives who rear the young ducks in the surrounding country know exactly the day when they will be ready for removal, and in two days after the shell is burst, the whole of the little creatures are sold, and conveyed to their new quarters."

More recently, King (1927) told us that Chinese incubators consist of large earthenware ovens (k'angs) which have a door on one side through which live charcoal is introduced. The fire is partly smothered under a layer of ashes. The oven itself is well insulated, cased in basket work and provided with a cover. Inside this oven rests a container of nearly the same size. Into this container is lowered a large basket with 600 to 1300 chicken eggs. Such incubators are arranged in rows. Immediately above each row, utilizing the warm air rising from them, is a continuous line of finishing hatcher's and brooders in the form of woven shallow trays, the sides of which are padded with cotton and the tops covered with sets of quilts of varying thickness. After the first four days all eggs are turned from two to five times in 24 hours. After 11 days the eggs are transferred to the finishing trays. It is said that hatches of from 90 to 98 percent of all fertile eggs are obtained by this method.

It is not surprising to learn that the art of incubation spread beyond the boundaries of continental China to Formosa, Annam (Indo-China) and the Philippines. A report by L. Kimura of the Governor General's office of Formosa on artificial incubation of duck eggs is available in a translation into Chinese by Ts'a Jui. According to this publication the practice of artificial incubation was introduced into Formosa about 1835 by a tea merchant from Ch'uan-chou in the Province of Fukien. Its popularity declined after the annexation of Formosa by Japan at the end of the Sino-Japanese war (1895). The procedure is described as follows:

Within a special incubating room trenches were dug along the walls of three sides. These trenches were 2 feet 8 inches wide, 2 feet 6 inches deep, and one of the trenches was about 38 feet in length (dimensions of room 15 x 40 ft.). Containers filled with eggs were put into these trenches and warmed husks of rice or wheat were then poured in to fill
the spaces around and between the egg receptacles. Shelves for finishing the hatching were in the center of the room. Prior to incubation the eggs were exposed to the sun for one hour. Ten layers of eggs with heated wheat husks were then put into the containers. Twice a day the eggs were moved to other receptacles, a fresh supply of warm husks being used. During cold weather charcoal heating plates were put into the trenches for the first two weeks of incubation. Each container held about 800 eggs and since there were 46 of them in an incubating room the total capacity was very considerable.

A method very similar to the Formosan is widely used in the Philippines for the hatching of duck eggs (Fronda, 1925-1926). Baskets arranged inside a wooden hut and insulated with firmly tamped rice hulls serve as incubator cabinets. Preliminary to the beginning of incubation, and provided that the weather is good, the eggs are exposed to sunshine until they become moist. They are then transferred to the baskets. A bag containing hot unhulled rice is put into the bottom of each basket, eggs in a cloth bag are placed on top of it, and bags of hot rice and eggs are alternated in layer upon layer until there are eight to ten bags of eggs in each basket. Two bags of warm rice are placed on top. The entire hut which holds the baskets is covered with cotton sheets. The rice is reheated every morning and afternoon, the eggs being turned at the same time. During the last part of the incubation period no additional heat is supplied. According to de la Gironnière (1860) and Saint-Loup (1895) an attendant remains within the hut for the whole period of incubation, a fact which may have given rise to the more fanciful accounts of Dumont d'Urville and Laplace quoted below. Jardel (1916) described the usage of a kindred system of incubation in Annam (Indo-China). Similar methods are currently used in Thailand for the incubation of duck eggs, and these incubators are always operated by Chinese (Fronda, 1952).

The travel stories of Dumont d'Urville and Rear-Admiral Laplace, as far as they relate to Philippine incubation practices, are quoted from de la Gironnière (1854). Dumont d'Urville's report reads as follows: "During our excursion to Los Baños, that which struck us most was the prodigious quantity of ducks and ducklings, which were sporting on this part of the lake; the surface was covered with them. The cause of this abundance of one kind of birds was soon understood from knowing the taste of the Tagals, of the Malays, and of the Chinese, who prefer them to other fowl. But we were puzzled to find out how such a wonderful quantity could be hatched; our guide, however, soon solved the difficulty. To serve as substitutes for the ovens that are used in China for artificial incubation, the Tagals have employed the agency of human heat, and they found, among their indolent servants some patient and steady hatchers. A sort of frame is made for that purpose, on which light sticks are laid across, well covered with thick blankets; the eggs are stowed up in the frame in a regular line, being laid close to each other, and kept
in their places by ashes which fill up the interstices. The whole is then raised up in a level position a little over the ground, and the sluggish hatcher lays himself at length on this strange kind of sofa; and then he eats, drinks, and smokes, and chews his betel, taking care not to injure the fragile shells he is to fecundate." A similar story was told by Rear-Admiral Laplace from which the following is quoted: "To my great astonishment, I learned that they (viz., the ducks) were the produce of eggs, hatched by men, who, for a small stipend, have the patience, or rather laziness, to remain constantly lying on the future ducklings. For this purpose the eggs are stowed side by side in a layer of ashes, so as to form an even surface, protected by a trellis frame, and covered thickly with wool or cotton. The whole apparatus is contained in a sort of truckle bed, slightly raised above the floor of the close hut in which it is placed."¹

Contemporary incubation practices in China have been described by Phillips, Johnson and Moyer (1915). They represent modifications of the ancient method recorded by Yang Hsin, and of that reported from the Philippines by Fronda. An extensive description and analysis of the k'ang incubation method, as used in North Tungchow, was published by Wang (1938) who gave many details which cannot be discussed here.

In Egypt, as in China, the origins of artificial incubation are lost in antiquity. The Egyptian incubating ovens of which de Réaumur justly said that "Egypt ought to be prouder of them than of her pyramids," as he described them and as they are still now in use, are built of sun-dried mud bricks (adobe) with double outer walls between which there is a mixture of sand or silt and chopped straw. Each oven consists of a lower and an upper compartment. Glowing bean straw serves as the source of heat. This is burned in the upper compartment, the eggs receiving heat by radiation from above. After seven days the amount of firing is reduced, and is entirely discontinued after the eleventh day. Up to the thirteenth day of incubation all eggs are kept in the lower compartment, but on that day half of them are moved to the upper chamber of the oven. The regulation of temperature and ventilation is accomplished by the opening and closing of holes to the outside. The eggs are moved three times daily for the first seven days, twice daily thereafter. Hatches of 80 to 87 percent of all fertile eggs are reported. No extensive description of these Egyptian incubators will be attempted here since detailed accounts are readily available in the literature, but a historical survey of the reports relating to the Egyptian art of hatching will be given below.

We have already seen that the art of hatching eggs artificially spread from China to the Philippine Islands, French Indo-China and Formosa.

¹ Randall (1960) has given a fascinating account of the iconographic role which the representation of men sitting on eggs played in medieval times as a motive of human folly. A modern variation on a similar theme can be found in Guy de Maupassant’s short story "Toine."
It appears that some of the neighbors of Egypt likewise profited by the methods of incubation which were in practice in that country. Brueyn (1540) and Azalus (writing in the fifteenth century; first printed 1544) tell us that incubating ovens, similar to those of Egypt, were in use in parts of Syria, and Lithgow (1632), in a narrative of his visit to Tunis in 1616, left the remarkable report which follows:

"—Captayne Waird sent twice one of his servants with me to see two sundry Ovens drawne, beeing full of young Chickens, which are not hatched by their mothers, but in the Fornace, being thus. The Oven is first spred over with warme Camel's dung, and upon it the Egges, closing the Oven."

"Then behind the Oven, there is a daily conveyance of heate, venting through a passage beneath the dung, just answerable to the naturall warmnesse of the Hens belly; upon which moderation, within twenty dayes they come to naturall perfection. The Oven producing at one time, three or four hundred living Chickens, and where defection is, every sharer beareth a part of the losse, for the Hatcher or Curator, is onely Recompensed according to the living numbers be delivered. Surely this is an usuall thing, almost through all Affricke, which maketh that the Hennes with them are so innumerable every where."

The Tunisian method of hatching, while presumably inspired by the Egyptian procedures, differs from them in various details. We shall have occasion to refer to this again. Brueyn (1540) reports from hearsay that artificial incubation was at his time practiced not only in Egypt and Syria, but also in Jerusalem and on the island of Rhodes. We have not been able to verify this. According to della Porta (1558) hatching ovens were at one time built on the island of Malta.

The earliest mention of artificial incubation in Egypt occurs in Aristotle's Historia Animalium, written in the fourth century B.C. In his discussion of poultry Aristotle reports that "in some cases, as in Egypt, they are hatched spontaneously in the ground, by being buried in dung heaps. — Instances have occurred of eggs being deposited in warm vessels and getting hatched spontaneously." To this statement we shall return below.

During the first century B.C. Diodorus Siculus, writing about the Egyptians, had this to say: "And that which is chiefly to be admir'd, is that their Industry is such in these matters, that they that keep Poultry and Geese, not content with the ordinary way of breeding these Creatures (as amongst other People) but by their Wit and Ingenuity cause them to increase to an infinite number, for they do not suffer them to hatch, but to admiration force out the Young with their Hands with so much Art and Skill, that it's done as effectually as by Nature it self." Pliny, in the first century of our calendar, recorded that "there be some eggs that
will come to be birds without sitting of the hen, even by the worke of Nature onely, as a man may see the experience in the dunghils of Aegypt. There goeth a pretie jeast of a notable drunkard of Syracusa, whose manner was when he went into the taverne to drinke, for to lay certaine egges in the earth, and cover them with mould: and hee would not rise nor give over bibbing, untill they were hatched. To conclude, a man or woman may hatch egges with the very heat onely of their bodie. — Livia Augusta the Empress, wife sometime of Nero (i.e. Tiberius Claudius Nero, an officer of Julius Caesar), when she was conceived by him, and went with that child [who afterwards proved to be Tyberius Caesar,] beeing very desirous (like a young fine lady as she was) to have a jolly boy, practised this girlish experiment to foreknow what she would have in the end: Shee tooke an egge, and ever carried it about her in her warme bosome, and if at any time she had occasion to lay it away, she would convey it closely out of her owne warme lap unto her nources, for feare it should chill. And verily this presage proved true: the egge became a cock-chicken, and she was delivered of a sonne. And hereof (it may well be) came the devise of late, to lay egges in some warm place, and to make a soft fire underneath of small straw or light chaffe to give a kind of moderate heat; but evermore the egges must be turned with a man or womens hand, both night and day, and so at the set time, they looked for chickens and had them."

Figure 3

Egyptian incubating practices as illustrated by John de Mandeville (From a manuscript entitiled: Montevilla, Reise ins heilige Land. Augsburg, 1481. Feldhaus, 1914).

Throughout the late middle-ages and the Renaissance we find references to the Egyptian art of hatching in historical and medical works, in travel accounts, and in books on agriculture.
Cardanus (1663) attested to the wide acquaintance with the fact that artificial incubation was practiced in Egypt. He also drew the interesting conclusion that in the process of incubation heat itself plays merely a role similar to that of producing a purer metal from one less pure ("Rursus, si quis obiceret — cui tamen non respondat-ignis calorem nihil posse generare, vt in prioribus libris demonstratum est: respondere posset, in Aegypto ouna excludi ignis calore, quod ab omnibus affirmatur: ita dicet, ex imperfecto metallo, vi ignis, perfectum, vt ex uno pullus, poterit generari." De rerum varietate, p. 206). This thought of Cardanus is reminiscent of the saying by the Roman poet Lucretius that the development of eggs into chicks shows that "sensations all can out of non-sensations be begot."

In the travel account of Sir John Mandeville, written in the fourteenth and first published in the fifteenth century, mention is made of the artificial hatching of eggs in Egypt. The early editions even contained an illustration (Fig. 2). This picture is, however, as fanciful as the text of Mandeville's book. A similar reference is to be found in Pietro dei Crescenzi's book on agriculture, which was composed between 1304 and 1309. The travel accounts of Niccolò di Martoni (1394, published 1895), the Rieter family (1460, see Kluge, 1910) and of Arnold von Harff (1496-1499) also contain brief references to the Egyptian manner of hatching eggs. Among later reports are those of Belon (1553), Paolo Giovio (1560), Boec (1577), Kirchherr von Suchen (1584), Benedictus Pererrus (1595), Leo Africanus (1600), Gesner (1604), Radziwil (1614), Fürer (1621), Ulysse Aldrovandi (1645), de Boullaye (1657), Vesling (1664), Monconys (1665), della Valle (1672), Thévenot (1674), Graves (1675), Metton (1681), Crouch (1683) and Montanari (1685). A brief reference to the Egyptian art of hatching even found its way into Grimmelshausen's famous "Simplicissimus" (1669). Knowledge of the Egyptian art of hatching presumably furnished the basis for a passage in Sir Thomas More's "Utopia" (1516) reading as follows in the English translation of Robyson (1556): "They brynge up a greate multitude of pulleyne, and that by a meruaylouse policy. For the hennes doae not sytt the vpo n the egges: but by keepynge theym in a cer tayn e equall heate they brynge lyfe into them, and hatche theym. The chykens, assone as they be come oute of the shel, follow men and women in stead of the hennes."

During the eighteenth century interest in the incubating ovens of Egypt was increasing. This is witnessed by the reports of Rantzau (1704), Lucas (1720), De Bruyn (1725), G flows (1725), Sicard (1729), Myllcr (1735), Campbell (1739), Perry (1743), Pococke (1743-1745), Tourtechot-Granger (1745), Norden (1755), Nelli (1759), de Pauw (1773), Niebuhr (1774-1778), Haller (1778) and Savary (1785-1786). More recent descriptions were given by de Rozière (1809), Rouyer (1809), Moubray (1816), Wilkinson (1835), Lane (1836), Cardwell (1890), Cadman (1921) and Askar (1927).

We have no definite information concerning the time at which arti-
ficial incubation was first employed in either China or Egypt. Nor do we possess historical accounts that tell us whether the invention was made independently in China and Egypt, or whether the practice of artificial hatching was transferred from one of the two countries to the other, although there is some indirect evidence suggesting that the cradle of this, as of so many other inventions, may have stood in China. It is likely that in both places artificial incubation was first applied to duck eggs and only later to the eggs of fowl.

In both countries these methods of incubation originated in sub-tropical or tropical regions and were used only during climatically favorable periods of the year, although in the Far East they spread to the North of China. The methods of incubation used in China seem to have varied considerably at different times and in different localities, and this is still true today, possibly because the incubating techniques there were in the hands of the people and were used over a considerable area. In Egypt, on the other hand, hatching was confined to a relatively small region; its use was restricted to holders of a monopoly and later to a guild-like group of artisans, and, presumably as a consequence, there was little change and innovation. Yet, in Egypt the techniques underwent also modifications in the course of time. Aldrovandi has called attention to the fact that neither Aristotle nor Diodorus mentioned the use of ovens in connection with Egyptian incubation and concluded that the methods had changed. The evidence, however, is uncertain and the probability great that ancient reports from distant countries were corrupted. On the other hand, if later descriptions are compared with the careful report which Abd-Allatif (Abd Al-Latif, a Muslim scientist who lived 1162-1231) left on Egyptian incubation, as practiced at his time, no doubt remains about the gradual change of and improvement in techniques. One remarkable instance of this kind is the fact that at the time of Abd-Allatif the Egyptian incubating ovens were only one story high (de Sacy, 1810).

In early times the production of chicks was a fiscal privilege in Egypt accorded to a restricted number of persons. Together with many other special privileges and monopolies this practice was abolished by Sultan Mohamed ben-Kelaoun in 1316 A.D. As is inevitable with such exclusive rights, they had led to serious abuse. For this we have the interesting testimony of the Arabic writer Ahmed Al Macrisi (1360-1442): "Among the abolished privileges was that which had been established for the production of chicks. There had been purveyors of monopoly in all districts of Egypt and they raised chicks for private persons. The situation had become a great vexation for the poor; it exposed widows to all kinds of chicanery and injustice. Many beneficiaries had their pensions assigned to the income from that monopoly, and nobody in all of Egypt could buy even one chick from anyone but a purveyor of this fiscal privilege. A person who was found guilty of having bought a chick from anybody else or who had sold chicks (without being privileged to do so)
saw death descend upon himself from all sides without being able to die" (de Sacy, 1810). It must be added that in spite of the suppression of the monopoly by Mohamed ben-Kelaoun, restrictive practices continued to exist or were reestablished at a later date.

González (1585) seems to have been the first to acquaint the West with Chinese ways of hatching. Knowledge of the Egyptian art of incubation, on the other hand, is of much longer standing. Attempts were repeatedly made to construct and use Egyptian incubating ovens in Western Europe. The most remarkable instance of this kind was that of Frederic II of Hohenstaufen, Holy Roman Emperor, King of Sicily and Jerusalem. In his "Art of Falconry", which was written during the first half of the thirteenth century, he says with reference to Egyptian incubation: "We ourselves saw this" — presumably during his crusade — "and we arranged to have it repeated in Apulia by experts whom we summoned from Egypt." Frederic II was probably the first person with a truly scientific interest in ornithology, and it may be assumed that his inquiries into incubation were motivated by a desire to learn the details of the technique.

Toward the close of the fifteenth century Alphonse II, King of Naples and Charles VIII, King of France, had Egyptian incubators built for their pleasure. André de la Vigne, secretary of Anne of Brittany, queen consort of France, tells us that Charles VIII on his expedition to Naples in 1495 saw such an incubating oven at Pougé-Réal, the pleasure home of Alphonse II, King of Naples:

Le samedi son armée diverse
Assez matin se partit dudit Verce,
Et tôt après il monta à cheval,
Pour aller boire dedans Pougé-Réal
Qui est un lieu de plaisance conuit,
Aussi Alphors pour son plaisir le fit
Auprès de Napples, où en toutes manières,
Y a des choses toutes singulières,

Aussi a ung four à œufs couver,
Dont l'on pourroit, sans geline, eslever
Mille poussins, qui en aurroit affaire,
Voir dix mille qui en voulroit tant faire.

After his return to France, Charles VIII had one of these hatching ovens built at Amboise in 1496 (Parmentier, 1803), and François I somewhat later had another one constructed at Montrichard in Touraine (Gohory, 1752). A passage in Bruyerin's book De re cibaria (1540) probably also relates to this event. Nollet (1771) makes reference to yet another such attempt at Chantilly.

Scientific interests persuaded Ferdinand II, Grand Duke of Toscana, who was in close touch with the famous Accademia del Cimento, founded
by his brother, to have two artisans brought from Cairo to Florence in order to build and operate Egyptian incubating ovens. This happened in 1644 (Galluzzi, 1781). The ovens were set up in a large room in the Giardino di Boboli, now a part of the gardens of the Palazzo Pitti. The first tests of the ovens gave poor results (61 chicks hatched from 144 eggs). Ferdinand II had the experiments varied and repeated "according to suggestions arrived at by reasoning and experience." In these experiments Ferdinand II, who during the preceding years and in collaboration with other members of the Accademia del Cimento had designed an alcohol thermometer, making use of this invention, "observed the daily variations in temperature at the various stages and made the necessary adjustments." An improvement in the hatching results was thus obtained, although it was found impossible to raise the chicks successfully (Magalotti, 1667; Antinori, 1841). Ferdinand II of Toscana is to be credited also with one of the earliest designs of a hygrometer.

Trials with artificial incubation, inspired by the Egyptian art, were pursued by Christian IV, King of Denmark, during the seventeenth century. Ferdinand II of Toscana had furnished sketches (reproduced by Bartholin, 1661) of his Egyptian hatching oven, and Vesling had communicated to Rhodius, the king's adviser, his pertinent observations in Egypt. The physician Olaf Worm, in a letter written to Rhodius in 1644 (Bartholin, 1661; Worm, 1751), said that in 1640 he had followed a professional call to Frederiksborg, a castle built by Christian IV, and that one day at the king's table, chicken being served, the king had asked him how he thought these chickens had been hatched. As a sequel to his mistaken reply that they had been brought forth by sitting hens, he was shown the king's hatching establishment, and of this he gave a brief account. A more extensive report was furnished by Bartholin, according to whom there were six ovens, similar in construction to those used at that time for the baking of bread, except that they were equipped with a special hearth of brass lamina and a small gridiron which held minute pieces of charcoal. The glowing charcoal was to insure a regular and gentle heat. The eggs were put into a shallow basket, lined with feathers, or placed on a silk cushion. They were turned two or three times a day. Only about one egg out of ten hatched. A sketch of one of these hatching ovens, drawn by Worm, is here reproduced from Bartholin (Fig. 4).

According to Bartholin the Danish king had yet another type of hatching oven which had double walls. The air space between the walls was connected with the oven part and served presumably to equalize the heat. After the death of Christian IV the ovens were allowed to go to ruin and, says Bartholin, "out of the wreckage I put into my Museum one of the cushions in memory of the king." Worm remarked that Christian IV "did not undertake this hatching for profit or gain. The ways of Nature are ten times better. But because the king wished to inquire into the truth of the Egyptian art, and so he started it and it gave him not a little pleasure."
Figure 4.

Hatching oven of Christian IV of Denmark. A, open oven; K, oven closed and ready for operation; B, ventilating hole with wooden plug; C, interior capacity of oven; D, square opening into which a brass gridiron was put; E, small pieces of charcoal. The opening was shut with a wooden door which, on the inside, was lined with brass lamina. The door was held in position by a rod, as shown in F, but it also rested on two iron supports, thereby leaving space for air to enter. G, a wooden rotating disk for turning the eggs; H, a silk cushion (which was put on G) on which the eggs were spread; they were covered with a similar cushion. I. Drawing by Worm from Bartholin (1661).

The operation of these incubators was not a success. Yet, as late as 1817 Mathieu urged the French government to finance the introduction of Egyptian incubating ovens and their adaptation to local conditions. The knowledge that artificial incubation was practiced in Egypt with good results did, however, stimulate in the course of time a number of attempts to devise methods for use in Europe. This will be discussed below.

One peculiar aspect of the reports on incubation in China and Egypt is the occasional mention of fermenting manure as a medium in which eggs were imbedded for hatching. As far as China is concerned, it should be noted that no Chinese sources refer to such procedures; they are only found in the travel reports of González and Grosier. As for Egypt, Aristotle tells us that eggs were “buried in dung heaps” and a similar remark is found in Pliny’s work, but no such statement is made by either Diodorus or in any later account of eye-witnesses.

An oblique reference, similar to that of Aristotle, is ascribed, in the Historia Augusta, to the Roman emperor Hadrian. Hadrian made a visit to Egypt in 130-131 A.D. In a letter of somewhat doubtful authenticity, written from Egypt to his brother-in-law Servianus, occur these uncomplimentary remarks about the Egyptians: “I have given these people every-
thing they asked for. I have confirmed all their ancient privileges, and added new, which they could not help acknowledging in my presence. But no sooner had I turned my back than they lavished every kind of insult on my son Verus and my friend Antinous. I wish them no worse than that they should feed on their own chickens, and how foully they hatch them I am ashamed to say—" (Gregorovius, 1898).

Our evidence being insufficient, we cannot definitely reject these statements as untrue. It appears very likely, however, that they are founded on a verbal misunderstanding. We may assume that travellers in China and Egypt were told that manure served as the “source of heat” for incubation. For the inhabitant of a warm and dry climate, such as Egypt and certain parts of South China, manure is a valuable fuel which, on account of its slow combustion, is particularly well suited to produce the low and even temperature needed in incubation. Moreover, in some instances (Yang Hsin, 1740) warmed, dry manure, which retains heat well, was employed for heating eggs in a fashion similar to that used with cereal husks. To most Europeans, however, manure would call forth the association of the steaming warmth of fermenting dung heaps; they were not likely to think of manure as something to be burned. It is probably in some such fashion that a misunderstanding arose which was to have reverberations for well over 2000 years. A somewhat similar interpretation was given by Keller (1913).

It was this misconception which, according to Bartholin (1657), led one Christian Thomae, counselor of Christian IV of Denmark, to attempt (reportedly with success) the hatching of chicks in manure, subsequently inspired Réaumur to his experiments, and as late as 1875 resulted in a patent issued by the U.S. Patent Office. This patent (No. 164,810) was granted to A. Corbett, manager of the “Gallinode Institute” in Hicksville, Queens County, New York. It covered a combination of incubator and brooder, fashioned after Réaumur’s ideas, consisting of a chamber to hold the hatching eggs which was to be surrounded on three sides by horse manure. By this time great interest had developed in incubation, and this must explain the fact that, though much superior inventions were already available, Corbett’s primitive design reaped him 45 medals and diplomas and resulted in a translation into Chinese of his publication on the subject (Corbett, 1874, 1876; Ferris, 1880). We are, however, anticipating historical events.

A peculiarly interesting essay, written by one Democritus, on “How it is possible to produce chickens without a hen”, is found in a work entitled “Geoponika.” This book, relating to various agricultural topics, was first compiled by Cassianus Bassus, also known as Scholasticus, at the end of the sixth or the beginning of the seventh century (Gemoll, 1884). Cassianus Bassus is believed to be indebted for much of his material to two writers of the fourth century, Vindanius Anatolius of Beirut and Didymus of Alexandria (Thorndike, 1929). The compilation was later
revised and became widely known about 950 A.D., during the reign of the East Roman emperor Constantine VII, Porphyrogenitus to whom the work is frequently ascribed. The book was first printed in 1538. Nothing certain is known about Democritus, the author of the chapter in which we are interested here. It may be assumed that his account was inspired by hearsay about incubation in Egypt. Here is what he has to say:

"You will have a number of chickens without incubation in this manner. When you set eggs under a hen that is sitting, the same day take some dung of fowls, pound it small, and sift it, and put it in pots, and lay hen's feathers all over the dung, and on these set the eggs perpendicularly, having the sharp end uppermost; then scatter some of the same dung over these again, until they are totally covered, and let them remain two or three days, and afterwards turn them every day, taking care that the eggs may not touch each other, that they may be equally cherished and after the twentieth day, when the hen's eggs begin to hatch, you will also find those in the pot cracked, wherefore they also set down the day on which the eggs have been set, that the number of the days may not be forgotten. On the twentieth day then take off the shell, and having cherished the chickens, put them in a basket, and introduce the hen, and she will take the management of all the chickens. That they may also have food, take some leaven of barley, and mix some gurgeoins with water; and put some ass or horse dung in the pots, and after three days worms will be produced to feed the young brood."

This advice may be based on misconceptions and may lack all foundations of actual experience; yet it bespeaks an attitude of sober realism which must be appreciated in an age in which beliefs were current such as the following quoted from Theophilus of Alexandria (turn of the fourth and fifth century): "For the Gentiles, whose skill in this art is well known, create basilisks in this wise. They have an underground chamber completely walled in on all sides with stone, and with two windows so small as scarcely to admit any light. In this they put two cocks of twelve or fifteen years and give them plenty of food. These, when they have grown fat, from the heat of their fat have commerce together and lay eggs. As soon as the eggs are laid the cocks are ejected and toads are put in to sit on the eggs and are fed upon bread. When the eggs are hatched chicks come forth who look like young roosters, but after seven days they grow serpents' tails and would straightway burrow into the ground, were the chamber not paved with stone" (Thorn-dike, 1929). These basilisks were then to be used in the making of gold.

The further history of artificial incubation is a curious sequence of real advances alternating with uncritical acceptance of legendary accounts relative to the methods used in Egypt.
Writing in the fifteenth century, Azalus (1544) spoke of seeing a woman in Udine (Italy) hatching chicken eggs by placing them between layers of horse manure. At about the same time Leonardo da Vinci entered in his diary a note to “ask the wife of Biogino Crivelli how the capon rears and hatches the eggs of the hen when he is in the mating season,” and another to the effect that these people “hatch the chickens by making use of the ovens by the fireplace.”

Charles Estienne (1567) reiterates the instructions found in the “Geoponika,” but with the advent of the seventeenth century we encounter real departures from tradition and independent thought. Olivier de Serres (1600) in his “Théâtre d’Agriculture” states that chicks can be hatched in a small oven which has been adapted for this purpose and which is heated by a slow, continuous fire. The oven is to be made of iron or copper; it is to be rounded on top (similar to the ovens used at that time for baking bread); its inner surface is to be lined with the same material as that used for ceilings. The top of the oven is to be of one piece, fitting into the lower part and removable so that the eggs may be turned easily. The eggs are to be surrounded by feathers and covered with a soft feather pillow. The heat is to come from four lamps which are lighted all the time and the flames of which touch the floor of the oven. This primitive incubator incorporated, at any rate, some provisions of insulation and a crude possibility of temperature regulation.

Gian Battista della Porta was an inventor of many mechanical contrivances and author of “Magia naturalis”, first published in 1558 and greatly enlarged in later editions. With reference to the instructions for incubation given in the “Geoponika” Porta tells us in his book that: “I tried this most diligently; and it took no effect, nor can I tell how it should be done.” Porta then gives an account of his own method which is here reproduced from the English edition.

“But what I have done myself, and I have seen others do, I shall briefly relate, that with little labour and without Hens, anyone may hatch eggs in a hot oven. Make a vessel of wood like a Hogshead, let it be round, and the Diameter so long as your arm is, that you thrust in, that you may lay and turn the Eggs, let it be four foot in Altitude. This we divide by three boards within into four parts: Let the first be a foot and a half, the second little above a foot, the third a foot, and the fourth least of all. Let every concavity divided with boards have a little door thereto, so large as you may thrust in your arm, and its shut to open and shut at pleasure. Let the first and second loft be made of thin boards, or wrought with twigs, let the third be of brass arched, and the fourth of solid wood. Let the first and second stage have a hole in the centre three fingers broad, through which must pass a brazen or iron pipe tinned over, that must come half a foot above the second story, and so in the lower
most, but in the bottom the orifice must be wider, like a Pyramis or funnel, that it can fitly receive the heat of the flame of a candle put under it; in the second story let the pipe be perforated about the top, that the heat breathing forth thence, the place may be kept warm, and the Eggs may be hot in the upper part, as they are under the Hen. Above these three rooms strew saw-dust, which I think is best to cover them: Let the saw-dust be highest about the sides of the Hogshead, but less in the middle; in the bottom where the pipe is lower, that the Eggs that lie upon it may receive the heat that comes from the pipe every way: In the third story where the pipe ends, let it be pressed down about the sides, and higher in the middle about the pipe, let a linnen cloth cover the saw-dust, a fine cloth, that if it be foul’d it may be washt again, and the Chicken hatch’d may go up on it. Lay upon every story a hundred Eggs, more or less, let the great ends of the Eggs lye downwards, the sharp end upwards. The walls of the Hogshead that are above the saw-dust within the concavities, and the upper part of the story must be covered with sheep skins, that their warmth may keep in the heat: in the lower concavity under the Funnel, must a light lamp be placed, at first with two weeks, in the end with three, in summer; but at the beginning of winter, first with three, and last with four or five: Let the light fall upon the middle of the Funnel, that the heat ascending by the pipe, the rooms may heat all alike. The place where this vessel stands must be warm and stand in a by place; in the lower part where the lamp is lighted, you must lay no Eggs, for that heat there will not hatch them. But where the Chickens are wet when they are first hatch’d, shut them in here to dry them by the warm heat of the lamp, marking twice or thrice every day whether the heat abate, be warm or very hot. We shall know it thus, take an Egg out of the place, and lay it on your Eye, for that will try it well: if it be too hot for you, the heat is great, if you feel it not, it is weak: a strong heat will hatch them, but a weak will make them addle. So you must add or take away from your lamp, to make the light adequate and proportionable after the fourth day that the Eggs begin to be warmed, take them out of the cells, and not shaking them hard, hold them gently against the Sun beams or light of a candle, and see whether they be not addle, for if you discern any fibres or bloody matter run about the Eggs, it is good, but if it be clear and transparent, it is naught, put another Egg in the place of it: All that are good must be daily turned at the lamp heat, and turn them round as the Hen is wont to do. We need not fear spoiling the Eggs, or if any man do handle them gently; in summer after nineteen or twenty days, or in winter after twenty five or twenty eight days, you shall take the Eggs in your hand, and hold them against the Sun, and see how the Chickens beak
stands, there break the shell, and by the hole of the Egg take the Chicken by the beak and pull out its head; then lay it in its place again, for the Chicken will come forth it self; and when it is come out, put it in the lower cell as I said: But let the lamp stand something from the parchement, lest the Chickens allured by the light, should pick at it and be burnt by it: And if you do work diligently as I have shewed you, in three hundred Eggs you shall hardly lose ten or twenty at most.”

It is said that these experiments gave della Porta the reputation of being a sorcerer and that he desisted from further work of this kind in order to avoid prosecution by the Inquisition (Devaux, 1892).¹

Cornelis Drebbel, the great Dutch mechanic who lived from 1572 to 1633 and who spent the latter part of his life in England, gained in his time some reputation by hatching eggs in incubators of his own construction (Tierie, 1932). On February 18, 1668, long after Drebbel's

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1. "Porta obtint quelques éclosions qui firent tant de bruit à l'époque qu'il passa pour sorcier et attira sur lui l'attention malveillante du Saint-Siège: il abandonna sa découverte pour ne pas déplaire à l'Inquisition." Devaux (1892). We did not succeed in discovering contemporary testimony about these events and the authenticity of the reports must be doubted.
death, his invention was discussed at a meeting of the Royal Society about which we have the following record: "Mr. Henshaw upon occasion mentions the way of hatching chickens by balneums formerly used in the Minorities by Dr. Kessler's brother (actually Kessler's father-in-law, viz., Drebbel); the particulars of which he was desired to bring in writing, which he promised to do" (Birch, 1756, vol. 2, p. 348). In a chronicle of Alkmaar, Drebbel's home town, van der Woude (1746) tells us that: "he was able, by means of a strange and amusing device, to hatch duck and chicken eggs all the years round, yes, even in the middle of winter, without using ducks or chickens for this, and everything went so punctually, that the young were born at the proper time, just as if they had been hatched by ducks or hens" (Dousa, 1850).

Figure 6

Drebbel's incubator with mercury-alcohol thermostat (From manuscript 2206, Ll. V 8, Part II, 1 in University Library, Cambridge, England).

The "strange and amusing device" was an ingenious invention, viz., an alcohol-mercury thermostat. Drebbel himself did not publish anything
about his incubator, but much information about his inventions was preserved by his son-in-law, Johan Sibertus Kuffler, and his grandson Augustus Kuffler, in a manuscript which now is in the library of the University of Cambridge.

The account given in this manuscript of Drebble's invention, with some punctuation added and a few parenthetic comments, is as follows:

"The Description of two Furnaces ruling themselves & Keeping at any Degree of Heate, the one for Hatching of Chickens."

"The First Figure placed at page 171 is for the Curious Chymist (not reproduced here) the 2d figure page 172 (see Fig. 6) is for Hatchin of Chickens & must Bee tended with greate Circumspection & dificultie. this Furnace must Bee without A grate having 2 or 3 holes. running from the Place where the \( \Delta \) is to the Edges which Blow the \( \Delta \) as A over the \( \Delta \) fire, Lyes An Iron Plate with A hole in the middle as B: thro which the Heate comes, over which is placed A Double foure Square Tinnen, Leaden or Copper Box in which the Eggs are laid in Towe & with in the Double sides Bottome & Topp the \( \nabla \) is put with which it must Bee filled thro a small Pipe Comineg out of the Topp of the Furnace as C & still as the \( \nabla \) water wastes (wastes), itt must Bee filled Againe thro the same in the Bottome of the water Box. Between the Double of itt Lay the glass \( \mathcal{D} \) which is filled with \( \mathcal{D} \) to the Neck & in the Necke \( \mathcal{F} \) to fill this Retorte you must first Put the \( \mathcal{G} \) in, then the \( \mathcal{D} \), then Turne itt upside downe, holding to the Mouth & the \( \mathcal{F} \) will come into the neck. Let the \( \Delta \) come round the Square water Box & it must Come out att a round small hole in the middle of the Topp of the Furnace as E upon which you must have a spoone to shut as F which spoone must have A Long handle playing upon A Crosse Pinn att G & at H. It hath A Screw By which means It may Be fitted Backward or forward, now there must Be another Pinn with A Screw att the end of which is Put A Little glass Pipe & fitted into the Neck of ye retorte as at I: See that when the \( \Delta \) groweth hotter the (read "than") ordinary the \( \mathcal{D} \) expands itt selfe pressing upon the \( \mathcal{D} \) & the \( \mathcal{G} \) the Pinn I & So closeth the hole E & dampe the \( \Delta \) till It comes to A just ("proper") heate."

Drebbe's invention includes two important innovations, the use of water as a source of indirect heat and the employment of a thermo-regulator. His thermostat is in principle identical with toluene thermostats as they are in use now. This invention, though it was promptly forgotten,

1. The symbols used in the manuscript are as follows:
   - \( \Delta \) fire, \( \nabla \) water, \( \mathcal{D} \) alcohol, \( \mathcal{F} \) mercury.
is of great historical interest. For, the invention of a self-regulating thermostat is generally credited to Bonnemain, who obtained a patent on a bimetallic thermostat in 1783 (Hammerl, 1882; Geer, 1902). As we have seen, it was actually anticipated and applied by Drebbel nearly 200 years earlier. Drebbel's interest in artificial incubation was probably stimulated by the account given in Porta's "Magia naturalis", a Dutch edition of which had appeared in 1566. Some attempts at thermo-regulation, based on the thermoscope of Heron of Alexandria (about 100 B.C.), had previously been made by alchemists and it may be presumed that the principles of Drebbel's regulator were derived from these predecessors. Yet, it cannot be denied that the design of his regulator and its application were original and resourceful.

One may be skeptical about the success which della Porta and Drebbel claimed for their methods, but one must concede that they made independent experimental efforts to arrive at workable techniques of incubation. Porta did not have the mechanical ingenuity of Drebbel, but his essays in this field seem at least as novel as the much later ones of Réaumur, and Drebbel's design of an incubator was potentially far superior to Réaumur's celebrated invention. A quotation from Birch (1757, 3, pp. 455-456) is proof of the difficulties which Drebbel and others encountered in producing normal and viable chicks. It seems to indicate also that the Kufflers (i.e., Drebbel's son-in-law and grandson) abandoned the use of thermostats and returned to more primitive techniques. According to Birch: "Mr. Henshaw farther gave an account of the manner, how Dr. Kuffler hatched chickens by the help of furnaces, the process of which he had seen; which was, that the doctor had a wire-grate placed over a balsamum at a foot distance with a cover over, pulled up by a pulley: in which grate he set the eggs, and so turned them every day for eighteen days together: then he laid them on a hair cloth in a stove near the ash-hole, where they hatched themselves with their own bills: in which stove he kept them for three days, till they could feed themselves, which was when the yolk was consumed in their bellies.—Sir Jonas Moore remarked that Sir Christopher Heydon together with Drebbel long since in the Minories hatched several hundred eggs; but mentioned not the way; but that it had this effect, that most of the chickens produced that way were lame and defective in some part or other" (January 16, 1679).

About the year 1659 two members of the Accademia del Cimento were working in Vienna on artificial incubation. They were Paolo del Buono and Geminiano Montanari. A disciple of Galileo, del Buono was Imperial Mathematician and director of the mint in Vienna. He had participated in the efforts of Grand Duke Ferdinand II of Toscana, alluded to earlier, to perfect the thermometer. Montanari was del Buono's student. In his book, "L'astrologia convinta di false", Montanari (1685) tells us that he and del Buono attempted to incubate chicken eggs in a kitchen stove which was heated with oil. The embryos developed, but
failed to hatch. What is important here is that these two investigators used a thermometer to determine the temperature underneath sitting hens, and that they attempted to adjust the heat of their oven accordingly.

The problem of temperature regulation in connection with incubation was at this time studied by two of the great founding members of the Royal Society of London, Sir Christopher Wren and Robert Hooke. Sprat (1667) says about Wren that “he has found out perpetual, at least long-liv’d Lamps, and Registers of Furnaces, and the like, for keeping a perpetual temper, in order to various uses; as hatching of Eggs, Insects—.” No details about these inventions are extant. Our only information comes from the minutes of the Royal Society in which we find the following relevant passages (Birch, 1756).

April 29, 1663. “Dr. Wren was desired to acquaint Mr. Hooke with the apparatus and progress, which he had made in the experiment of hatching eggs by the equal and moderate heat of a lamp,—”

February 14, 1666-7. “Dr. Wren mentioning, that he had a new kind of lamp, the operator was ordered to attend him, to receive his instructions how to make it.”

February 21, 1666-7. “The operator was again ordered to attend Dr. Wren to receive the directions for the making his new kind of lamp,—”

April 11, 1667. “Dr. Wren’s new lamp was produced and approved. He intimated, that the main point in it was to balance it well. He was desired to make a scheme thereof, with some discourse upon it in writing; which he promised to do.”

The rebuilding of London and its churches presumably kept Sir Christopher Wren from carrying out this promise. Robert Hooke, his colleague in the Royal Society as well as in the surveying and rebuilding of London, busied himself with the same problems. Apparently it was chiefly between 1675 and 1677 that his attention was on these matters (Hooke, 1935). In his “Lampas” Hooke (1677) gave a detailed account of his efforts to devise self-regulating lamps. The problem that he set himself is stated as follows: “to shew a way how to make the Receptacle of a Lamp in such manner as that it shall continue to supply the Pabulum to the flame equally and for a very long time till it be all consumed. The consideration of which Problem first put me upon the enquiry after a counterpoise for Liquors or Fluids—.” About the purpose of such counterpoises Hooke said that they are “to keep the superificies of the Liquor (whether Oyl, Spirit of Wine, Oyl of Turpentine, or the like) whatever quantity there be in the Vessel, always to the same height, so that the said Pabulum shall always be equally distant from the bottom of the flame, and the wick or flame being once placed at a convenient height or distance above the superificies of the Oyl, shall not be deserted by the said Superificies till the whole quantity be consumed.”
Self-regulating lamps designed by Robert Hooke. The two upper lamps were spheres containing the fuel. These spheres rotated and were counterpoised in such a fashion that the level of the fluid remained constant. The lower part of the figure illustrates lamps in which the wick was attached to a float, the socket of the wick sinking with the level of the oil (From Hooke, 1677).
Self-regulating lamps designed by Robert Hooke. The oil in these lamps was in a receptacle from which it reached the flame through a syphon. A counterpoise raised the receptacle as the oil was consumed (From Hooke, 1677).
Figure 9

Leutmann's incubator. Explanation of letters: b, ash door; c, grate; d, furnace with cover e; g, opening into extension of stove; k, pipe for hot air which rests on a grate and opens at i into the oven; n, smoke stack; p, dish for water to supply humidity; s, thermometer, fastened to a board, r; t, sand on which the eggs rested. There was a sliding tile door at g for temperature regulation. Further temperature adjustments could be made by opening or closing ash door, sliding doors on the oven and oven door itself (From Leutmann, 1735).

Some of these lamps are shown in Figs. 7 and 8. Two such lamps were at one time in the collections of the Royal Society (Grew, 1681), but apparently have not come down to us. Among the uses to which his lamps might be put Hooke listed: "Distillations, Digestions, Fermentations, Putrefactions, Dissolutions, hatching the Eggs of Birds or Insects."

The Royal Society at one time also was in possession of a "Lamp-Furnace" designed by Hooke, and of this Grew left the following description: "Towards the bottom is a partition with a hole in the middle; below which, stands a Vessel of Oil with a Wick, and a Cork to float it, so as to stand within the said hole. Over this is placed a Pan, viz. with
the bottom about two inches distant from the partition. Within which, is fine sand. Design'd for the hatching of Eggs, in order to observe the Process of Generation. As also for digesting of Liquors." Nothing further is known about this incubator or about trials with it.

Yet another of the early members of the Royal Society, Sir Kenelm Digby (1669) used methods of artificial incubation for embryological observations. He left this account: “Therefore, to satisfy our selves herein, it were well we made our remarks in some creatures, that might be continually in our power to observe in them the course of nature, every day and hour. Sir John Heydon, the Lieutenant of his Majesties Ordnance (that generous and knowing Gentleman, and consummate Souldier both in Theory and Practice) was the first that instructed me how to do this; by means of a furnace, so made as to imitate the warmth of a sitting Hen. In which you may lay several eggs to hatch; and by breaking them out at several ages, you may distinctly observe every hourly mutation in them, if you please.—”. Sir John was the son of Sir Christopher Heydon mentioned earlier.

Another contemporary, the French philosopher Nicolas de Malebranche, also used artificial incubation for embryological studies. All that we know about this comes from a letter written by the Abbé Daniel on April 10, 1670. He informs his correspondent that “the Reverend Father de Malebranche has honored me with a letter saying that he has at present an oven in which he incubates eggs, and that he has already opened some in which he saw the formed and beating heart, together with some arteries” (Blampignon, 1861). The inventions and observations of Wren, Hooke and Malebranche had no reverberations and during the remainder of the seventeenth century we find nothing but an inconsequential reference in John Worlidge’s (1697) “Systema Agriculturae”.

An important event occurred with the publication of Leutmann’s book on furnaces and ovens which ran through five editions between 1720 and 1764. Leutmann stated clearly three basic principles which must be fulfilled if the artificial hatching of eggs is to be successful. These were as follows: (1) a careful study of the temperature prevailing underneath sitting hens; (2) the construction of an oven which not only will hold fire for at least 12 hours, but which can be regulated in such a fashion that the temperature of its incubating compartment corresponds closely to that under a sitting hen; (3) the adjustment of humidity according to natural conditions.

In implementing his first principle Leutmann was successor to del Buovo and Montanari. The instrument which he constructed for this purpose consisted of a tin “egg”, painted white, which was attached to a lead tube, bent at right angles, and with a thermometer (Florentine alcohol thermoscope) inserted into the top of this tube. This device
was used to make daily temperature determinations under sitting hens and also to measure the warmth within the incubator. The incubator and thermometer are illustrated in Figure 9. Leutmann also offered suggestions for the brooding of chicks.

In 1748 Cederhielm reported about hatching experiments which he had pursued on behalf of the Royal Swedish Academy of Sciences. His work was inspired by reports on incubation in Egypt, but he was apparently quite unaware of earlier attempts, such as those of Bartholin, Drebbel and Leutmann. His own work, published in Swedish, remained unknown to most of his contemporaries and successors including Réaumur. Various types of hatching ovens were built by Cederhielm, the one that presumably gave the most satisfactory results being shown in Fig. 10. These ovens were regulated with dampers and insulated with sand. Cederhielm’s first concern was to determine the proper incubation temperature. He found that the body warmth of a sitting hen was about 37° on the scale of an Ekström thermometer. He aimed at maintaining this temperature in his hatching trials, but had to cope with fluctuations between 35° and 39°.

In getting his ovens ready for incubation the lower one was heated first: the eggs were then put into it and a fire was started in the upper oven in order to maintain a proper temperature below. The eggs were put into boxes half filled with dry and pulverized cow manure which was to help in equalizing the temperature. Boxes and manure were regularly moistened. For the first two weeks the eggs were turned twice daily, three times a day thereafter. Cederhielm finally succeeded in hatching some normal chicks. He had, at any rate, clearly recognized all important principles of incubation and his work could well have served as a sound foundation for further development.

Two publications of great interest appeared in 1749, one by Beguelin, the other by de Réaumur. Nicolas Beguelin, a Swiss and tutor of Frederick William II who was later to succeed Frederick the Great as King of Prussia, designed for the amusement of his “auguste élève” an incubator so that his pupil might from day to day follow the development of the embryo and see the hatching of chicks. The incubator consisted of two cylindrical sheet iron containers, fitting into each other, the inner one being considerably smaller than the outer and resting on supports at the bottom of the outer container. On top the two containers were united by a metal ring. There was a hole to fill the space between the cylinders with water and a faucet to drain the water. The outer wall of the incubator was insulated with wood, cardboard or flannel. The top cover was of wood and could be opened or closed for adjustment of the temperature. Heat was provided by an oil lamp underneath the incubator. Beguelin noted that the temperature in the incubator was more easily kept constant with a greater volume of water in the jacket.
In order to facilitate observation of the developing embryo Beguelin removed the shell at the broad end of the eggs and used a piece of shell from another egg as cover. Embryos were thus kept alive for 15 days. It is related that out of one batch of 26 eggs which had not been opened, all but one of those fertile produced hatched chicks. In another publication Beguelin (1750) described improvements of a method of incubation which had been devised by Sulzer. The latter’s incubator was a galvanized iron box with a double bottom. Steam was introduced between the two bottoms. The top of the box was open and the eggs were laid on a cloth, stretched over the top, and were covered with tow.

The appearance of de Réaumur’s book created somewhat of a sensation. In the words of Achard de Péaticux (1850) it “tourna bien des têtes
et occasionna la ruine de plusieurs personnes.” In 1747 Réaumur had given a lecture on incubation before the Académie des Sciences in Paris. This was followed by the publication of his book in 1749 (English translation 1750), and that of a shorter practical guide in 1751. Two methods were recommended by Réaumur. In the first, specially fitted casks or boxes were partially sunk into horse manure, the heat of the fermenting manure providing the necessary temperature. The casks or boxes had an outer lining of plaster or other material to check the penetration of moisture.

The second type of incubator was built on top of bakery ovens and utilized the heat given off by these ovens. Réaumur used his thermometers in attempting to maintain a proper and constant warmth; he was aware of the necessity to prevent excess moisture (he determined the degree of moisture by introducing a cold egg into the incubator and observing the amount of water condensation on the shell); he devised some means of ventilation; and he insisted on the need for regular turning of the eggs.

From a mechanical point of view Réaumur’s inventions were primitive and inferior to some that had been designed much earlier. There are presumably several reasons which account for the interest aroused by Réaumur’s work. To start with, he was one of the leading scientists of his time; his observations were documented by careful records and based on meticulous attention to detail; his treatise was written with considerable enthusiasm and in the spirit of the promoter. Most important of all perhaps, Réaumur devised a method of brooding newly-hatched chicks, thus pointing the way for utilizing to advantage the results of artificial incubation.

Just how successful Réaumur and his followers were in hatching chicks we do not know; according to Féry-D’Esclands (1877), Réaumur obtained hatches of only 10 to 15 percent. There can be no doubt, however, that Réaumur’s methods were for a time widely regarded as a revolutionary advancement. Even on this continent they were put into practice almost immediately. Dr. Jean François Gaultier, a French physician who lived in Canada between 1742 and 1756, wrote to Réaumur in 1753 and 1754 about his having used the new ways of hatching chicks. Réaumur had supplied the thermometers for the purpose.

“During the past year, and to an even greater extent during the present, people have eaten young chickens in February which had never before happened in Canada,” Gaultier wrote, and in another letter, relating the benefit of incubation, he told Réaumur that “this is one more debt which Canada owes you” (Vallée, 1930). It must be admitted, however, that the initial enthusiasm was dissipated quickly. There were some attempts to revive Réaumur’s ideas, e.g. in 1781 by an anonymous German author, in 1831 by Léonard in France, and later still by Corbett (1874, 1876) in the United States, but nothing came of them.
Yet it is significant that an editorial footnote to Léonard’s article could, as late as 1831, make the statement that the technique of Réaumur "seems superior to many machines which have been recommended." Presumably inspired by Réaumur’s experiments with manure, du Bignon (1763) reported that it was possible to utilize the heat of fermentation of tanbark for incubating eggs.

Our account of Réaumur’s contribution to the development of artificial incubation must not be concluded, however, without reporting that, prior to Réaumur and du Bignon, Richard Bradley (1736) already had, if in a much less sophisticated fashion, utilized the heat of fermenting horse manure and tanbark for the hatching of eggs. We quote: "My way is in a hot Bed, either made of Horse-Dung or Tanners Bark. Take an Earthen Vessel, like a garden Pot, but not quite so deep, fill it half way with Wool or Cotton, and lay as many Eggs on the Bed of Wool as will make a single Layer, so as not to come within an inch of the sides of the Vessel; then fill up the Pot with Wool, covering the Eggs about four Inches, and set the Pot up to the Rims in the Bed, and cover the Bed with a Frame and glasses, such as you use for Cucumbers, and these will hatch in due time. - If you can make Fowls lay, you may always hatch them."

Réaumur’s experiments led to several attempts to invent means for the mechanical regulation of the temperature in incubators. Romas (Krüinitz, 1791) constructed two different devices for this purpose. One was based on the temperature expansion of an iron rod, the motion of expansion being successively transmitted to three different levers, the last of which was to open a register for the escape of warm air. The other appliance utilized the expansion of fluids with increasing temperature. A special thermometer was built for this purpose which had an expansion chamber above the bulb. It was adjusted in such a way that the thermometer remained in a horizontal position and its liquid did not reach the expansion chamber when the instrument was, at an ambient temperature of 32° R., suspended by a thread attached between bulb and expansion chamber. With rising temperature the liquid of the thermometer entered the expansion chamber, thereby upsetting the balance of the thermometer. The downward movement of one end of the thermometer was to pull open a register.

Krüinitz (1791) recommended an instrument in which expanding fluid raised a piston in a tube. The piston in turn was to lift a register. It was of considerable merit that Krüinitz suggested mercury for use in this instrument.

The design of two other mechanical temperature regulators was due to Prince de Conti (Krüinitz, 1791). The principle of both these regulators was similar to the device of Krüinitz, but one of them utilized the expansion of air with rising temperature.
Soon after the publication of Réaumur's book R. Huzard built an incubator of considerably superior design (Brechemin, 1926). This incubator had very large dimensions (capacity 6000 eggs). It was constructed of masonry with ducts and windows for ventilation and an entrance door. The exterior was insulated with wool. Heat was supplied by warm water circulating from a tank through copper tubes. Open containers with water, placed inside the incubator, supplied additional moisture. After initial difficulties Huzard's hatching results are said to have been better than those of Réaumur.

Another remarkable event in the history of incubation was the publication in 1780 of a book by Abbé Copineau, entitled "Ornithotrophie artificielle ou art de faire éclore et d'élever la volaille par le moyen d'une chaleur artificielle." This work was printed in four editions (with varying titles) between 1780 and 1799, indicating a considerable public interest. Copineau gave a critical evaluation of Réaumur's incubators, pointing out that their greatest faults lay in the impossibility to regulate the temperature properly and to obtain quickly an even distribution of heat and the necessary amount of ventilation. Copineau's own incubator was similar to that of Huzard. It was built of brick, circular in shape, and had a capacity of 8000 eggs. It was heated by circulating hot water. The lower, but not the upper, part of the outside wall was insulated. There were provisions for ventilation and windows for reducing the temperature in the incubator. As an important innovation Copineau made regular determinations of air humidity with the hygrometer invented by Deluc (1775) and which a little later was to be greatly improved by de Saussure (1783). Fény-D'Esclands (1877) stated that Copineau had hatches of up to 20 percent.

At about this time some experiments were made with frictional electricity. Achard (A**, 1799) thought that eggs thus treated at room temperature could develop, if at a somewhat retarded rate. Prince Gallitzin (1780) exposed eggs on the ninth day of development for half an hour to frictional electricity, incubation being completed by a sitting hen, and he believed that the treatment had improved the chances of hatching.

The reinvention of the thermostat and its application to incubation by Bonnemain (1816, 1824, 1828; see also Parmentier, 1827) were probably the most important single events that, much later, led to the perfection of our modern incubators. Bonnemain started his work contemporaneously with Copineau. On August 14, 1782 a commission of the Académie Royale des Sciences observed the hatching of chicks in Bonnemain's establishment and reported that the new "fire regulator" has the "éloges et l'approbation de l'académie." During the next year Bonnemain obtained a patent on his invention. This was the first bimetallic (iron-brass) thermoregulator.

In his initial report (1816) Bonnemain had not revealed any details of his invention, but when he applied later for a subvention of his work,
the French government, fairly enough, made a grant of public funds conditional on the publication of a full description of technical details (Bonnemain, 1824, 1828).

The novel principles of Bonnemain’s incubator included an ingenious system of hot water circulation and thermostatic control of the draft door on his stove. There were special provisions for fully utilizing, prior to its escape into the chimney, the warmth of the air rising from the fire. A source of humidity was provided by placing shallow pans of water into the incubator. It is said that the temperature could be maintained within one-half of one degree Réaumur. It seems that Bonnemain had considerable commercial success with his incubators, supplying the markets of Paris with quantities of poultry, but eventually political conditions of the time brought his activities to a close because “the majority of his regular customers either had left the country or had stopped entertaining.”

Le Roi (1868) tells us that in 1804 one Foucalt established in Versailles a hatching business by heating the room of a house with hot air which was passed between pieces of sheet metal, the latter heating the room by radiation. The enterprise is said to have been successful.

For a similar scheme John Champion had obtained Letters Patent from the British Crown in 1770, a description of which was registered with the High Court of Chancery. The method simply consisted in heating “an apartment lined with flues, such as in bothouses – to the degree of blood heat.” The eggs were spread on a table.

It is evident, however, that for one reason or another the new schemes of incubation did not find ready acceptance. In 1812 Thomas Jefferson complained in a letter to Dr. Thomas Cooper about the lack of generally useful methods of incubation. He wrote: “You know the just esteem which attached itself to Dr. Franklin’s science, because he always endeavored to direct it to something useful in private life. The chemists have not been attentive enough to this. I have wished to see their science applied to domestic objects, to malting, for instance, brewing, making cider, to fermentation and distillation generally, to the making of bread, butter, cheese, soap, to the incubation of eggs, etc. And I am happy to observe some of these titles in the syllabus of your lecture. I hope you will make the chemistry of these subjects intelligible to our good housewives” (Lipscomb and Bergh, 1904).

Meanwhile, in France more primitive methods of incubation came to the fore again. In 1813 Bose reported for a commission of the Institut de France on a technique developed by a Mademoiselle Portebois. In order to make either male or female fowl sit on eggs, the birds were put into a box so small that they could not move. A cover prevented the birds from rising. These nests with the birds in them were kept in the dark. With female chickens, ducks and turkeys the top board could
usually be removed after a day without the birds leaving the eggs. Males were somewhat more recalcitrant, but submitted to sitting on eggs after a few days. The birds were used for three or four successive incubation periods.

This procedure apparently gained considerable popularity, for in 1867 Geyelin in a report on the poultry establishments of France wrote that a system was in use there which he proposes to call “living hatching machine” and that this technique was practiced by specialists (“couveurs”). The method was essentially that described by Bose, except that only turkeys were used as sitters. The procedure was as follows: Nest boxes were set up next to each other along the walls of a dark room. Each nest was provided with a few plaster of Paris eggs. Turkey hens were put into the boxes and the boxes were covered with lattice or wire netting. After about 48 hours the plaster eggs were exchanged for two dozen hatching eggs to each turkey. Once a day the turkeys were removed from the nest and force-fed. At the same time the nest boxes were cleaned. The chicks were removed as soon as they emerged from the shells and new hatching eggs were put under the turkeys. The same birds could be used for from three to six months or even longer. Some establishments had as many as 100 turkeys sitting simultaneously. (2400 eggs!).

Geyelin refers to this technique as “the very best and cheapest way of hatching.” A similar account has been given by Gobin. These methods are of interest in view of what we know now about the stimulating effect of light on the pituitary and on activity of the gonads, quiescence of the gonads and the brooding instinct apparently being promoted by darkness.

In 1824 Walthew announced the use of steam for heating an 1100-egg-capacity incubator of his own design. Barlow (1824) made a similar claim and was in turn accused by Walthew of stealing his idea. Felgère (1828) recommended the use of water of hot springs for heating incubators and also for maintaining the proper temperature of brooder rooms. There are several eye witness reports for the success of this procedure (Gaultier, 1831; Chevalier, 1831), and it became well established in the community of Chaudes-Aigues (Department Cantal). In fact, the use of hot springs for the hatching of eggs obviously had a long history in France. For, Astruc (1737) had already reported such practices at Balaruc in Languedoc (Department Hérault). Moreover, Astruc very reasonably suggested on the basis of these observations that, instead of attempting to imitate the Egyptian manner of incubation, it might be more practical to employ hot water as the source of heat for artificial incubation.

Bonnemain’s ideas on artificial incubation were revived and improved upon by Borne (1828), who failed, however, to give an account of his procedures, and by Sorel (Herpin, 1840). Contemporaneously, Bonnes (1831) developed an incubator of his own construction which, while very original in design, was mechanically inferior to that of Bonne-
Bonnemain's incubator was of brick and masonry construction and built into the corner of a room. The inside walls formed a hexagon to aid the reflection and equal distribution of heat. Hot air was introduced into the incubator by a pipe which was heated in a charcoal oven outside the incubator. Triangular holes near the top served to reduce the temperature. The eggs were put on circular trays rotating around an axle. In the center of the turning trays was a gadget designed to aid in the equalization of temperature. As a source of humidity there were six small pails of water which were connected with each other by pipes and which could be filled and drained from the outside. The capacity of this incubator was in excess of 1000 eggs. After an initial failure on account of a faulty thermometer, Bonnes reported that 310 chicks were hatched from 340 eggs which started development.

Bonnes expressed the belief that the claims Bonnemain had made for the efficiency of his method had been exaggerated because otherwise Bonnemain's method would have been adopted universally. The acceptance or eclipse of inventions unfortunately, however, is not determined by such simple standards of value. At any rate, Bonnes' own invention was forgotten promptly.

Delpech and Coste (1834) designed for their embryological observations a small incubator which had the shape of an Etruscan vase (Fig. 11). This incubator consisted of two metal shells, fitted into each other. The outer shell contained some water which was heated by an adjustable burner in the base. The wall of the inner shell was thus warmed by steam. Air currents produced by a pipe which opened into the inner space served to equalize the temperature. A basket made of silver-plated copper wire contained the eggs. A thermometer was inserted through a hole in the cover. We have no information about the performance of this machine. During the following year Lemare (1835) announced an incubator which incorporated a thermoregulator of novel design. The incubator was heated by hot water. With increasing temperature, expansion of the water lifted a float in a tube connected with the water tank and thereby partially closed the stove draft.

Yet even as we enter the era of commercial manufacture of incubators, we find that these machines had no provisions for automatic temperature regulation. This was true, for instance, for "Cantelo's Patent Incubator" which introduced top-contact heat (Cantelo, 1849) and for the incubators of Voitellier (1880) and Christy (1881). No wonder then that as late as 1866 the great embryologist Karl Ernst von Baer complained that incubators undermine the operator's health because of the attention they require during the night.

The second half of the last century brought the invention and manufacture of a large variety of incubators. Many details about these early commercially-produced machines can be learned from the publications of Ferris (1880), Tomlinson (1880), E. Brown (1881), Montauban (1881),
Figure 11

Incubator of Delpech and Coste. Explanation of letters: a, thermometer; b, cover; c, egg basket; d, air space; e, pipe opening into inner chamber and producing air currents; f, outer container, partly filled with water; h, adjustable alcohol lamp (From Delpech et Coste, 1834).
The history of artificial incubation, as it has been related here, poses many and complex questions. The fact that the ancient methods of China and Egypt could not be successfully transplanted to Europe probably finds its explanation in climatic conditions. In the south of China and in the north of Egypt temperature and humidity remain fairly constant during certain parts of the year, and the temperature is such that relatively little artificial heat is needed to provide the proper conditions of incubation. In such a situation simple devices may suffice to afford adequate control of the physical environment. In the less stable climate of Europe the same methods could not but fail. The same contrast held probably with even greater force for the raising of chicks which had been hatched artificially.

It is more difficult to explain why so frequently in the history of artificial incubation ingenious inventions proved to be abortive. Let us take as an example Cornelis Drebbel's invention of a thermostat. One cannot admit in this instance the truth of the generalization that "great men, no matter how notable their genius, in all spheres formulate and solve those tasks which have been raised for accomplishment by the historical development of productive forces and production relationships" (Hessen, 1931). On the contrary, Drebbel's accomplishments like many others illustrate the inescapable conclusion that "one of the paradoxes of history is that science is a product of human demands, and yet is not necessarily used when it becomes available" (Crowther, 1941). On account of poor communication facilities and language barriers, investigators and inventors, especially in earlier times, frequently remained unaware of work done by predecessors.

Numerous and varied circumstances probably contributed to the failure of the efforts of such men as Ferdinand II of Toscana, Paolo del Buono, Geminiano Montanari, Cornelis Drebbel, Sir Christopher Wren, Robert Hooke, Leutmann, Bonnemain, and others to produce practical methods of incubation. The causes presumably were partly technological, partly economic, partly psychological. For general discussions on these problems the reader is referred to Gilfillan (1935), Stern (1937), and Bernal (1929). Technologically, it is evident that the early essays into artificial incubation could not give consistently satisfactory results.

We have quoted evidence for the discouraging results of many of these trials. A further account by Paris (1821), relating to the close of the eighteenth century, may here find its place: "During the period that I was at College, the late Sir Buswick Harwood, the ingenious professor of anatomy in the University of Cambridge, frequently attempted to develop the egg by the heat of his hotbed; but he only raised monsters, a result which he attributed to the unsteady application of heat."
Moreover, no serviceable provisions were available for raising chicks that had been hatched artificially. Encouragement for development of inventions and for further experimentation was lacking. This was particularly true in the field of agriculture. Until recent times the markets for the produce of poultry husbandry were very restricted and the raising of poultry an unimportant by-product of general farming which did not seem to merit special efforts or investments. It was for such reasons that Meall (1854), speaking of artificial incubation, saw "most insuperable objections to its ever being successfully adopted". For, he felt that "there was no adequate motive to pursue it in this country, where a quantity of poultry, fully equal, and even superior to the demand, may be raised by the natural means."

Above all, it may be assumed that psychological obstacles barred the road for many of the inventions relating to artificial incubation. We quote a lucid statement by Alexander Hamilton (1791):

"Experience teaches, that men are often so much governed by what they are accustomed to see and practice, that the simplest and most obvious improvements, in the most ordinary occupations, are adopted with hesitation, reluctance, and by slow gradations. The spontaneous transition to new pursuits, in a community long habituated to different ones, may be expected to be attended with proportionately greater difficulty. — To produce the desirable changes as early as may be expedient may therefore require the incitement and patronage of government. The apprehension of failing in new attempts is, perhaps, a more serious impediment. There are dispositions apt to be attracted by the mere novelty of an undertaking, but these are not always the best calculated to give it success. To this it is of importance that the confidence of cautious, sagacious capitalists, both citizens and foreigners, should be excited. And to inspire this description of persons with confidence, it is essential that they should be made to see in any project which is new — and for that reason alone, if for no other, precarious — the prospect of such a degree of countenance and support from government as may be capable of overcoming the obstacles inseparable from first experiments."

Government support of research and invention, planned for the public good, is still inadequate today, as are the safe-guards against the growth of special privilege which, as experience shows, is likely to attend the subsidy of private interests.

The fitful course of the evolution of artificial incubation is not unlike that of many other techniques. It illustrates dramatically how much ingenuity is wasted because the possible value of inventions fre-
quently is not tested, fails to be brought into its proper perspective,\(^1\) lacks the necessary support or subvention, is allowed to be suppressed by or to fall into oblivion on account of private interests or prejudices, and generally is not, as it ought to be, made a part of public planning for the future.

While the general use of incubation equipment had to await the proper historical setting, it should be noted that the unsolved problem of artificial incubation served as a potent stimulus to the invention (thermostatic devices, self-regulating lamps) and the improvement (thermometer, hygrometer) of instruments which found many important applications in other fields. It is clear that the history of an idea, even if it concerns a very concrete and applied technique, is quite different from the history of specific inventions made relative to the same subject.

**THE PHYSICAL ENVIRONMENT OF HATCHING EGGS**

**Prior to incubation**

For obvious reasons eggs cannot be stored indefinitely prior to incubation. In fact, the period for which eggs can be held without impairing the hatching results is rather short. Its length depends on the temperature of the storage room (de Réaumur, 1749; de Lavison, 1862; Daveste, 1882, 1883a, 1887). The first requirement for successful storage of hatching eggs is the maintenance of a temperature in the storage room which is below “physiological zero”, i.e., below the point at which some, if very slow, development of the embryo will take place. Physiological zero for chicken eggs was established by Edwards (1902) as between 20°C and 21°C (68-70°F.), but more recent investigations by Funk and Biellier (1944) suggest that it may actually be several degrees higher. Prolonged storage may, especially under unfavorable conditions, lead to bacterial invasion and spoilage of hatching eggs; special precautions may be required (Bean and MacLaury, 1959).

Funk (1934 a) observed that with a storage temperature of 45-60°F. (7.2-15.6°C.) hatchability in relation to time of storage varied as shown in Table 1. There is a progressive decrease of hatchability. Similar results have been reported by Otrygan’ev (1938) and Mookerjee (1953). It is likely that such figures do not show the full extent to which prolonged storage interferes with development since it may be assumed that with a longer duration of storage there is an increasing percentage of eggs

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1. The unhappy influence of too close adherence to particular initial aspects of discoveries or inventions has been forcefully brought out by Goethe. We quote from his "Zur Naturgeschichte im allgemeinen": "Eine höchst wichtige Betrachtung in der Geschichte der Wissenschaften ist die, dass sich aus den ersten Anfängen einer Entdeckung manches in den Gang des Wissens hinein und durchzieht, welches den Fortschritt hindert, sogar öfters behindert. ... So hat auch jeder Weg, durch den wir zu einer neuen Entdeckung gelangen. Einfluss auf Ansicht und Theorie. Wir erwehren uns kaum zu denken: was uns zu einer Erscheinung geleite, sei auch der Beginn, die Ursache derselben; dabei beharren wir, anstatt von der umgekehrten Seite heranzugehen und die Probe auf unsere erste Ansicht zu machen, um das Ganze zu gewinnen."
which will never start development and which on this account will be classified as infertile. It must be noted, however, that according to Funk, Forward and Kempster (1950) eggs put into incubators on the day of laying hatch less well than after brief storage. Lamson and Kirkpatrick (1918), in studies conducted at Storrs, found that eggs stored for three to five days gave a hatch of 71.1 percent (501 fertile eggs), while eggs stored for 11 to 12 days gave a hatch of only 65.5 percent (441 fertile eggs). The higher the temperature of the storage room, the sooner will the hatching of the eggs begin to suffer. Under favorable storage conditions no significant deterioration of hatching quality seems to take place during the first six days, while beginning with the seventh day the chances for successful incubation diminish progressively. The Romans were already aware of these facts. Writing in the middle of the first century A.D., Columella, in his interesting discussion of poultry husbandry, said that “the freshest eggs are most suitable for hatching; those, however, which have been kept for sometime can also be set, provided that they are not more than ten days old.” Extensive observations were made by Waite (1919, 1923-1924); they yielded analogous results (Fig. 12). Studies by Olsen and Haynes (1948) led to similar conclusions. They reported that storage temperatures between 50° and 55° F. are optimal.

### Table 1

<table>
<thead>
<tr>
<th>Age of eggs when set</th>
<th>Number of eggs</th>
<th>Percentage of fertile eggs hatched</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-7</td>
<td>8253</td>
<td>76.2</td>
</tr>
<tr>
<td>8-14</td>
<td>930</td>
<td>74.0</td>
</tr>
<tr>
<td>15-21</td>
<td>109</td>
<td>61.6</td>
</tr>
<tr>
<td>22-28</td>
<td>61</td>
<td>32.0</td>
</tr>
<tr>
<td>29-31</td>
<td>19</td>
<td>0</td>
</tr>
</tbody>
</table>

Figure 12

The effect of storage of eggs on hatchability (From Waite, 1919).
and that at the lower end of this temperature range high hatching quality is preserved for a longer time. After storage at 30°F for 2 to 8 days the incidence of embryo abnormalities was increased.

Careful studies by Moran (1925) had indicated that the optimum storage temperature lies between 8° and 10° C. (46.4°–50°F.), Phillips (1945) reported that storage of eggs from New Hampshire pullets for one to seven days at 32°, 38° and 52° F., respectively, did not result in significant differences of hatchability, but Funk, Forward and Kempster (1950) found that storage for as short as seven days or less was harmful to hatchability if the holding temperature was below 45°F. (7.2° C.) or above 60°F. (15.6° C.). The damage from temperatures outside the optimal range was greater, however, among eggs held from 8 to 13 days.

On the basis of fairly extensive observations Pritsker (1940 b) concluded that preheating eggs at high temperatures for 30 to 60 minutes before the beginning of regular incubation has a favorable effect on hatchability. The incubation temperatures employed during this preliminary heating ranged up to 48° C. (118.4° F.), with temperatures at the level of the blastoderm of as much as 44.5° C. (112° F.). When fresh eggs (three to five days after laying) were used, consistently higher hatches than in the controls (no preheating) resulted, but older eggs did not give comparable results (see also Karapetyan, 1957). Becker and Bease (1958) obtained an improvement in the hatchability of stored eggs by pre-heating them before the beginning of incubation, either by warming them for one or five hours at 100°F. (37.8° C.) or by leaving them overnight at 70-73° F. (21-23° C.). Contrary to Pritsker, Becker and Bease found that the eggs that had been stored longest profited most by this procedure.

Kosin (1956) studied the effects of daily brief periods of warming eggs during a storage period of 14 days. Each day the eggs were exposed for one hour to an ambient temperature of 99°3/4°F. (37.6° C.). This treatment clearly produced an improvement in subsequent hatching, thereby confirming an early report by Jackson (1912). Recent reports by Milby and Sherwood (1960) and by McConachie, Jerome and Pepper (1960) should be consulted.

Storage at low temperature is the best means now available to preserve the hatching quality of eggs for at least a limited period. It is worthy of note, however, that de Réaumur in 1785 suggested dipping eggs in melted mutton fat in order to prolong the time during which good hatching results can be obtained. He recommended removal of the fat with warm water before using the eggs for incubation. This is a crude technique, to be sure, but the idea itself may merit further study.

Kato and Funahashi (1935) reported that tropical climate does not interfere with the hatching quality of eggs, provided the eggs are transferred to a cool storage room soon after laying. They found, as did other investigators, that the longer prior to incubation the eggs were exposed to unfavorable temperatures, the greater was embryo mortality during early stages of development. In a temperate climate such stringent precautions are unnecessary (Skoglund and Brown, 1956).
Heywang (1944) obtained results, however, which are at variance with those of Kato and Funahashi. His data show that hatchability was significantly reduced among eggs which had been laid at average maximum temperatures of 101.8° and 106.8° F. (ranges of 100.0 to 104.9° and 105.0 to 109.9° F., respectively), even though the eggs had been put into a refrigerator within one hour after laying. More recent observations by Heywang (1945) indicate that cooling of the eggs at the end of the day of laying is necessary for good hatching results, but that no improvement of hatchability was obtained by repeated gathering of eggs during the day and immediate chilling. It should be pointed out that the observations of Kato and Funahashi were made in the highly humid climate of a tropical country, whereas those of Heywang were gathered in the dry atmosphere of Arizona. Huston and Carmon (1958), working with New Hampshires, White Plymouth Rocks and White Leghorns, did not observe an adverse effect on hatchability when laying hens were kept at high environmental temperatures.

The effect of exposing eggs, prior to incubation, to temperatures below the freezing point of water has been studied by a number of investigators (Colesanti, 1874-1875; Pictet, 1893; Rabaud, 1899; Mancini, 1908; Mauro, 1922; Dougherty, 1926-1927; Jull, McCartney, and El-Ibiary, 1918). Not all these reports are in good agreement with each other, but it is evident that short chilling to somewhat below the freezing point does not impair the hatching power of eggs, and holding eggs at the freezing point for two days was found to have no effect on their hatchability (Mussel and Barcroft, 1924-1925; Funk, Forward and Kempster, 1950). When eggs are held at or below the freezing point for longer periods, hatchability deteriorates progressively, but brief exposure to very low temperatures may be tolerated without damage (Jull, McCartney and El-Ibiary, 1918). Eggs from genetically different stocks of fowl may show varying degrees of damage after storage at 32° F. for three to five days (Olsen, 1951).

North (1941) suggested that at high altitudes it may be desirable to raise the humidity during storage. Even at low altitudes North noted a slight improvement of hatching results by humidification of the storage room. Further observations on humidity requirements during storage were made by Cooney (1913), Funk and Forward (1951), and Schwarz (1956). The data of these authors do not provide convincing evidence for special humidity requirements during storage, except possibly at very high holding temperatures.

Reduced atmospheric pressure does not affect the hatching quality of eggs unless the pressure falls below 0.5 inches Hg. At such extremely low air pressure loss of water from the eggs becomes excessive and hatchability is reduced (Fraps, 1945).

Duration of storage, that is, age of the eggs at the beginning of incubation, appears to have a definite effect on length of the incubation
period. Funk (1934 a) reports the observations reproduced in Table 2. The results are shown graphically in Figure 13.

![Figure 13](image)

*Figure 13*

The effect of age (time of storage) of eggs on length of the incubation period (From Funk, 1934 a).

Kaufman (1938) made some interesting inquiries into the biological effects of egg storage on embryonic development. Her studies relate to eggs which had been stored at a temperature of 12° C. (53.6° F.) for 24, 28 and 34 days, respectively. Eggs of the same hens and of similar weight

<table>
<thead>
<tr>
<th>Test</th>
<th>Age of eggs Days</th>
<th>Range</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>1-7</td>
<td>492-523</td>
<td>512</td>
</tr>
<tr>
<td></td>
<td>8-14</td>
<td>498-546</td>
<td>522</td>
</tr>
<tr>
<td></td>
<td>15-17</td>
<td>516-546</td>
<td>530</td>
</tr>
<tr>
<td>II</td>
<td>1-7</td>
<td>498-540</td>
<td>513</td>
</tr>
<tr>
<td></td>
<td>8-14</td>
<td>504-540</td>
<td>518</td>
</tr>
<tr>
<td></td>
<td>15-21</td>
<td>510-540</td>
<td>527</td>
</tr>
</tbody>
</table>
were put into the incubator, one day after they had been laid, to serve as controls. It was found that after prolonged storage embryonic mortality was especially high in early stages of incubation. The relative water content of the albumen was decreased in stored eggs, whereas that of the yolk was increased. Embryos developing in eggs which had been stored showed a higher water content than those in control eggs. Body size (weight) of 7- and 14-day embryos was considerably reduced in the storage material, but the relative growth rate was higher, during the last two weeks of incubation, in embryos of stored eggs than in the controls. Kaufman confirmed Funk's observation that hatching is delayed in stored eggs, and found that the initiation of development is also delayed.

Ancel and Vintemberger (1925 a) had earlier made interesting studies concerning the effect of the age of eggs on embryonic development. Kaufman (1939) reported that changes in the catalase content of eggs occurred during storage, the concentration of this enzyme falling in the albumen and rising in the yolk. Catalase content, however, did not seem to have any relation to embryonic mortality (although this possibility is suggested by the work of Ogorodnyi, 1939 b). The injection of small amounts of glutathione into eggs during the second week of storage (total period of storage 30 days) reduced embryonic mortality and produced a corresponding rise in hatchability. This suggests that at least one of the noxious factors of storage results in a disturbance of the embryonic oxidation-reduction mechanism. In a later publication Kaufman (1948 a) confirmed the decrease in catalase content of the albumen after more than two weeks of storage, and also the beneficial effect of glutathione injections upon embryo mortality. No significant variations in yolk catalase were found. Albumen catalase content varied significantly between hens, but no relation to hatchability was observed after prolonged storage.

Turning of the eggs prior to incubation is unnecessary according to Jackson (1912), Waite (1919) and Funk (1934 a). Funk and Forward (1951) claimed that turning is beneficial when eggs are held longer than one week, but the reported differences are of doubtful statistical significance and at best very slight. Variations in oxygen and carbon dioxide concentration of the surrounding air during the pre-incubation period do not seem to affect embryo viability (Ancel, 1928, 1928-1929).

It is a common belief among poultrysten that jarring of eggs during shipment may seriously reduce their hatchability. Inquiries into this problem have been made by I. Geoffroy-Saint-Hilaire (1837), de Lavison (1862), Dareste (1883 b, 1885, 1891), Gowell (1902), Bouges (1923), Gutteridge (1930-1931), Knox and Olsen (1936) and Seck (1939). Dareste found in one instance that eggs which after shipment had been allowed to rest for two days produced normal embryos when incubated, whereas those which had been put into the incubator at once after having been received, gave a majority of abnormal embryos. Dareste, then, proceeded to ex-
pose eggs to vibration previous to incubation. With the machine which he used for his experiments the eggs were jarred 1,620 times per minute, the vertical displacement amounted to approximately 15 mm., and the time of exposure was varied from 15 to 60 minutes. The eggs were kept in a vertical position. It was found that normal embryos developed in most of the eggs if they were shaken with the large end up, but that abnormal development occurred in most cases if the position had been the reverse, i.e., small end up. The time of exposure to this treatment, within the limits stated above, did not seem to influence the results; nor did a period of rest after treatment prevent the occurrence of abnormal embryos in eggs which had been shaken with the small end upward.

Gutteridge (1930-1931) observed a definite lowering of hatchability due to railroad transportation of eggs. Knox and Olsen (1936) reported that the shipping of eggs tended to give rise to "tremulous air cells," i.e., a loosening of the inner shell membrane in the vicinity of the air cell, and that such eggs gave poor hatching results. These authors then proceeded to produce tremulous air cells by manual jarring of eggs (the eggs being held large end down during the procedure) and again obtained a definite lowering of hatchability. Seck (1939) found no adverse effect on hatchability from jarring, but he did not make a systematic and well-planned inquiry. Schwarz (1959), on the other hand, has provided a drastic illustration for the damage that can be done to hatchability by violent and prolonged vibrations exerted on eggs before or during early incubation.

Damage to membranes is not the only cause of reduced hatchability after the exposure of eggs to shaking. In experiments conducted at the Storrs Agricultural Experiment Station (Landauer and Baumann, 1943) it was found that the incidence of all types of commonly occurring malformations was increased after the shaking of eggs prior to incubation. The most common abnormality resulting from such treatment was rumplelessness, and this also was the most frequent defect in the control material. Position of the egg, duration of treatment, age of the eggs at the time of shaking and seasonal factors were all found to influence the results. A rest period between the end of shaking and the beginning of incubation was beneficial in reducing the incidence of rumplelessness, provided the period of shaking had not been too long. Critical periods were found during the first 24 hours of embryonic development during which the appearance of rumplelessness was induced more readily than at other times. Finally, it was observed that the individuality of the laying hen (her hereditary constitution) played an important role in determining the frequency with which rumplelessness occurred either sporadically or after shaking. Since rumplelessness (of the sporadic type) in the great majority of cases is (or associated factors are) a bar to hatching, it follows that all the agencies which have been enumerated do under the conditions of these experiments affect hatchability. The amount of damage done by treatments of this nature depends, of course, on the severity
of shaking; with a mild procedure the loss of hatchability may be slight (Randles and Romanoff, 1954). The cleaning of eggs by dry buffing appears not to interfere with subsequent hatchability (Shannon and Keenleyside, 1958; Shannon and Donnelly, 1959).

Sandvik (1958) exposed eggs prior to incubation to the gamma rays of a source of radioactive cobalt. He found that no egg receiving more than 1080 r hatched. In the group receiving between 930 and 1080 r hatching amounted to six percent of that of the controls. Following an exposure to 500-600 r the hatching rate was about 60 percent of the controls and after 270 r it was 96 percent. Experiments with still much smaller dosages were carried out by Samoletov, Kostin and Salgannik (1958) who used the radioactivity of uranium and thorium salts. They exposed eggs for 5 to 10 minutes to energies of 0.0001 to 0.0003 r/min. before setting and every third day thereafter, a total of seven times, and reported an improvement of hatching at all dosages (no statistical evaluation).

**During incubation**

There are three important physical factors which influence hatching quality during incubation: temperature, humidity, and turning of the eggs.

Maintenance of an optimal temperature is of prime importance for satisfactory hatching results. Embryonic development is initiated at temperatures far below the optimum, but only as the temperature approaches the correct level does development proceed to hatching. The older literature concerning the temperature range within which development of the chicken embryo takes place has been reviewed by Groebbels (1937). At the upper and lower limits of this range development is abnormal (Baudrimont and Martin-Saint-Ange, 1843, 1847; Tirelli, 1899, 1900; Féret, 1900; Alsop, 1918-1919; Harman, 1928; Deuchar, 1952). Philips and Brooks (1923) and Burke (1925) studied the optimum temperature requirements for incubation. Under natural incubation conditions (hens) and in still-air incubators, where heat is applied from above and where a temperature gradient exists with the maximum temperature at the top of the eggs, the optimum temperature at the upper level of the eggs is between 102° and 103° F. (38.9-39.4° C.). In forced-draft incubators with uniform heat distribution the optimum is between 99° and 100° F. (37.2-37.8° C.).

For a long time it was assumed, by analogy with conditions of natural incubation, that good results of artificial incubation depend on the existence of a temperature gradient, declining from upper to lower surface of the eggs. This view had for a time much influence on the design of incubators and was defended by Fischer as late as 1913, but is proven to be without foundation by the excellent performance of forced-draft machines.
Towards the end of the incubation period the temperature, according to Romanoff (1936a), can be lowered by as much as 5°F (3°C) without ill effects. According to Kalliourov (1936a) it is desirable to have the temperature somewhat higher at the beginning of incubation and somewhat lower at the end than during the remaining time. All statements with regard to optimum temperature, however, are subject to modification according to variations in relative humidity of the air.

Chicken embryos are fairly resistant to temporary cooling during incubation. In the experience of Taylor, Gunn and Moses (1933) cooling for 12 hours to about 70°F (21°C) reduced the hatch by only 3.4 percent. Kaufman (1934) found that exposure of eggs for 24 hours to a temperature below physiological zero, that is, below the temperature at which development takes place, did not produce harmful results. Both studies demonstrated that the resistance to cooling is definitely greater during the first week of incubation than during the last two weeks. The time of hatch is, of course, delayed by cooling, but, according to Kaufman, the delay is somewhat less than the period of cooling itself. This contention is supported by observations of Canevazzi (1940). Romanoff and Faber (1933) and Pritzker (1939) similarly observed the occurrence of compensations in growth rate under different temperature conditions. Thus, rapid growth in early developmental stages, on account of relatively high incubation temperatures, was followed later by somewhat retarded growth, although the incubation temperature remained unchanged; relatively low incubation temperature was, vice versa, responsible for retarded early growth and a compensatory higher growth rate toward the end of the incubation period. Compensatory adjustments of developmental rate have also been found after exposure of blastoderms to x-rays (Bless and Romanoff, 1943). Ancel (1958, 1959) and Ancel and Calame (1959) studied the effect of interrupting incubation for two and three days between the third and tenth day. They found as a consequence of such treatment malformations the nature of which, not unexpectedly, varied with the age of the embryos at the time incubation had been stopped.

Temporary cooling which does not produce an entire cessation of development (i.e., to points above physiological zero) may be more harmful than complete stoppage. According to Kaufman (1948b) it may lead to disharmonious growth of various organs, ending in death of the embryos.

Taylor, Gunn and Moses (1933) observed that the number of deformed and/or weak chicks was about doubled if, at any time during the incubation period, the current of electric incubators was interrupted for 12 hours with a consequent gradual drop of the temperature to 75°F (24°C). Keeping eggs at subnormal incubation temperature from the sixteenth day on resulted in delayed and irregular hatching, but the mortality was low (Romanoff and Faber, 1933). Grodzinski (1933, 1934) exposed eggs, previous to incubation, for four days to a temperature of
Such eggs, on account of complete suppression of the mesoderm, developed germinal discs without embryos or blood vessels. If eggs which had been incubated normally from 9 to 14 hours were exposed to $-3^\circ$ C. for 30 to 120 hours, a considerable mortality and many defective embryos resulted, but there were also some normal embryos. Chilling experiments of a more extreme nature were performed by Moreng and Bryant (1954 a and b, 1955). They exposed eggs during various stages of incubation for 75 to 125 minutes to a temperature of $-10^\circ$ F. ($-23^\circ$ C.). Resistance to this treatment was highest during the first two days of incubation and lowest towards the end of the incubation period. Few embryos survived such chilling at any stage if it lasted more than 75 minutes. Following less drastic cooling Moreng and Bryant (1956) found that resistance and survival declined sharply after the fourth day of incubation.

Periodic cooling (at room temperature) used to be a routine procedure of incubation. But it was shown by Stewart and Atwood (1909), Lamson (1917-1918), Lamson and Kirkpatrick (1918) and others that this is unnecessary with modern incubation equipment. It should be added, however, that Mashtaler (1948), Tret'yakov (1953, 1954) and other Russian investigators, referred to by Tret'yakov (1953), still claim advantages from regular periods of cooling.

In contrast to the relatively high resistance to temporary cooling, it is known by general experience that developing chicken embryos are very sensitive to even slight increases of the temperature above the optimum; in other words, the optimum is close to the upper limit above which normal development cannot take place.

As we have seen, development of the embryo will begin at temperatures far below the optimum. Such conditions are likely, however, to cause more than a simple slowing down of normal events. If incubation at low temperatures is continued beyond a certain time, irreparable damage may ensue. In experiments at Storrs it was observed, for instance, that after incubation (in a still-air incubator) for seven days at $93^\circ$ F., followed by optimal conditions (in a forced-draft incubator), all embryos died eventually. Similar observations have been reported by Harrison and Klein (1954).

Pritzker (1940 a and b; 1941) found that the level of temperature during incubation has some effect on the size of various organs, such as heart and liver, of newly hatched chicks and on chemical composition of the body. He suggested that it may be desirable to vary the temperature of incubation according to the temperature at which the hatched chicks are to be brooded. This statement clearly reflects the influence of Lysenko's biological dogmas and finds no support in general experience.

At an optimum temperature the developing chick appears to utilize to greatest advantage the food supplies available in the egg. This conclusion seems to follow from the finding of Romanoff (1936 a) that the
ratio of the weight of the chick at hatching to the original weight of the egg is highest at those temperatures which yield the best hatches.

The optimal temperature for incubation is not a constant, but varies with the humidity of the air. Humidity itself is of great importance for normal development of the chicken embryo (Baudrimont and Martin-Saint-Auge, 1843, 1847). Early observations on the importance of providing proper humidity conditions during incubation were due to Dryden (1907, 1908) and Lewis (1912). In work at Storrs Lamson and Kirkpatrick (1918) observed the effects of varying humidity on weight loss of eggs and on hatchability, the temperature being kept constant (Table 3).

Table 3

<table>
<thead>
<tr>
<th>Relative humidity</th>
<th>Loss of weight of eggs</th>
<th>Fertile eggs hatched</th>
</tr>
</thead>
<tbody>
<tr>
<td>70-80</td>
<td>5.3</td>
<td>45.5</td>
</tr>
<tr>
<td>60-70</td>
<td>8.7</td>
<td>62.1</td>
</tr>
<tr>
<td>50-60</td>
<td>9.8</td>
<td>69.3</td>
</tr>
<tr>
<td>40-50</td>
<td>10.2</td>
<td>68.6</td>
</tr>
<tr>
<td>30-40</td>
<td>11.5</td>
<td>68.6</td>
</tr>
<tr>
<td>20-30</td>
<td>14.5</td>
<td>60.6</td>
</tr>
<tr>
<td>15-20</td>
<td>17.4</td>
<td>48.0</td>
</tr>
</tbody>
</table>

The effect of incubation temperature on percentage of fertile eggs hatched. Relative humidity 60 percent, oxygen 21 percent, carbon dioxide below 0.5 percent. (From Barott, 1937.)
According to Barott (1937) the humidity determinations of Lamson and Kirkpatrick should be increased by 5 to 15 percent on account of inadequacies of their technique. Similar results were reported by Palmer and Dykes (1927).

Low humidity causes excessive evaporation of water, while high humidity prevents the evaporation of sufficient amounts of water from eggs. In both cases hatchability is reduced. Excessive humidity towards the end of the incubation period seems likely to cause a considerable increase in embryo mortality (Romanoff, 1929; 1930 a). A lowering of humidity, with constant temperature, lengthens the time of development, and the chicks hatching under such conditions are smaller than normal (Romanoff, 1930 a; Townsley, 1931). Observations by Orlov (1941) and others indicate that excessive and insufficient amounts of humidity have similar effects on the rate of embryonic mortality, embryo growth and time of hatch.

![Figure 15](image)

The effect of relative humidity at two different incubation temperatures on percentage of fertile eggs hatched. Oxygen 21 percent, carbon dioxide below 0.5 percent. (From Barott, 1937).
been shown by Marshall and Cruickshank (1938) that small eggs lose weight more rapidly during incubation than do large ones. It is not surprising, therefore, that for good hatching the eggs of Bantam and Jungle fowl require higher humidity or lower temperature toward the end of incubation than the eggs of larger breeds.

Table 4

<table>
<thead>
<tr>
<th></th>
<th>Day of hatching</th>
<th>7 days prior to hatching</th>
<th>14 days prior to hatching</th>
<th>21 days of incubation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Correlation coefficient</td>
<td>.31</td>
<td>.55</td>
<td>.69</td>
<td>.68</td>
</tr>
<tr>
<td>Standard error</td>
<td>.18</td>
<td>.14</td>
<td>.10</td>
<td>.11</td>
</tr>
</tbody>
</table>

Texture of the shell, unquestionably, plays an important role in rate of water evaporation, and the optimum humidity may be influenced thereby. The existence of genetic differences in shell texture and in rate of water loss will be discussed later.

High altitudes may call for minor modifications of incubation technique, presumably in order to correct for an increased rate of water evaporation from the eggs (as a consequence of low atmospheric humidity, Aggazzoti, 1913) and for reduced oxygen pressure. According to North (1941) a quarter of a degree rise in temperature and a 3 percent increase in relative humidity will bring about the compensations necessary at an altitude of 7000 feet. It may be doubted, however, that the significance of such slight variations is securely established. In a subsequent publication North (1944) recommended lowering of the temperature during the hatching period and adjustments in the rate of air flow. Earlier investigations by Giacomini (1894) have a bearing on these problems. Thompson (1952) made a searching analysis of humidity conditions as they affect incubation at high altitudes. He reached the conclusion that dryness of the shell pores becomes, toward the end of incubation, a critical factor at all altitudes, and that – in as much as evaporation of water from eggs varies with speed of air movement, absolute humidity and barometric pressure – it becomes ever more important at increasing altitudes to make provisions for sufficient evaporation during late stages of incubation, i.e. to guard against excessive humidity. Kohn (1930) found no effect of high altitude on hatchability, but recent experiments by Ellis and Morris (1947), made at an altitude of 7200 feet, led to the conclusion that the introduction of supplementary oxygen into the incubators over the entire period of development improved hatches by about 18 percent. This was confirmed by Meshew (1949) and Stephenson (1950). Meshew claimed that for optimum hatches at high altitudes the concen-
Particularly careful observations concerning the influence of temperature and humidity on development and hatching were made by Barott (1937) under still-air conditions. His results with regard to the effects of temperature, other factors being kept constant, are graphically illustrated in Figure 14, whereas Figure 15 shows the effect of varying degrees of relative humidity at two different levels of incubation temperature. Best hatches were obtained with 58% of humidity at 102°F. (38.9°C.) and with 61% humidity at 100°F. (37.8°C.).

As is evident from the preceding discussion, there is a definite relation between temperature and humidity requirements. Townsley (1930, 1931), for instance, reports that a relative humidity of 70 percent with 98°F. (36.7°C.) temperature resulted in about the same hatchability as did a relative humidity of 56 percent with 99°F. (37.2°C.) temperature. In other words, as the percentage of humidity is increased, the temperature in a general way needs to be decreased for optimal results. This seems to hold, at any rate, if humidity and temperature are kept at the same level throughout the incubation period. The exact relationship between these two factors, unfortunately, has not been determined as yet and the need for further studies has rightly been emphasized by Romijn (1950). It must be kept in mind, however, that conditions during one part of the incubation period determine, within limits, the beneficial or detrimental nature of certain situations during another part, e.g., high humidity toward hatching time will be necessary if sufficient evaporation from the eggs had occurred previously, but will be detrimental if the humidity was high at all times.

It is of interest to note that according to Callenbach and Hiller (1933) and Romanoff (1934) pheasant eggs require a higher relative humidity at the beginning than towards the end of incubation, whereas the reverse appears to be true for quail and chicken eggs, even though all these different species belong to the family Phasianidae. It should be noted, however, that Otryganev and Kuchkovskaya (1941) and Otryganev (1941 a) obtained good hatchability after relatively high levels of temperature and humidity during the first five days of incubation of chicken eggs.

The effect of sub-optimal humidity on embryo survival is illustrated by coefficients of correlation, calculated by Cave and Jones (1925), between degree of relative humidity of the air surrounding an incubator and the percentage of eggs hatched (Table 4). No correlation would have been found if humidity within the incubators had been optimal.

The most favorable conditions of temperature and humidity probably are, within fairly narrow limits, the same for different breeds of fowl. It is known from practical experience, however, though no exact studies have been made, that the eggs of Bantam fowl differ from those of the large breeds in their humidity and temperature requirements. This is presumably due to the fact that with decreasing egg size the shell surface increases in proportion to egg content, and it has actually
tration of carbon dioxide as well as that of oxygen should be increased. Wilgus and Sadler (1954) obtained, at an altitude of 5000 feet, optimal hatching with an oxygen tension of 23 to 23.5 percent and a carbon dioxide concentration of about 0.5 percent. They observed also, however, that there was a marked variance in resistance to hypoxia between progenies of different mothers. Davis (1955) confirmed the beneficial effect of supplementary oxygen at an altitude of 7200 feet. The rates of improvement were of similar magnitude for the eggs of mothers which, in the absence of supplementary oxygen, had shown differences in hatchability. Davis, in addition, recorded the important observation that in the absence of supplementary oxygen a gradual improvement of hatchability occurred as a consequence of natural selection. Buss (1956) found, in observations made at an altitude of 5000 feet, that “embryos from poor hatching hens have retarded hemoglobin development.” The allantoic blood of such embryos gave significantly lower values on the thirteenth and fourteenth days of incubation.

Tret’yakova (1941) made interesting studies relative to the influence of different levels of humidity on physico-chemical properties of the albumen and yolk of developing eggs (refractive index, buffer value, electrical conductivity, resilience, surface tension, hydrogen-ion concentration). It may be assumed that these effects reflect metabolic changes in embryonic development in response to variations in the external environment.

The position of eggs and turning are further important factors during incubation. It was recognized early that proper orientation, viz. large end up, is essential for good hatchability (Lihrzik, 1858). Byrcky and Olsen (1930-1931) made observations relative to the effect of incubating eggs with the small end upward. They found that in this case an increased percentage of embryos occupy a position with the head in the small end of the egg, a barrier to hatching. This change in position is obviously due to gravity. Yet an appreciable proportion of embryos remains in their normal position. If now, in addition to keeping the eggs with the small end upward, the shell at the large end (over the air space) is covered with paraffin, the percentage of embryos which have their head in the small end of the egg becomes much increased. The explanation seems to be that, as long as the shell over the air space is in a normal condition, many embryos remain with their heads towards this source of air, while after the shell is sealed over the air space, the combined effect of gravity and “air-hunger” induces the embryos to turn. The general question of malpositions will be discussed in a later chapter.

According to Olsen (1930) sitting hens move their eggs 96 times in 24 hours. Kuiper and Ubbels (1951) found a frequency of only 24 times during the same period. This is, of course, done in a hit-or-miss fashion and cannot be directly compared with the more efficient mechanical turning devices employed in incubators. Very few eggs hatch if no turning whatever is done (Eycleshymer, 1907). In trials at the Storrs
Agricultural Experiment Station Lamson and Kirkpatrick (1918) compared the turning of eggs twice and five times daily in still-air incubators. The average hatchability in nine tests amounted to 55.4 percent when the eggs were turned twice and to 61.1 percent when turned five times. This is not a very striking difference, but its significance has been attested by experiments of other investigators. Chattcock (1925) found that eggs turned four to five times daily hatched from 6 to 10 percent better than those turned only twice; Insko and Martin (1933) reported that turning four times always resulted in better hatchability than turning only twice (see also Hannas, 1919-1920). A similar improvement was observed by Kuiper and Ubbels (1951) and Ubbels (1953) in comparing the results of turning 3 and 24 times. Kaltofen and Ubbels (1953) and Kaltofen (1955, also 1958) observed a slight but significant gain in hatchability (about 3 percent) from turning 24 times as compared with 8 times. Hatchability in these tests amounted to 78.0 and 74.7 percent, respectively; it seems unlikely that under otherwise satisfactory incubation conditions an appreciable improvement of hatchability can be expected from turning more than 8 times during 24 hours (Kotliarov, 1936 b).

Olsen and Byerly (1936) compared the results of turning eggs three times daily in a hit-or-miss fashion with those obtained by moving the eggs 48 and 96 times a day (by rotating them back and forth about their long axes and tilting them up and down about their short axes), and found in the latter cases an improvement of hatchability by 6.8 and 7.0 percent, respectively, in two trials. Mechanical turning of the same type, carried out but a few times daily, might have given the same results. That this is so was, in fact, demonstrated by experiments on multiple-plane turning (Funk and Forward, 1952, 1960). Olsen and Byerly justly pointed out, however, that gentleness of turning is a factor to be considered. Funk and Forward (1953) found that eggs hatch better when the incubator trays are turned through angles of 40° or 45° rather than 30°; hatching appeared to be slightly better following turning to 45°, as compared with 40°, but the differences were not evaluated statistically. Turning at greater angles did not seem to improve hatchability.

The period of incubation during which turning of the eggs is required and the physiological significance of turning have not been fully elucidated. It was recognized early (Card, 1926) that turning is most necessary during the first week of incubation. According to New (1957) turning the eggs between the fourth and seventh day of incubation gives a hatchability similar to that of eggs turned throughout the incubation period; yet, Insko and Martin (1933) had reported earlier that turning more than twice a day apparently reduced embryo mortality during the first three days of incubation. According to Olsen and Byerly (1936) frequent turning in only one direction leads to high embryo mortality (causes: rupture of yolk sac; disruption of chorion, allantois and shell membrane; twisting of chalazae; rupture of blood vessels). New (1957) believes that preventing an abnormal adhesion between chorion and
shell membrane is the principal function of turning. Randles and Romanoff (1949), on the other hand, had suggested earlier that turning is necessary for normal functioning of the amnion.

Except for observations at high altitudes, we have at present only very incomplete knowledge concerning the possible effects of increased and reduced atmospheric pressure on development of the chicken embryo. Cunningham (1927) has presented evidence suggesting that as a consequence of extended periods of increased air pressure embryonic growth proceeds faster than normally. This acceleration of growth is not due to a change in the rate of water lost by eggs during incubation (Cunningham, 1938). More recent studies by Nelsen (1946 a and b, 1947, 1955) produced no evidence for an acceleration of development following a 24-hours exposure of eggs to increased pressure. Above a certain level of tolerance, pressure becomes progressively more harmful. Reduced pressure (165 mm.) is responsible for the occurrence of malformations (Becher, 1939).

Jarring and vibration may interfere with normal development and may, thereby, reduce hatchability. Etienne Geoffroy-Saint-Hilaire (1825) was the first to observe that shaking of eggs during early stages of incubation is likely to lead to the appearance of various types of malformations. Later experiments were performed by Stiles and Watson (1937), and more extensive studies were made by Olsen and Byerly (1938). The latter authors exposed incubating eggs to three different types of mechanical disturbances. In a first series of experiments eggs were put into a shaking machine in which the eggs received 229 oscillations per minute through distances of 3 inches. The eggs were treated in the horizontal or the vertical position. The tests extended from the beginning of incubation to the twentieth day. Mortality after treatment was greatest when the eggs had been shaken parallel to their short axis: embryos between 4 and 13 days were especially susceptible. Most of the mortality attributable to shaking occurred within 72 hours after treatment, and the greatest part of this mortality was due to rupture of the yolk sac or to hemorrhage. There was little or no delayed mortality and no apparent teratogenic response to treatment at any point within the incubation period.

In a second series of experiments Olsen and Byerly centrifuged eggs with either the blunt or the pointed end foremost in the centrifuge cup. Centrifuging lasted for one minute. The average force exerted on the eggs amounted to 710 dynes. The results were similar to those of the first series. Those eggs which had had the large end in the centrifuge cup showed high embryo mortality, especially between the fourth and fifteenth day of incubation. In eggs centrifuged with the small end in the centrifuge cup embryo mortality was much less pronounced. In a third series of experiments eggs were jarred by striking either the blunt or the pointed end against the operator’s hand. High embryo mortality resulted from both kinds of treatment, but it was more extreme among those eggs
in which force was applied to the large end. Incubating eggs which had been rocked by near-by dynamite blasts also showed high subsequent mortality. On the other hand, Fronda (1938) found that an earthquake of intensity VI - VII had no detrimental effect on hatchability, irrespective of whether the eggs at the time of the earthquake were in the first, second or third week of incubation. Sound intensities of 96 decibels had no measurable effect on hatchability (Stadelman, 1958). When cocks were exposed to intermittent noises (intensity 120 decibels) and their semen was used for artificial insemination, Kosin (1958, a) found a significant lowering of hatchability in one trial, but not in a second one. It is well recognized, of course, that "significant" differences may arise by chance.

Barott (1937) observed that, with otherwise constant conditions, velocities of air movement past the eggs ranging between 10 and 75 cm. per minute did not lead to detectable differences in hatchability. According to Konoplev (1954), however, an air velocity of approximately 2 meters/sec. is optimal, as tested during the first 48 hours of incubation, and in combination with a temperature of about 38.4°C (101°F.) and a humidity of about 80 percent.

THE CHEMICAL ENVIRONMENT DURING INCUBATION

At one time it was believed that developing embryos are independent of the surrounding air (Erman, 1818), but closer observation soon showed that an adequate supply of oxygen is imperative for successful hatching (Schwann, 1834). It is equally necessary to remove from incubators excessive amounts of carbon dioxide. Efficient ventilation will take care of both these needs.

Baudrimont and Martin-Saint-Ange (1843, 1847, 1851) made important early inquiries into the chemical and physical conditions of incubation. After further preliminary experiments by Brigham (1901), Edmond (1907), Dryden (1907), Thom (1908) and Graham, Day, Thom, Harcourt and Fulmer (1908), Lamson and Edmond (1914) made a careful study at Storrs concerning the amount of carbon dioxide found under sitting hens and in incubators. They observed that chicken embryos can withstand wide variations of carbon dioxide concentration, but that for best results not more than 60 parts of carbon dioxide should be present in 10,000 parts of air. If the carbon dioxide concentration exceeded 150 parts in 10,000, hatchability decreased definitely, and with more than 200 parts present, asphyxiation of the embryos occurred. Romanoff (1930 b) found similarly that carbon dioxide concentration above 1 percent resulted in slow growth, formation of abnormalities, and early death of the embryo (see also Barott, 1937).

Barott (1937) studied the role which varying oxygen concentrations play in hatchability. Preliminary observations had been made by Preyer (1885), Wesselkin (1913) and Riddle (1924). The results of
Barott's investigations are shown in Figure 16. It can be seen from this graph that best hatches were obtained with 21 percent of oxygen.

The effects of varying concentrations of oxygen and carbon dioxide during the first four days of development have been observed in detail and with great care by Taylor, Sjodin and Gunn (1956). Their principal results, in their own words, were as follows: "Normal hatchability resulted from CO₂ levels ranging from approximately zero to one percent. At concentrations of 1.1 percent or higher, hatchability was significantly reduced in direct proportion to the increase in CO₂ levels. No level of CO₂ consistently produced significantly better hatchability than the control incubators operating at 0.05 to 0.12 percent CO₂. Reduction of the period of exposure to the first 24 or 48 hours of incubation reduced the relative decrease in hatchability associated with high CO₂ levels, but failed to produce any improvement in hatchability over control conditions. O₂ levels below 18 percent tended to reduce hatchability proportionately to the decrease in O₂ concentration. Levels of 18 to 50 percent O₂ produced normal hatchability. Increasing O₂ concentration to 75 percent or higher reduced hatchability significantly. The early chick embryo is very susceptible to conditions of reduced O₂ supply or high concentrations of carbon dioxide; it is very resistant to extremely high concentrations of oxygen. -Commercial incubators tested had O₂ and CO₂ levels well within the range of tolerance of the early chick embryo for optimal hatching results." These observations put in doubt earlier claims that the presence of small amounts of carbon dioxide is necessary during early development (Romanoff, 1930 b; Romanoff and Romanoff,
that chicken embryos need little, if any, oxygen from outside the eggs during the first two days of incubation (Portmann and Jedlin, 1936) and that high concentrations of oxygen (31%) during the first five days of incubation improve subsequent development and hatching (Cruz and Romanoff, 1944). It is presumably true, however, that chicken embryos are not harmed if eggs are kept in pure carbon dioxide prior to incubation (Ancel, 1928) and that during the first few hours of incubation the oxygen requirements are minimal (Nelsen, 1958).—The special conditions obtaining at high altitudes have already been discussed (p. 61-62). For extensive literature on the teratogenic effects of low oxygen tension during the early stages of incubation the reader is referred to Landauer (1957, a) and Grabowski and Paar (1959).

**EGG TRAITS WHICH INFLUENCE HATCHABILITY**

**Size**

Any appreciable degree of relation between egg size and hatchability should be of immediate practical importance since it would thereby become possible to select for incubation those eggs which, because of their size, promise best hatching results. It is not surprising, therefore, that this problem has been studied repeatedly.

*Benjamin* (1920), working with White Leghorns, did not find a definite relationship between egg size and hatchability, but *Dunn* (1922), using inbred White Leghorn pullets belonging to the flock of the Storrs Agricultural Experiment Station, secured positive results. Dwarf and double-yolk eggs were excluded from this analysis. When the eggs were distributed in two classes according to weight, the following averages were obtained (Table 5):

<table>
<thead>
<tr>
<th>Egg weight (g)</th>
<th>Number of fertile eggs</th>
<th>Fertile eggs hatched (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>52.5-59.9</td>
<td>290</td>
<td>62.06 ± 2.85</td>
</tr>
<tr>
<td>60.0-73.9</td>
<td>93</td>
<td>44.09 ± 5.14</td>
</tr>
</tbody>
</table>

The difference between the hatching averages of the two groups amounted to 17.97 ± 5.88 percent; it is three times its standard error and clearly significant. The mean weight of all eggs was 55.39 ± 0.21 g. Egg weight which was considerably above the mean appeared to reduce the hatching quality. The results from hen eggs pointed to the same conclusion as those from pullet eggs, though in this case, presumably on account of small numbers, the difference was not significant. Closer analysis showed, however, that deviations from mean egg weight of the individual, rather than deviation from the flock mean, influenced hatch-
ability. There was no correlation between mean egg weight of individual birds and mean hatchability percentage for the same individuals. Regardless of mean egg weight of the flock, it was true for each individual that those eggs tended to hatch less well which were above the mean of the eggs of the particular bird. This situation clearly indicates that physiological factors connected with egg formation are, at least in part, responsible for the reduced hatching quality of eggs above the mean weight. Czannecka (1954), Axelsson (1954) and Coles (1956b) have also emphasized that adverse effects on hatchability are related to deviations of egg weight from the mean for the individual laying hen rather than to variation in mean egg weight of pens or flocks. This important fact should be kept in mind in evaluating the reports to be discussed below.

Halbersleben and Mussehl (1921-1922) found likewise that abnormally large eggs hatch less well than medium-sized ones. Their observations suggest that the same holds, if less strikingly, for abnormally small eggs. Shibata and Murata (1936) similarly reported that heavy eggs tend to show a reduced rate of hatching. Full and Haynes (1925) gave data obtained from twenty-four Barred Plymouth Rock pullets (Table 6). Again, the largest eggs showed the poorest hatching results, though in this case, presumably due to the smallness of the sample, the difference in hatchability between the large and the medium-weight class was not significant. Contrary to previous studies, the eggs in the smallest weight class showed the highest average hatchability, though again the difference was not significant. Mean weight of those eggs in which embryos died either early or late in incubation did not differ significantly from the mean weight of the eggs that hatched. The authors concluded that in “normal” eggs, weight has no bearing on hatching quality. If low variability of egg weight is considered normal, this conclusion seems justified.

### Table 6

<table>
<thead>
<tr>
<th>Egg weight (g)</th>
<th>Number of fertile eggs</th>
<th>Fertile eggs hatched (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>40.00-52.99</td>
<td>123</td>
<td>67.48 ± 3.02</td>
</tr>
<tr>
<td>53.00-59.99</td>
<td>992</td>
<td>65.32 ± 2.00</td>
</tr>
<tr>
<td>60.00-66.99</td>
<td>23</td>
<td>52.17 ± 14.03</td>
</tr>
</tbody>
</table>

The differences in the material analyzed by Dunn and by Full and Haynes are strikingly shown by the coefficients of variation of egg weight. In Dunn’s material v amounted to 8.92 percent, in that of Full and Haynes v was only 4.20 percent. In eggs of very uniform weight and with only rare extreme variants it is obviously difficult to determine the effect of size factors, and it is not surprising that no significant differences with regard to the effect of weight on hatchability should emerge from such data. Similar doubts hold for the negative findings of Hays and Sumbardo (1926-1927). The eggs used for their study came from a Rhode
Island Red family bred for high hatchability, and it seems likely that egg size was much more uniform in this material than it would be in a random population.

Further data on this problem were secured by Axelsson (1932 a). White Leghorns, Rhode Island Reds, Barnevelders, and the F₁ and F₂ generations from crosses of these breeds were used for study. All data came from one-year-old birds. Within each group the mean weight of those eggs from which chicks hatched did not differ significantly from the mean weight of all eggs put into the incubator, but for the total of all groups mean weight of the eggs which produced hatched chicks was lower (though not significantly so) than mean weight of all eggs. However, within the groups it was found in six out of seven cases that the standard deviation of the distribution was greater for all eggs incubated than it was for those from which chicks hatched. Taking the eggs of all groups together the difference amounted to 0.37 ± 0.079g. This difference is 4.68 times its error. The results indicate that medium-sized eggs hatched best. This conclusion is confirmed if for each of the breeds and crosses the percentage hatch of eggs weighing 51 to 60 g. is compared with the hatchability of all other eggs, that is, the smaller and the larger ones. In six out of seven groups the eggs weighing 51 to 60 g. yielded better hatches than the smaller and the larger eggs taken together. For the whole material the results are shown in Table 7.

The difference in hatchability between these two groups amounted to 5.03 times its standard error, leaving no doubt about its statistical significance. Figure 17 gives the regression of hatchling percentage on egg weight for this material, based on a total of 4,507 eggs. It can be seen that the maximum percentage hatch (viz. 65.6 percent) occurred at 56.4 g.

<table>
<thead>
<tr>
<th>Egg Weight 51-60 g.</th>
<th>Egg weight less than 50 g. or more than 60 g.</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>Hatch %</td>
</tr>
<tr>
<td>3193</td>
<td>66.6 ± 0.82</td>
</tr>
</tbody>
</table>

The difference in hatchability between these two groups amounted to 5.03 times its standard error, leaving no doubt about its statistical significance. Figure 17 gives the regression of hatchling percentage on egg weight for this material, based on a total of 4,507 eggs. It can be seen that the maximum percentage hatch (viz. 65.6 percent) occurred at 56.4 g.

There is general agreement with regard to the reduced hatching quality of very large eggs. Further evidence for this conclusion was presented by Funk (1934 a), Warren (1934) and Scott and Warren (1941). On the other hand, some doubt seems still to exist as to whether or not a
similar, if less pronounced, reduction of hatching quality is typical of eggs below mean weight. Warren, using White Leghorn and Rhode Island Red material, presented the results shown in Table 8. There can be little doubt that the coefficients, though small, are statistically significant, suggesting that in this material hatchability decreased with increasing egg size. This is confirmed by a separate tabulation for the Rhode Island Red group (Table 9).

Table 8

<table>
<thead>
<tr>
<th>Breed</th>
<th>Number of birds</th>
<th>Egg size</th>
<th>Hatchability of fertile eggs %</th>
<th>Coefficient of correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean g.</td>
<td>σ g.</td>
<td>Mean</td>
</tr>
<tr>
<td>White Leghorn</td>
<td>222</td>
<td>53.7</td>
<td>3.7</td>
<td>71.5</td>
</tr>
<tr>
<td>Rhode Island Red</td>
<td>161</td>
<td>56.5</td>
<td>4.6</td>
<td>58.0</td>
</tr>
</tbody>
</table>

Table 9

<table>
<thead>
<tr>
<th>Size group of eggs</th>
<th>Range of egg weight g.</th>
<th>Hatchability of fertile eggs in %</th>
<th>Difference between first and last group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small</td>
<td>44-51.9</td>
<td>69.1±3.0</td>
<td></td>
</tr>
<tr>
<td>Medium</td>
<td>52-57.9</td>
<td>59.4</td>
<td></td>
</tr>
<tr>
<td>Large</td>
<td>58-67.0</td>
<td>51.8±2.4</td>
<td>17.3±3.9</td>
</tr>
</tbody>
</table>

Figure 17

The regression of hatching percentage on weight of eggs. X: egg weight, Y: hatching percentage (From Axelsson, 1932 a).
These results are similar to those reported by Jull and Haynes; they suggest, much more definitely than the data given by the latter authors, that small egg weight may be associated with high hatching quality. Additional evidence for this conclusion has been published by Obenko and Antakov (1956).

Godfrey (1936) made an interesting analysis of hatchability as influenced by egg size. He used the eggs of 367 birds belonging to various breeds (100 Rhode Island Reds, 56 White Wyandottes, 53 Light Sussex, 24 White Plymouth Rocks, 17 Jersey Black Giants, 14 Barred Plymouth Rocks, 7 White Leghorns, and 96 Jersey Black Giant x White Leghorn crossbreds). The analysis of covariance of egg weight and hatchability led to the conclusion that egg weight does not have an appreciable linear effect on hatchability. On the other hand, the curvilinear trend (Figure 18) was significant. There was a rapid increase of hatchability from egg weight 46 g. (hatchability about 51 percent) to 50 g. (hatchability about 76 percent); within the 50 to 58 g. egg-weight range hatchability remained nearly constant (near 75 percent), while above 58 g. it declined steeply.

Wilhelm (1939) found in White Leghorn material a correlation of $0.259 \pm 0.089$ between egg weight and hatchability. We know now, however, that such correlation coefficients are of doubtful value since the relation of egg weight to hatchability obviously is non-linear. Scott and Warren (1941) confirmed with White Leghorn stock that large egg size tends to reduce hatchability, but with regard to small egg size the evidence was again conflicting; the groups of females laying the smallest eggs gave the highest average hatchability in one year and the lowest in another. Hébert and Laugier (1943) presented data in support of the conclusion that hatchability is reduced in excessively small as well as in very large

![Figure 18](image)

**Figure 18**

Relationship between percentage hatchability and average egg weight per bird, based on the records of 367 hens and of one hatching season. (From Godfrey, 1936).
eggs. Their results are not acceptable, however, since they are based on the total number of eggs rather than the number of fertile eggs used in their tests; for, a relation might well exist between egg size and fertility. In the material of Penionshkevich (1945) the largest and smallest eggs hatched less well than those nearer the center of the weight distribution. The same is true for data presented by Skoglund, Tomhave and Momford (1948), Kumanov (1948) and Lerner and Gunns (1952).

Scott and Warren (1941) found that eggs in which the proportion of white to yolk is approximately 2:1 have a better chance of hatching than have eggs with wider or narrower ratios (see also Penionshkevitsch, 1936). They observed, further, that eggs which are large in proportion to the body weight of the hen producing them tend to hatch poorly. This latter relationship presumably represents but the composite result of a positive correlation between body size and egg size on the one hand and of the effect of egg size upon hatchability on the other. Smith, Abbott and Jones (1958) confirmed, by experimental X-ray treatments, that eggs with a reduced relative content of albumen hatched poorly.

Considering all available information, it can be said definitely that large egg size decreases hatchability somewhat. With regard to small egg size the evidence is conflicting. It appears certain that in some instances small egg size also reduces hatchability to some extent, while other data do not show such an effect.

Lerner and Gunns (1952) have justly pointed out that many of the discrepancies in the reports bearing on the relations between egg size and hatchability are the result of imperfections and inadequacies of the data of various authors. From their own careful analysis Lerner and Gunns drew the following conclusions:

"1. The reproductive fitness of birds laying eggs of intermediate weight is greater than that of birds characterized by smaller or larger egg weight."

"2. In flocks where some artificial selection for large egg size is practiced, maximum hatchability is obtained in eggs somewhat below the mean egg size characteristic for the time of setting."

"3. The optimum egg size for hatching may be expected to vary from population to population, and particularly from season to season within a given flock as the mean egg size varies."

"4. Hatchability (or reproductive fitness in general), while related to the egg size of each individual egg (in the sense of Dunn, 1922) is nevertheless also a property of the bird's genotype for egg weight (in the manner established by Funk, 1934). The first of these relationships has no doubt a physiological significance, the second forms an aspect of genetic homeostasis."

It is evident that we are dealing with a very complex situation. Some factors have a direct bearing on the relations between egg size and
hatchability. This is true, for instance, with regard to the effect of surface area on rate of water loss; it may also apply to the quantitative relations of albumen and yolk, as these vary with size of eggs. Other factors, of a hereditary or environmental nature, influence egg size, and thereby hatchability, in an indirect way. This is presumably true, for instance, for current egg production (to be discussed subsequently).

According to Byerly (1934) egg weight is an important cause of variation in length of the incubation period, the heavier eggs generally requiring a longer time for incubation than the lighter ones. Hays (1941) failed to find such an association, but his comparison was only between hens, and the relationship of weight to hatchability for the eggs of individual hens was not taken into account.

McNally and Byerly (1936) reported that in most eggs the heavier they were the more advanced was embryo development after 48 hours of incubation (as judged by number of somites), but that there was a tendency for small eggs to contain embryos which are developed further than would be predicted from their weight (Figure 19). It was shown by these authors that hatchability is somewhat increased when the embryo is at a more advanced stage at the end of 48 hours of incubation, but

![Figure 19](image-url)

**Figure 19**

Relationship between average deviation from average somite number after 48 hours of incubation and average deviation from average egg weight (From McNally and Byerly, 1936).
that it declines rapidly beyond an optimum (Figure 25, p. 123). The slightly reduced hatchability of eggs below the mean weight, and the more definitely reduced hatching quality of eggs above the mean weight, can both be referred to the association between egg weight and the degree of development already attained at the time of laying or reached soon after incubation begins. Scott and Warren (1936), however, found no difference in degree of embryonic development between the first and second eggs of the clutch of individual hens, though the first egg of the clutch is usually larger.

In connection with this discussion of the influence of egg size on hatchability it should be noted that double-yolked eggs rarely, if ever, produce hatched chicks (Broca, 1862), although, as a curiosity, it is worth noting that Claude Bernard (1850), the famous physiologist, gave an account (second-hand?) of 18 vigorous chicks, hatched from nine double-yolked eggs, all of which had been laid by one hen.

Shape

Benjamin (1920), working with White Leghorn eggs, and Jull and Haynes (1925), analyzing data from Barred Plymouth Rock and Rhode Island Red eggs, failed to find any influence of the shape of eggs on hatchability. Negative results with regard to the relation of egg shape to hatchability were also reported by Hays and Sumbardo (1926-1927) and by Skoglund (1951). While there is no reason to question the correctness of this conclusion as far as the ordinary range of variability in length and breadth is concerned, some doubt remains with regard to the extreme variants. Very long and narrow eggs (low shape index) in common experience rarely yield hatched chicks. The fate of such extreme and relatively rare variants may easily escape attention if a large body of data is analyzed statistically. In experiments with White Leghorn stock Olsen and Haynes (1949) found the following hatching percentages: 47 misshapen eggs 48.9%, 34 eggs with loose air cells 32.4%, 317 eggs with misplaced air cells 68.1%, 2494 control eggs 87.2% (see also Anghi, 1941).

Pearl and Surface (1914) made a comparison of the variability in length and breadth of chicken eggs and eggs of wild birds (rook, English sparrow, etc.). They found the coefficients of variation shown in Table 10.

<table>
<thead>
<tr>
<th></th>
<th>Egg length</th>
<th>Egg breadth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average for 12 wild species (unweighted mean)</td>
<td>4.48</td>
<td>2.98</td>
</tr>
<tr>
<td>Domestic fowl</td>
<td>4.29</td>
<td>3.79</td>
</tr>
</tbody>
</table>

The differences between wild birds and domestic fowl were not statistically significant, but the fact that the eggs of different species of
wild birds similarly pointed to a greater variability in length and a smaller one in breadth than is found among chicken eggs would seem to make a reinvestigation of this problem well worth while. Pearl and Surface concluded from their data that it is not essential to the survival of a wild bird that its eggs should be less variable in shape than those of domestic fowl.

**Shell characters**

The most obvious significance of the shell is that of providing the embryo with protection against external injuries of various kinds. In addition to this, however, we know that the shell plays an important role as a source of calcium for the developing embryo (the mammillary membrane of the shell being, according to Sajner 1955, its principal source of calcium), and as the medium through which gaseous exchange takes place between the egg contents and the surrounding air. It is to be expected from a knowledge of these facts that structural changes in the shell are reflected in the hatching quality of eggs.

Between thickness of the shell and hatchability Wilhelm (1939) found in White Leghorn material a correlation of $0.164 \pm 0.016$. A low, but significant, positive correlation was reported also by Leydolph and Schneiderhöhn (1952). Voitellier (1936) had earlier made the statement, without supporting data, that thickness of the shell plays a role in the hatchability of eggs. Rauch and Steinke (1953) in a study of the relations between thickness of egg shell and hatchability found on a material of 1434 eggs of Brown Leghorn hens, the data reproduced in Table 11. Their results show clearly that there is a shell diameter that is optimal for good hatching results. Data suggestive of similar relations were published by Znojilova, Zoufaly and Páltková (1959). In view of these data it is astonishing that Rudy and Marble (1939) could not find a significant correlation between weight of the dry shell and hatchability.

<table>
<thead>
<tr>
<th>Shell thickness in mm</th>
<th>0.18-0.22</th>
<th>0.22-0.26</th>
<th>0.26-0.30</th>
<th>0.30-0.34</th>
<th>0.34-0.38</th>
<th>0.38-0.42</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of eggs</td>
<td>18</td>
<td>168</td>
<td>668</td>
<td>492</td>
<td>76</td>
<td>12</td>
</tr>
<tr>
<td>Percent hatch</td>
<td>61</td>
<td>79</td>
<td>88</td>
<td>80</td>
<td>58</td>
<td>50</td>
</tr>
</tbody>
</table>

During storage as well as during incubation eggs lose weight by evaporation of water through the shell. This was first observed by Geoffroy-Saint-Hilaire (1830). Before him it had even been thought possible that eggs might gain weight by absorbing essential substances from the sitting hen's "perspiration"; but it was pointed out by the German philosopher Christian Wolff (1725, 1737) that this was unlikely because of the possibility of successful artificial incubation. It seems reasonable to assume that the amount of water evaporated during a given period and at a constant temperature is determined by the degree of porosity of the shell. The porosity in turn will depend on the number and size
of the pores, and on whether or not the individual pores are open or are obstructed by calcium or organic deposits. Furthermore, Marshall and Cruickshank (1938) demonstrated that the cuticular areas ("plaques") surrounding the shell pore exit serve as evaporating surfaces, and this fact must be kept in mind in future studies relating to shell porosity and hatchability.

The first extensive inquiry into this problem was made by Dunn (1922-1923; 1923-1924) at the Storrs Agricultural Experiment Station with eggs from a flock of moderately inbred White Leghorns. One result which emerged from this work was that eggs with visibly porous shells and a high rate of water loss showed a very poor performance with regard to hatchability. This is evident from the data in Table 12, obtained from four hens which laid many eggs with very porous shells, recognizable by a dead white or bluish color tint of the shell (perhaps identical with the "mottled" eggs of Henderson; see below). The determinations of weight loss were made on one set of eggs, the hatching records were obtained on another set. Not all of the eggs incubated were abnormally porous, and the more nearly normal eggs were predominantly the ones which gave hatched chicks. Hence, the hatching results do not picture the full extent of loss of hatchability due to defectiveness of the shell. Hen 287 in Table 12 laid exclusively eggs of the very porous type. In two breeding seasons this hen left no progeny, all embryos dying before the end of the incubation period.

If this evidence established the fact that extreme porosity of the shell, and hence excessive loss of water by evaporation, acts as a barrier to hatching, the question remained whether a relation between water loss (porosity) and hatchability exists also within the more nearly normal range of variability of eggs. Such a relation would be of far greater practical importance since the extremely porous variants constitute only a small proportion of all eggs. In order to obtain information about this question eggs were weighed when fresh (on day of laying), and again after 7 and 14 days of incubation, respectively. The data for weights taken after seven days of incubation fail to show statistically significant

<table>
<thead>
<tr>
<th>Hen number</th>
<th>Weight lost during 20 days storage %</th>
<th>Weight lost per sq. cm. of surface g.</th>
<th>Number of eggs incubated</th>
<th>Fertile eggs hatched %</th>
</tr>
</thead>
<tbody>
<tr>
<td>146</td>
<td>3.99</td>
<td>0.0368</td>
<td>29</td>
<td>22.0</td>
</tr>
<tr>
<td>149</td>
<td>3.60</td>
<td>0.0323</td>
<td>18</td>
<td>47.0</td>
</tr>
<tr>
<td>287</td>
<td>4.28</td>
<td>0.0375</td>
<td>13</td>
<td>0.0</td>
</tr>
<tr>
<td>342</td>
<td>2.67</td>
<td>0.0214</td>
<td>25</td>
<td>32.0</td>
</tr>
<tr>
<td>Mean or normal eggs</td>
<td>1.96</td>
<td>0.0170</td>
<td>250</td>
<td>59.8</td>
</tr>
<tr>
<td>Range of normal eggs</td>
<td>1.30-2.79</td>
<td>0.0113-0.0229</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
differences in weight loss between infertile eggs, eggs which died during the first week, eggs which died during the remainder of the incubation period, and eggs which hatched. Still, it should be pointed out that the highest hatching percentages were among the classes with lowest weight loss, and, vice versa, the lowest hatching percentages were among the classes with highest weight loss. The data obtained with reference to weight loss during the first two weeks of incubation were of a similar nature. Table 13 gives the results of the latter experiment.

The first two classes showed very similar percentages of hatch, while the third class (with the highest weight loss) gave a lower hatch. The difference between the second and the third class was 20.91 ± 13.28 percent. This difference is not statistically significant. The mean weight loss of those eggs which died after the fourteenth day was 11.04 ± 0.39 percent and that of the eggs which hatched was 10.49 ± 0.24 percent. These data did not exclude the possibility that with a larger material the existence of a relationship between weight loss and hatchability might be demonstrated to exist within the normal range of variability of eggs, but it seemed unlikely that such a relationship should play a major role as a causative agency in embryonic mortality. Funk (1934 a) could not establish a difference in hatchability by grouping eggs into two classes according to good or poor shell texture as determined by a candling lamp. Hays and Sumbardo (1926-1927) found no consistent relation of shell thickness or of number of pores per square millimeter to hatchability; but since their material came from stock selected for high hatchability, no general conclusion can be drawn from it.

An extensive study of weight loss as related to hatchability was made by Axelsson (1932 a) who determined the loss of weight during the 24 hours following the day of laying (average storage temperature 22° C.; average relative humidity 60 percent), and then incubated the same eggs. This method has a great advantage in that the rate of weight loss was determined under strictly comparable conditions for those eggs which later produced hatched chicks and for those in which the embryos died. The eggs for these determinations came from White Leghorns, Rhode Island Reds, Barnevelders, and crosses between these breeds. A summary of the data obtained in 1931 is shown in Table 14. It was found

<table>
<thead>
<tr>
<th>Weight loss %</th>
<th>Number of eggs with living embryos on 14th day</th>
<th>Number of chicks hatched</th>
<th>Hatch from eggs which had living embryos on 14th day %</th>
</tr>
</thead>
<tbody>
<tr>
<td>6.00-8.50</td>
<td>19</td>
<td>13</td>
<td>68.42 ± 10.66</td>
</tr>
<tr>
<td>9.00-11.50</td>
<td>55</td>
<td>39</td>
<td>70.91 ± 6.12</td>
</tr>
<tr>
<td>12.00-16.50</td>
<td>18</td>
<td>9</td>
<td>50.00 ± 11.79</td>
</tr>
<tr>
<td>Total</td>
<td>92</td>
<td>61</td>
<td>66.30</td>
</tr>
</tbody>
</table>
that the coefficient of correlation between the percentage of hatch and the average loss of weight amounted to $-0.734 \pm 0.154$. This is certainly a significant correlation, indicating that the lower the weight loss, the better the hatch. A similar correlation value was found for the relation of percentage hatch and standard deviation of weight loss ($r = -0.687 \pm 0.176$), an expression of the fact that the periods with greater average loss of weight and with lower average hatchability were also periods in which loss of weight (shell porosity) generally was more variable.

Further data are given by Axelsson to show that during the early part of the incubating season there was a general tendency for weight loss (shell porosity) to increase, and for hatchability to decrease. From the fact, however, that during a rest period (pause) the shell quality improved (decrease of weight loss), while hatchability did not immediately increase correspondingly, it was concluded that other factors complicated the picture. It was also found that after a long and severe winter, average and standard deviation of weight loss were higher than usual. In general, the best hatching percentages were obtained for eggs which during the 24-hour test period lost between 0.081 and 0.160 g. of weight; no egg which lost more than 0.240 g. of weight produced a hatched chick.

Judging from the results obtained during two consecutive years, it appears that in this material the loss of hatchability due to poor shell quality amounted to approximately 8 percent of all fertile eggs. It was possible to demonstrate that eggs with low weight loss had a somewhat heavier shell than those with high loss of weight. The shells of the former contained 95.8 percent of substance soluble in acetic acid, while the shells of eggs with high weight loss yielded only 91.6 percent of acetic acid soluble matter. Since calcium carbonate forms 93 to 94 percent of the mineral substance of egg shells, it seems fair to assume that the differences in acetic acid soluble substance are due to corresponding changes in the amounts of calcium carbonate in the shells of eggs with low and high loss of weight. This is not necessarily the only difference between these two groups of eggs.
Axelsson's data demonstrate clearly that weight loss (shell quality) is a highly variable character, and that it is easily influenced by environmental factors. Yet his observations show also that there are definite differences between individual hens with regard both to loss of weight and percentage hatch. This can be seen from the data of Table 15.

Table 15

<table>
<thead>
<tr>
<th>Average weight loss of eggs of individual hens</th>
<th>Number of hens</th>
<th>Average hatching %</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.081-0.120</td>
<td>11</td>
<td>54.49</td>
</tr>
<tr>
<td>0.121-0.160</td>
<td>76</td>
<td>63.78</td>
</tr>
<tr>
<td>0.161-0.200</td>
<td>17</td>
<td>47.12</td>
</tr>
<tr>
<td>0.201-0.240</td>
<td>4</td>
<td>25.90</td>
</tr>
<tr>
<td>0.241-0.280</td>
<td>1</td>
<td>0.00</td>
</tr>
</tbody>
</table>

The eggs of hens belonging to the first two classes (average weight loss 0.081 to 0.160 g.) had an average hatchability of 62.58 ± 1.45 percent, while the eggs of hens belonging to the last three classes (average weight loss 0.161 to 0.280 g.) produced an average hatch of 41.12 ± 3.04 percent. The difference between these two groups amounts to 21.46 ± 3.37 percent, and is certainly significant. Voitellier (1936) confirmed that water loss through the shell is an important factor in hatchability. That increased loss of weight during incubation is associated with reduced hatchability was also confirmed by Shibata and Murata (1936) and Axelsson (1954).

Additional extensive data on the same problems have been provided by Rauch (1952) and Rauch and Steinke (1953). The results of measurements on 1077 eggs of Brown Leghorn fowl are shown in Table 16, and those for 813 eggs of Legbar fowl are reproduced in Table 17. The observations of these investigators indicate that a curvilinear relationship exists between diameter of the shell pores and hatchability, eggs with pore diameters of the shell below and above the optimum hatching less well than those near the center of distribution. In addition, an interesting difference was found between the two breeds in the distribution of the diameter of the shell pores. One wonders how the number of pores per unit area was related to the size of the pores. Bouges (1923) had already earlier claimed that breed differences in shell quality exist which affect evaporation of water during incubation.

By determining loss of weight of eggs during 24 hours prior to the beginning of incubation Rauch and Steinke could demonstrate a relationship to subsequent hatching results. These determinations were made on 1560 eggs of Brown Leghorn fowl after storage for 24 hours at a temperature of 21°C (69.8°F) and a relative humidity of 40 percent. The results are summarized in Table 18.
Table 16

<table>
<thead>
<tr>
<th>Pore width in μ</th>
<th>0-5</th>
<th>6-12</th>
<th>12-18</th>
<th>18-24</th>
<th>24-30</th>
<th>30-36</th>
<th>36-42</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of eggs</td>
<td>0</td>
<td>48</td>
<td>168</td>
<td>411</td>
<td>315</td>
<td>93</td>
<td>42</td>
</tr>
<tr>
<td>Percent hatch</td>
<td>—</td>
<td>38</td>
<td>66</td>
<td>82</td>
<td>90</td>
<td>81</td>
<td>64</td>
</tr>
</tbody>
</table>

Table 17

<table>
<thead>
<tr>
<th>Pore width in μ</th>
<th>0.5-10</th>
<th>10-15</th>
<th>15-20</th>
<th>20-25</th>
<th>25-30</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of eggs</td>
<td>15</td>
<td>48</td>
<td>399</td>
<td>264</td>
<td>66</td>
</tr>
<tr>
<td>Percent hatch</td>
<td>40</td>
<td>75</td>
<td>51</td>
<td>55</td>
<td>29</td>
</tr>
</tbody>
</table>

Table 18

<table>
<thead>
<tr>
<th>Weight loss %</th>
<th>0.05-0.10</th>
<th>0.10-0.15</th>
<th>0.15-0.20</th>
<th>0.20-0.25</th>
<th>0.25-0.30</th>
<th>0.30-0.35</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of eggs</td>
<td>6</td>
<td>312</td>
<td>804</td>
<td>372</td>
<td>54</td>
<td>12</td>
</tr>
<tr>
<td>Percent hatch</td>
<td>50</td>
<td>75</td>
<td>77</td>
<td>72</td>
<td>56</td>
<td>25</td>
</tr>
</tbody>
</table>

Since the foregoing evidence shows that shell quality is, at least in part, an individual trait of hens, the question arises how this trait is transmitted genetically. Axelsson secured interesting information bearing on this problem. Table 19 gives data for the three breeds which he used and for first crosses between them. The fact that all values for weight loss are higher for 1931 than for 1930 is, according to Axelsson, due to the application of a different correction factor for egg size and also to the lateness of spring in 1931 with a consequent effect on shell quality during the early part of the incubating season. The differences in magnitude between groups, however, are of similar order and in the same direction in the two years.

Among the three pure breeds, the eggs of White Leghorns showed the lowest, those of Barnevelders the highest loss of weight, and the difference between these two breeds is statistically significant. The data from F₁ birds of crosses between the three breeds suggest that the lower
loss of weight (lower porosity or better shell quality) is incompletely dominant to higher weight loss. Quinn, Gordon and Godfrey (1945) confirmed for White Leghorns that egg shell quality, as expressed by loss of weight of the eggs during the first two weeks of incubation, is a genetic trait.

Axelsson’s observation that the eggs of Rhode Island Reds lose relatively more weight during incubation than do the eggs of White Leghorns has been confirmed by Godfrey and Olsen (1937) and Vladimirova (1954). Godfrey and Olsen also established the existence of significant differences in egg-weight loss during incubation between individual females within one breed.

Additional evidence relating to the importance of shell texture (weight loss) for hatchability was secured by Hays and Spear (1951) with Rhode Island Reds. The observations on Rhode Island Reds and White Leghorns do not support earlier statements, preferred with little supporting evidence, that the rate of water evaporation generally is greater from white-shelled than from brown-shelled eggs (Gilbert, 1895; McCue, 1900 b; Laurie, 1911). A critical examination of this problem is wanting, but the demonstration by Marshall and Griswold (1938) that brown eggs are less porous than white ones is of interest in this connection. More recent, but again rather inconclusive, observations by Godfrey (1947) suggest that among breeds which lay brown eggs those with dark pigmentation of the shell tend to have better hatchability than the lightly tinted ones. Godfrey believes that the lightly pigmented eggs have less calcium in their shells and lose more moisture during incubation than eggs with dark shells. Low positive correlation coefficients were found between intensity of coloration of the shell and its thickness or its breaking strength (Godfrey, 1949 a). Funk and Forward (1949 b, 1951) confirmed on eggs of New Hampshire fowl that those with lightly tinted shells produced fewer hatched chicks than did the eggs with dark brown shells (55.0 and 74.1 percent, respectively), and that the eggs with light brown shells tended to show a higher rate of water evaporation. Skoglund (1950) observed similar, but statistically non-significant, relations between shell color and hatchability of New Hampshire eggs, whereas Rosenberg and Tanaka (1951) came to the conclusion that intensity of shell color has no bearing on hatchability. New studies by Raimo (1951) have, however, produced results similar to those of Godfrey and of Funk and Forward. Raimo made observations on 4400 eggs of New Hampshire fowl by dividing them into five groups according to color of the shell, the groups ranging from “very light” to “very dark”. He found that the eggs with lightest colored shells hatched less well than those with more deeply tinted shells. Shape of the eggs did not seem to vary significantly between groups, but the eggs with the lightest shells had a smaller mean weight than the remaining ones (not evaluated statistically). This difference in weight of the eggs may well be accounted for by the relations
the eggs laid by $F_1$ hens. The difference between the $F_2$ groups amounts to 3.66 times the error.

Axelson argues further that, if all inherited differences of weight loss were due to sex-linked factors, the results of certain groups and crosses should be essentially the same. The pertinent data are reproduced in Table 22. In all four instances the results agree with what might be expected if, in addition to sex-linked factors, autosomal ones were operative and in two cases the differences appear to be statistically significant. Axelson, therefore, assumes that both sex-linked and auto-

### Table 20

<table>
<thead>
<tr>
<th>Cross</th>
<th>Weight loss of eggs g.</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Wh. Leghn. $\varnothing$ x R.I.R. $\delta$) $F_1$</td>
<td>0.137 ± 0.0013</td>
</tr>
<tr>
<td>(R.I.R. $\varnothing$ x Wh. Leghn. $\delta$) $F_1$</td>
<td>0.123 ± 0.0012</td>
</tr>
<tr>
<td><strong>Difference</strong></td>
<td><strong>0.014 ± 0.0018; $\frac{D}{e(D)} = 7.78</strong></td>
</tr>
<tr>
<td>(Wh. Leghn. $\varnothing$ x Barnev. $\delta$) $F_1$</td>
<td>0.143 ± 0.0029</td>
</tr>
<tr>
<td>(Barnev. $\varnothing$ x Wh. Leghn. $\delta$) $F_1$</td>
<td>0.131 ± 0.0012</td>
</tr>
<tr>
<td><strong>Difference</strong></td>
<td><strong>0.012 ± 0.0033; $\frac{D}{e(D)} = 3.64</strong></td>
</tr>
<tr>
<td>(R.I.R. $\varnothing$ x Barnev. $\delta$) $F_1$</td>
<td>0.157 ± 0.0032</td>
</tr>
<tr>
<td>(Barnev. $\varnothing$ x R.I.R. $\delta$) $F_1$</td>
<td>0.139 ± 0.0024</td>
</tr>
<tr>
<td><strong>Difference</strong></td>
<td><strong>0.018 ± 0.0040; $\frac{D}{e(D)} = 4.50</strong></td>
</tr>
</tbody>
</table>

### Table 21

<table>
<thead>
<tr>
<th>Number of eggs</th>
<th>Hatchability $%$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$F_1$ hens from matings in which the breed with lowest weight loss and highest hatching percentage was <strong>maternal</strong> &lt;br&gt; (Wh. Leghn. x R.I.R.; Wh. Leghn. x Barnev.; R.I.R. x Barnev.)</td>
<td>823</td>
</tr>
<tr>
<td>$F_1$ hens from matings in which the breed with lowest weight loss and highest hatching percentage was <strong>paternal</strong> &lt;br&gt; (R.I.R. x Wh. Leghn.; Barnev. x Wh. Leghn.; Barnev. x R.I.R.)</td>
<td>820</td>
</tr>
<tr>
<td><strong>Difference</strong></td>
<td><strong>8.7 ± 2.38</strong></td>
</tr>
</tbody>
</table>

somal factors influence weight loss (porosity of the shell), and that both kinds of genetic agencies influence the results in the same direction (incomplete dominance of low weight loss). Further evidence is presented
between degree of coloring of the shell and its diameter (and structure), as reported previously and as confirmed by new studies of Godfrey (1949 d). Godfrey found highly significant correlations (with \( P < .01 \)) between color intensity and breaking strength of the shells (\(+ .368\)) as well as between degree of coloring and diameter of the shell (\(+ .372\)), depth of color increasing with thickness and strength of the shell. It is interesting to note that in this, as in many other situations, the discrepancies between the results and conclusions of various investigators appear to have been a consequence of dissimilarities between flocks in the variance of the trait under investigation. No doubt remains, at any rate, that in flocks which show a wide variation in intensity of shell color the eggs with the lightest coloring hatch least well.

Another elaborate inquiry into the problems related to loss of weight of eggs during storage and incubation was undertaken by Vladimirova (1954, with references to other Russian literature). Her principal conclusions were the following: 1. The smaller the loss of weight during storage the better is subsequent hatchability. 2. Winter eggs tend to lose less weight than summer eggs. 3. The rate of weight loss of eggs decreases with advancing age of the laying hens. 4. Large eggs lose relatively less weight than small eggs. 5. A direct relation exists between porosity and diameter of the shell on the one hand and loss of weight on the other. 6. Loss of weight during storage is positively correlated with loss of weight during incubation. 7. Eggs with a low rate of weight loss show a higher electrical conductivity of the albumen (all layers) than those with a high rate of weight loss. For many of her data Vladimirova unfortunately did not give a statistical evaluation. Some of her conclusions agree well with what had been known, others are new and, if confirmed, may have considerable importance. Vladimirova’s claim that the rate of weight loss decreases with advancing age of the layers is difficult to reconcile with the observation that shell porosity is greater during the second than during the first laying year (Bolton, 1957), and in a comparison of eggs from pullets and old hens Bolton did, in fact, find that the eggs laid by the old birds lost weight at an appreciably higher rate than those laid by pullets.

It is interesting to make comparisons between Axelsson’s data (for 1931) from the \( F_1 \) females out of the several reciprocal crosses. The values of weight loss are corrected for egg size (Table 20). In each of the three instances the \( F_1 \) females of reciprocal crosses are significantly different with regard to weight loss of their eggs, and in each case weight loss was higher in that \( F_1 \) in which the father belonged to the breed with higher weight loss of the eggs. Such results are expected if we are dealing with sex-linked inheritance. Further support for this conclusion can be seen in the data presented in Table 21. Since the responsible genetic factor or factors act through the mother’s organism, the results of sex-linked inheritance become apparent only in the \( F_2 \) generation, that is,
in support of this conclusion, though admittedly the problem deserves continued study.

Table 22

<table>
<thead>
<tr>
<th>Cross</th>
<th>Weight loss of eggs g.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhode Island Red</td>
<td></td>
</tr>
<tr>
<td>(Wh. Leghn. ♀ x R.I.R. ♂) F₁</td>
<td>0.144 ± 0.0022</td>
</tr>
<tr>
<td></td>
<td>0.157 ± 0.0013</td>
</tr>
<tr>
<td>Difference</td>
<td>0.007 ± 0.0026;</td>
</tr>
<tr>
<td></td>
<td>−e (D) −2.69</td>
</tr>
<tr>
<td>Barnevelder</td>
<td></td>
</tr>
<tr>
<td>(Wh. Leghn. ♀ x Barnev. ♂) F₁</td>
<td>0.150 ± 0.0018</td>
</tr>
<tr>
<td></td>
<td>0.143 ± 0.0029</td>
</tr>
<tr>
<td>Difference</td>
<td>0.017 ± 0.0031;</td>
</tr>
<tr>
<td></td>
<td>−e (D) −5.00</td>
</tr>
<tr>
<td>Barnevelder</td>
<td></td>
</tr>
<tr>
<td>(R.I.R. ♀ x Barnev. ♂) F₁</td>
<td>0.160 ± 0.0018</td>
</tr>
<tr>
<td></td>
<td>0.157 ± 0.0032</td>
</tr>
<tr>
<td>Difference</td>
<td>0.003 ± 0.0037;</td>
</tr>
<tr>
<td></td>
<td>−e (D) −0.81</td>
</tr>
<tr>
<td>(Barnev. ♀ x Wh. Leghn. ♂) F₁</td>
<td>0.131 ± 0.0012</td>
</tr>
<tr>
<td>(R.I.R. ♀ x Wh. Leghn. ♂) F₁</td>
<td>0.123 ± 0.0012</td>
</tr>
<tr>
<td>Difference</td>
<td>0.008 ± 0.0017;</td>
</tr>
<tr>
<td></td>
<td>−e (D) −4.71</td>
</tr>
</tbody>
</table>

On the whole, the evidence that has been reviewed supports the conclusions that (1) excessive porosity of the shell is a definite barrier to hatching; and that (2) a more general relation exists between shell porosity (weight loss) and hatchability, resulting in reduced hatching quality of eggs with a shell porosity above the optimum.

Shell texture is influenced by genetic and environmental factors. A high degree of mottling of the shell increases, according to Henderson (1941), the amount of water lost during incubation, and in another report Henderson (1942a) showed that poor shell quality significantly depresses the hatchability of eggs.

Mueller and Scott (1940) made a new study of the relationship between loss of egg weight during incubation and hatchability. They used White Leghorns. A summary of their results is given in Table 23. These data fail to show any significant relationship between shell porosity and hatchability. Negative results (although with a trend similar to that observed by Axelsson) were also recorded by Eriksson (1951). The reasons for these discrepancies remain obscure. It seems possible, however, that the explanation must be looked for in differences of incubation technique. In modern incubators, which have provisions for regulating humidity, weight loss is unquestionably less variable than it is in machines with more primitive humidity control. The less favorable atmospheric environment of old-type incubators is likely to bring into sharper relief
the role of shell porosity. For, under adverse humidity conditions eggs with varying degrees of shell porosity may lose water in significantly different amounts, whereas such results may be lacking when more optimal humidity prevails. Such an interpretation is in agreement with the following facts: (1) an excessive rate of evaporation is definitely harmful to the embryo; (2) there is a positive correlation between weight loss of eggs (evaporation) during incubation and porosity of their shells (Almqvist and Holst, 1931; Bryan and Sharp, 1934) and also between thickness of the shell and rate of evaporation (Murray, 1925); (3) the relation of shell porosity to evaporation tends to disappear at optimal humidity levels (Stewart, 1933); (4) Dunn, Axelsson, Rauch and Steinke, and Vladimirova used still-air incubators, whereas Mueller and Scott employed a forced-draft machine.

Table 23

<table>
<thead>
<tr>
<th>Porosity index*</th>
<th>Mean</th>
<th>Number of hens</th>
<th>Mean percentage hatchability</th>
</tr>
</thead>
<tbody>
<tr>
<td>6.99 and below</td>
<td>6.25</td>
<td>80</td>
<td>70.0</td>
</tr>
<tr>
<td>7.00 - 7.99</td>
<td>7.35</td>
<td>64</td>
<td>69.5</td>
</tr>
<tr>
<td>8.00 and above</td>
<td>8.89</td>
<td>50</td>
<td>69.6</td>
</tr>
</tbody>
</table>

*The “porosity index” equals the 24-hour loss of egg weight in milligram per cm² of surface area.

Mueller and Scott found in their observations that large and small eggs did not differ significantly with respect to the degree of shell porosity and that eggs of one and the same hen were remarkably constant in their extent of shell porosity.

An interesting, though unfortunately very incomplete, report concerning the probable existence of hereditary shell defects and their unfavorable influence on hatchability is due to R. E. and A. S. Serebrovsky (1926). They found that in the Pawloff breed of fowl extremely poor hatches are frequently encountered and believe that the cause is to be found in improper shell formation with consequent excessive desiccation during incubation.

Mussehl and Halbersleben (1923) determined for 802 fertile eggs the correlation between “specific gravity” of the whole egg and hatchability. The coefficient was found to be 0.204 ± 0.034; small, but significant. The “specific gravity” of the shell is twice that of the egg contents (averages of 2.14 and 1.07, respectively), and the authors assume that variations in “specific gravity” of the whole egg are most likely due to variations in thickness of the shell, and that the observed correlation is the expression of a slight increase in hatching quality with increasing “specific gravity” of the shell.

The problem of “specific gravity” of eggs, as it relates to their hatchability, has received further attention by the work of Munro (1940),
Determinations of "specific gravity" were made on large numbers of White Leghorn and Barred Plymouth Rock eggs by immersing them in salt solutions of different concentrations and by noting the concentration at which they floated just beneath the surface of the solution. These observations were analyzed with reference to subsequent hatchability of the eggs.

It is not immediately clear just what is measured by such determinations. The relative amount of shell material bears an inverse relationship to egg size, and this geometrical factor unquestionably complicates the meaning of the results which Munro obtained by his procedure. The same criticism applies to the work of Muschel and Halbersleben. In any event, it was found that there is a distinct curvilinear relationship between the floating character of the eggs and their hatching quality (Figure 20). A breed difference was reported: the critical point below which hatchability was very poor being 1.078 for Barred Plymouth Rock eggs and 1.086 for White Leghorn eggs (not tested statistically). It was also found that the floating quality of their eggs is a distinct trait of individual hens. Additional observations (Munro, 1942) indicated, however,

![Figure 20](image)

Figure 20
Relation of "specific gravity" of the egg to hatchability. Solid line: Barred Plymouth Rock eggs; broken line: Leghorn eggs (From Munro, 1940; modified).
that in some flocks no relationship could be discovered between the floating quality of the eggs and hatchability. This occurred in flocks in which the variance of floating quality was exceptionally low. More recent observations by Svensson (1957) on eggs of White Leghorn, Rhode Island Red and New Hampshire fowl led the author to the conclusion that a “specific gravity” between 1.075 and 1.080 was optimal for hatchability. A low, but significant, correlation between “specific gravity” and loss of weight of eggs was found in one year, but in another year the two traits were completely independent.

It should be added here, that shell defects leading to reduced hatchability may be brought about by withholding calcium from the diet. This was shown by Buckner, Martin and Peter (1924-1925). In their experiment three groups of White Leghorns were kept under identical conditions, except that group I had grass range and oyster shell ad libitum, group II had no range but oyster shell, and group III had neither range nor oyster shell. The experiment was begun November 1. When incubation was started on March 1 of the following year, the average dry weight of the egg shells in the three groups amounted to 5.2, 5.4 and 3.5 g., respectively; that is, in group III dry weight of the shell was strikingly reduced.

The results of incubating eggs from the three groups are shown in Table 24. The following conclusions seem justified. Egg production was much reduced when calcium was withheld. Fertility was not interfered with. The hatching quality of the eggs became progressively lower, and embryo mortality tended to shift from the final to earlier periods of development.

The crucial confirmation was obtained when, subsequent to these tests, oyster shell was supplied to group III and withheld from groups I and II. Hatchability decreased in groups I and II, while in group III it rose to 20.7, 32.5 and 36.1 percent, respectively, in three successive incubation trials. The loss in hatching quality of the eggs as a consequence of calcium deficiency in the diet is probably caused, at least in part, by increased weight loss (increased shell porosity); but it is possible that other factors, such as inadequate calcium supply to the embryo, play a role. In a later communication, however, Buckner, Martin and Peter (1929) made the following statement: “While the absence of calcium carbonate from the diet is accompanied by marked decrease in the weight of the egg shell, this circumstance does not appear to be connected with the loss of hatchability. The cause seems to be deeper seated and probably should be sought in connection with the metabolism of the mother hen.”

This conclusion seems chiefly to be based on the observation that infertile eggs from the lot without range and without calcium supplement did not lose more weight during 18 days of incubation than did eggs from the control group. But data from infertile eggs scarcely furnish a
fair basis for judgment. It must be kept in mind that the embryo removes calcium from the egg shell, and in thin-shelled eggs this may lead to an increased rate of evaporation. The fact that hatched chicks from the calcium-deficient group showed a reduced dry weight of the carcass relative to the initial weight of the egg, may well be due to stunted growth as a consequence of increased evaporation of water.

Table 24

<table>
<thead>
<tr>
<th>Date when eggs set</th>
<th>Group</th>
<th>Number of eggs</th>
<th>Infertile</th>
<th>Mortality to 18th day</th>
<th>Mortality after 18th day</th>
<th>Hatched</th>
</tr>
</thead>
<tbody>
<tr>
<td>March 14</td>
<td>I</td>
<td>76</td>
<td>10.5</td>
<td>7.9</td>
<td>15.8</td>
<td>65.8</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>69</td>
<td>16.0</td>
<td>16.0</td>
<td>27.5</td>
<td>40.6</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>19</td>
<td>5.5</td>
<td>31.6</td>
<td>42.1</td>
<td>21.0</td>
</tr>
<tr>
<td>March 28</td>
<td>I</td>
<td>58</td>
<td>12.1</td>
<td>12.1</td>
<td>12.1</td>
<td>63.8</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>42</td>
<td>7.1</td>
<td>21.4</td>
<td>35.7</td>
<td>35.7</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>17</td>
<td>11.8</td>
<td>29.4</td>
<td>41.2</td>
<td>17.7</td>
</tr>
<tr>
<td>April 11</td>
<td>I</td>
<td>78</td>
<td>14.1</td>
<td>17.9</td>
<td>24.4</td>
<td>43.6</td>
</tr>
<tr>
<td></td>
<td>II</td>
<td>59</td>
<td>0</td>
<td>20.3</td>
<td>22.0</td>
<td>57.6</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>18</td>
<td>16.7</td>
<td>61.2</td>
<td>22.2</td>
<td>0</td>
</tr>
</tbody>
</table>

Stuart and Hart (1938) tested the effect which different levels of calcium intake have on shell strength and confirmed that inadequate calcium consumption reduces hatchability. Axelsson (1932 b) found that addition of cod liver oil, sprouted grain, or vigantol (a vitamin-D preparation) to the diet of hens decreased, in the order named, the loss of weight of their eggs. Excessive calcium content of the diet also has a detrimental effect on egg shell formation (Tyler 1945), and hence, presumably, on hatchability.

The significance of other shell qualities for hatchability, for example variations in the formation of the outer shell coating, has not as yet been investigated.

Studies by Penjonschkewitsch (1937) call attention to the possible importance of the inner shell membrane for hatchability. In contrast, distinction to results reported by Ferdinandov (quoted by Penjonschkewitsch) the author found that the water content of the inner shell membrane increases with progressing incubation, and that desiccation of this membrane leads to increased permeability for gases. Since it appears that there are breed differences in thickness of the outer as well as of the inner shell membrane, their relationship to hatchability deserves further attention. Penjonschkewitsch may be right in contending that drying out of the inner shell membrane cannot lead to suffocation of the embryo, as Ferdinandov had supposed, but there can be little doubt that the parchment-like condition of the inner shell membrane, frequently caused by low humidity, may form a mechanical obstacle to hatching.

**Albumen characters**

The importance of the amount of albumen in eggs on their hatching quality was studied by Godfrey (1936). His material consisted of eggs
from 115 birds (Rhode Island Red, Light Sussex, Wyandotte). The eggs of these hens, produced during a period of ten weeks, were incubated to determine hatchability, and subsequently about ten eggs of each hen served for various measurements. A low but significant negative correlation was found between weight of total albumen per egg and hatchability, and also between weight of thick albumen and hatchability. In general, then, the less total albumen there is in an egg or the less thick albumen it contains, the better are the chances that it will produce a hatched chick. No significant difference in this respect could be established between the three breeds used. The relation between total albumen weight and hatchability is closely similar to that between egg weight and hatchability (Figure 21), and it seems likely that the latter is partly or wholly an expression of the former. Observations by Scott and Warren (1941), bearing on these problems, have already been discussed (p. 72). These relations presumably hold only within certain limits. In experiments by Smith, Abbott and Jones (1958) the quantity of albumen was reduced (but also its quality affected) by prior X-ray irradiation of the albumen-producing region of the oviduct of laying hens; such eggs had a high early embryo mortality and reduced hatchability.

The relationship to hatchability of the “score of the condition” of the firm albumen, i.e., of the degree to which the firm albumen will preserve its shape around the yolk when the egg is carefully broken upon

Figure 21
Relationship between percentage hatchability and: A, average egg weight; B, average amount of albumen per egg; C, average amount of thick albumen per egg; D, average percentage thick of total albumen. Data from 115 birds during one hatching season (From Godfrey, 1936).
a suitable surface, has been studied by a number of investigators. It was first reported by van Wagennen (1935), van Wagennen and Hall (1936) and Hall and van Wagennen (1936) that this physical trait of the firm albumen had an influence on hatchability, the eggs with a high score of the albumen hatching better than those with a low score, but subsequent investigations failed to confirm the existence of such a correlation (Wilhelm 1939; Rudy and Marble, 1939).

In studies with White Leghorns Rudy and Marble (1939) found a significant correlation, for the data of one year, between the amount of firm albumen in percentage of total albumen and hatchability, but the material of another year did not confirm this result. Other studies also failed to show a significant association between these traits (Godfrey, 1936; Hall and van Wagennen, 1936; Broekhuizen, van Albada, Appelman and Ubbels, 1952).

The cohesive quality of the albumen and the height of the firm albumen apparently are not related to hatchability (Rudy and Marble, 1939). The same seems to be true for the relative amount of outer thin albumen (Hall and van Wagennen, 1936). The percentage of solids in the albumen, as determined by the refractive index, also has no influence on hatchability (Bronkhorst, 1933; Bronkhorst and Hall, 1935 b), though in a general way the observations of these authors tend to confirm the conclusion that eggs with low hatching quality show greater variability in relative amounts of solids in the albumen than do eggs with high hatching quality (Powell, 1925). According to Voitellier (1936) water content of the albumen is a factor in hatchability, but no details are given in support of this statement. That organic constituents of the egg white are important for embryonic development, beginning with early stages of incubation, has been shown by Schmidt (1937).

**Yolk characters**

With the possible exception of vitamin content, to be discussed subsequently, there is little evidence available tending to demonstrate that yolk qualities play a role in hatchability. No relation was found between the amounts of solids in the yolk and hatching quality of eggs (Bronkhorst, 1933; Bronkhorst and Hall, 1935 b), nor between the shape index of the yolk and hatchability (Hall and van Wagennen, 1936), nor between yolk weight and hatchability (Rudy and Marble, 1939).

Since a large part of the yolk is not utilized by the embryo until fairly late in development, it is not surprising that it should be of less importance for survival than the albumen, though it is important to keep in mind that the thin yolk beneath the germinal disk forms the source of nourishment of embryos in early stages of development. Penjonschkewitsch (1936) presented evidence for the conclusion that efficiency of yolk utilization by the embryo may be a significant factor in hatchability.
Barancheev (1936) studied the relation between yolk color and hatchability in White Leghorn eggs. All eggs came from a flock which was kept under uniform conditions. Only eggs weighing between 50 and 60 g. were used for incubation. By comparison with standards, the eggs were divided into three groups according to the intensity of yolk color. Group I contained the eggs with the darkest colored yolk, group III those in which the yolk color was lightest. There were 107 fertile eggs in group I, 285 in group II, and 280 in group III. Hatchability amounted to 77.6% in group I, 54.4% in group II, and 37.9% in group III. Moreover, the percentage of strong chicks among those hatched decreased from group I (96.6%) to group III (84.2%). Similar results have been reported by Kirsanoff (1935) for goose eggs. It was shown by Bishey, Appleby, Weis and Cover (1934) that there is a relationship between color of the yolk and its richness in carotene and xanthophyll, the color being darker if the amount of these pigments is greater. But it remains to be investigated whether the relationship between yolk color and hatchability is only an expression of vitamin A concentration (see below) or whether still other factors play a role.

Yolk mobility of unincubated eggs may give some clue with regard to the potential hatching value of eggs. This was first demonstrated by Byerly and Haynes (1938) and subsequently studied in greater detail by Henderson (1942 b). Yolk mobility is the relative speed of the yolk shadow as an egg is rotated in front of a candling lamp. Henderson collected data on the relation of yolk mobility to hatchability by scoring the eggs on an arbitrary scale, ranging from “1” (no visible or very slow movement) to “5” (highly mobile), and by analyzing these scores with reference to subsequent hatchability. A significant relation was found, the eggs with highly mobile yolks hatching less well than those with slight or no mobility. Yolk mobility increases with pre-incubation age of eggs and is probably an expression of physical properties of the albumen. Broekhuizen, van Albada, Appelman and Ubbels (1952) could not detect a relation between strength of the yolk sac membrane and hatchability.

With regard to egg contents as a whole, Cross (1912) failed to find a correlation between the amounts of proteins and fats in eggs of certain hens and the hatching quality of their eggs. Negative results of this kind do not exclude the possibility, of course, that the presence or absence of definite kinds of proteins may be a significant factor in hatchability.

**NUTRITIONAL FACTORS IN HATCHABILITY**

A variety of substances are indispensable for normal growth and development of the chicken embryo. If such substances are lacking in the fertilized egg or are present in insufficient amounts, death of the embryo may occur sooner or later. It is true that an inadequate diet will frequently lead to decline and cessation of egg production rather than to the laying of deficient and unhatchable eggs, yet there is abundant evidence that nutritional factors of various kinds affect the hatching quality
of eggs via the organism of the mother. No complete survey of the pertinent literature will be attempted here. Additional literature on the relations of maternal nutrition to hatchability can be found in a book by Heuser (1955).

Little is known concerning hereditary differences which influence the economy of utilization of various foodstuffs, and, thereby, affect the hatching quality of eggs. It was shown, however, by Lillie, Olsen and Bird (1951) that general physiological conditions, possibly relating to absorption from the digestive tract or to other mechanisms involved in the transfer of nutrients from mother to egg and embryo, may produce significant variations between mothers in hatchability of their eggs; in two groups of birds hatchability could be differentiated in a similar manner by dietary deficiency in either riboflavin, vitamin B₁₂ or manganese. Hereditary inadequacies of maternal riboflavin transfer to eggs will be reported below. No evidence seems to be available which would suggest that nutritional deficiencies in the diet of cocks influence the hatchability of eggs fertilized by them.

**Vitamins and hormones**

The presence in eggs of sufficient amounts of vitamin A is necessary for normal hatchability. Holmes, Doolittle and Moore (1927) demonstrated that low hatching quality caused by a diet deficient in vitamin A could be improved by supplementing the feed with cod liver oil as a source of this vitamin. Within certain limits hatchability increases in proportion to the amount of vitamin A supplied with the feed. This was demonstrated by Sherwood and Fraps (1932) in tests in which the effect of a white corn, a mixed white and yellow corn, and a yellow corn diet (white corn lowest, yellow corn highest vitamin A content) were compared with each other.

No similarly direct relation was found between the vitamin A content of the yolk and the hatching quality of eggs produced by the hens of these three experimental groups; but when the two groups which received the highest and lowest amounts of vitamin A with the feed, and whose eggs had the highest and lowest hatchability, respectively, were compared with each other, it was found that in every one of four tests the eggs of the group with high hatching quality contained more vitamin A in the yolk than did the eggs of the group with low hatching quality. Similar results were obtained in a test in which alfalfa leaf meal served as supplementary source of vitamin A (Sherwood and Fraps, 1934). The results of this experiment are given in Table 25. Though by far the greatest part of vitamin A is found in the egg yolk, it is quite possible that the fraction contained in the albumen is more important as far as hatchability is concerned.

Additional extensive evidence concerning the necessity of vitamin A for the developing embryo, and the need for its presence in the feed of
hens which produce hatching eggs, was furnished by the work of Payne and Hughes (1933), R. M. Smith (1933), Sherwood and Fraps (1935, 1940), Russell, Platt, Taylor and Chichester (1936), Almquist and Mechi (1939), Polk and Sipe (1940), Hart and Stuart (1944), Temperton and Dudley (1946-1948), McElymont and Hart (1948), Kotaj (1957) and others. Bearse and Miller (1937) presented further data showing that an improvement of the hatchability of eggs takes place as the level of vitamin A (alfalfa) is increased in the ration. With only 0.5 percent of alfalfa in the ration (62.5 Sherman units of vitamin A per 100 g. of feed) eggs did not hatch; with 1 percent of alfalfa hatchability amounted to 68.3 percent and with 4 percent alfalfa (500 Sherman units) 95.8 percent of all fertile eggs hatched. No further increase of hatchability was obtained with higher levels of vitamin A intake. Fertility was not affected by the vitamin A content of the ration. The amounts of vitamin A in the yolk of eggs increased with a greater intake of this vitamin by the laying hens. There is evidence suggesting that excessive amounts of dietary vitamin A may lead to a condition of hypervitaminosis with increased embryonic mortality (Temperton and Dudley, 1947), but the evidence for this conclusion is not critical. The lower the level of vitamin-A intake or the more severe the depletion of the body of laying hens, the earlier during incubation is embryo mortality said to occur (Temperton and Dudley, 1946).

Studies by Williams, Lampman and Bolin (1939) led to the conclusion that vitamin A deficiency depresses hatchability only if it is suffi-

<table>
<thead>
<tr>
<th>Date of hatch</th>
<th>No-alfalfa group</th>
<th>4%-alfalfa group</th>
<th>8%-alfalfa group</th>
<th>Estimated units of vitamin A per gram of egg yolk</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>units vitamin A fed per day</td>
<td>Hatch %</td>
<td>units vitamin A fed per day</td>
<td>Hatch %</td>
</tr>
<tr>
<td>May 1, 1933</td>
<td>224</td>
<td>13.8</td>
<td>31.3</td>
<td>33.3</td>
</tr>
<tr>
<td>June 9, 1933</td>
<td>336</td>
<td>47.0</td>
<td>50.2</td>
<td>60.2</td>
</tr>
<tr>
<td>Average</td>
<td>38.4</td>
<td>46.0</td>
<td>52.4</td>
<td>9.5</td>
</tr>
</tbody>
</table>

1. Sherman and international units of vitamin A are not directly comparable. It has been found that the factor for converting Sherman units into international units may vary between 0.8 and 2.5.
Taylor, Stern, Russel and Jungherr (1947) recommended a minimum of 2,000 international units of pro-vitamin A per pound of feed.

Thiamine (vitamin B₁) is so plentiful in all cereal grains that a deficiency in it is unlikely to occur in the nutrition of fowl. This is not saying, of course, that thiamine is unimportant in development of the chicken embryo. By injecting thiamine analogs into developing eggs Naber, Cravens, Baumann and Bird (1954) could produce typical symptoms of thiamine deficiency and high embryo mortality.

Bethke, Record and Kennard (1933, 1936) have shown that riboflavin (B₂) is essential for normal embryonic development. This was confirmed by Davis, Norris and Heuser (1938 b) and Schumacher and Heuser (1939 a). It was further demonstrated that the riboflavin content of eggs is influenced by the ration fed to laying hens (Heiman, 1935; Bethke, Record and Wilder, 1936). With regard to what has been said before concerning the relative importance of albumen and yolk for hatchability, it is interesting to note that vitamin B₁ was found to be confined to the egg yolk, while riboflavin is present both in albumen and yolk. Further evidence for the necessity of riboflavin for high hatchability was presented by Norris, Heuser, Ringrose, Wilgus and Heiman (1934), Norris, Wilgus, Ringrose, Heiman and Heuser (1936) and Sergeev and Kudriavtsev (1941). The results of Norris, Wilgus, Ringrose, Heiman and Heuser are graphically shown in Figure 22 which demonstrates that up to a certain concentration of riboflavin in the feed there is a nearly direct proportionality of increase in hatchability with increase in riboflavin intake by the laying hens, while after a satisfactory level has been reached, no further improvement results.

Further data concerning the effect of riboflavin deficiency on embryonic mortality and hatchability were given by Davis, Norris and Heuser (1938 a). These authors demonstrated also that riboflavin deficiency leads to a retardation of embryo growth.

Investigations by Lepkovsky, Taylor, Jukes and Almquist (1938) showed that the characteristic embryonic abnormalities produced by riboflavin-deficient diets consisted of edema, commonly found in embryos dying between 9 and 14 days; of degeneration of the embryonic Wolffian bodies, generally observed in embryos dying between 17 and 21 days; of “clubbed” down and dwarving in body size.

 Apparently riboflavin deficiency plays also a role in producing embryonic anemia, though still other agencies may be at work in this respect. According to Rozenbakh (1941), Romanoff and Bauerfeind (1912) and McClymont and Hart (1947) embryonic micromelia is another symptom of riboflavin-deficiency. The distribution of embryo mortality on rations with and without riboflavin is shown in Figure 23. Romanoff and Bauerfeind (1942) obtained a similar curve of embryonic mortality, but made the important observation that riboflavin depletion occurred
Figure 22
The quantitative relationship between intake of vitamin B₂ (G) by laying hens and hatching quality of their eggs (From Norris, Wilgus, Ringrose, Heiman and Heuser, 1936).

at different rates in different hens and that, to an appreciable extent, the three peaks of mortality among the progeny represent a composite picture, the highest peak of embryo mortality being shifted the more to earlier incubation stages the greater is the riboflavin depletion of the maternal body and, as a consequence, of the eggs. The occurrence of myelin sheath degeneration of the peripheral nerves was shown by Engel, Phillips and Halpin (1940) in a large percentage of embryos developing in riboflavin deficient eggs.

In order to obtain eggs with good hatching quality the feed of laying hens must contain at least 220 to 230 micrograms of riboflavin in each 100 grams (Hunt, Winter and Bethke, 1939). Under somewhat different experimental conditions such an amount was found quite adequate by Petersen, Lampman and Stamborg (1947). According to these investigators 360 micrograms per 100 grams of feed was marginal, any higher concentrations giving satisfactory results. Observations by W. O. Brown (1951, 1952), by Hill, Norris and Scott (1954), Coles and Cumber (1955) and by Morimoto, Hizikuro and Arivoshi (1957) led to similar conclusions. Hill, Norris and Scott reported, in addition, that for normal development the yolk of eggs must contain at least 2.5 to 3 micrograms/gram of riboflavin. Further information concerning the role of riboflavin in practical breeding rations may be found in a publication by
Figure 23
Distribution of embryonic mortality on rations with and without riboflavin.
(From Leipkovsky, Taylor, Jukes and Almquist, 1938).
There is a possibility that hereditary factors exist which influence the requirements and/or utilization of riboflavin, and thereby influence the quantitative importance of this vitamin for hatchability. (Davis, Norris and Heuser, 1938 b; Lamoreux and Hutt, 1948; Oregon Agricultural Experiment Station, 1950). Mayfield, Odland, Page and Halbrook (1953) observed differences between individual hens in the riboflavin content of their eggs, independent of rate of production. Maw (1954) found evidence in a flock of White Leghorns that certain females were unable to deposit adequate amounts of riboflavin in their eggs. The embryos in such eggs died between the tenth and fourteenth day of incubation. Injection into these eggs of a sufficient amount of riboflavin led to normal development and the hatching of viable chicks. Preliminary data suggest that this "metabolic error" of the mothers is a hereditary trait. Further work seems to have established that the trait is due to a single recessive mutant gene (rd).

Buss, Boucher and Maw (1959) have reported the following values, in mcg/g, for free riboflavin content of the yolk of eggs, laid by hens of the three genotypes: RdRd 4.30, rdRd 2.50 and rdrd 0.41. Injection into eggs of rdrd mothers of 60 mcg riboflavin at 10 days of incubation led to a 96 percent hatch. Furthermore, it is very interesting that this metabolic error does not interfere with the production of normal amounts of flavin adenine dinucleotide and flavin mononucleotide of laying rdrd hens. For free riboflavin of the blood of laying birds Boucher, Buss and Maw (1959) found the following concentrations in mcg/g: RdRd 0.434, rdrd 0.272 and rdrd 0.008. The free riboflavin level in the blood of laying rdrd hens is identical with that of the non-laying birds of the two other genotypes. A brief report by McNary and Bell (1957) suggests the possible existence of a similar situation in an inbred family of fowl. The discrepancy, as far as embryo malformations are concerned, between the effects of riboflavin-deficient maternal diets and the consequences of the mutant condition which prevents the rise in blood-riboflavin level at sexual maturity and hence storage of sufficient amounts of the vitamin in eggs, remains to be elucidated.

Pantothenic acid (the so-called antidermatosis vitamin or filtrate factor component of the vitamin G complex) was believed by Lepkovsky, Taylor, Jukes and Almquist (1938) to have no effect on hatchability. The investigations of Bauernfeind and Norris (1939 a and b), Taylor, Thacker and Pennington (1941) and especially those of Gillis, Heuser and Norris (1942 a and b; 1947, 1948) have shown beyond doubt, however, that the presence of pantothenic acid in the diet of laying hens is essential for the production of hatchable eggs. The latter authors found that the pantothenic acid requirement for good hatchability is between 650 and 1000 micrograms per 100 grams of diet. On pantothenic acid deficient diets the embryos die late in incubation without showing characteristic abnormalities. It was also found that the effectiveness of pantothenic acid is increased by adding heated liver extract to the diet. Accord-
ing to Balloun and Phillips (1957) 3 mg/lb. feed of pantothenic acid are adequate for satisfactory hatchability if the diet of laying hens contains sufficient amounts of vitamin B₁₂, but more than 4.5 mg/lb. are needed on a B₁₂-deficient diet. It was found that on a diet low in pantothenic acid, added amounts of vitamin B₁₂ appreciably increased the deposition of pantothenic acid in the eggs. Hence the authors see in this interesting relationship a confirmation of an hypothesis advanced by Evans, Groschke and Butts (1951), according to which vitamin B₁₂ aids in the transfer of pantothenic acid from the liver to other parts of the body. An analog of pantothenic acid interfered with embryonic development (Kimura and Ariyama, 1959).

Briggs, Groschke and Lillie (1946) demonstrated that nicotinic acid (vitamin B₃) is indispensable for hatchability. The amount required in a ration depends on the amino acid balance of the feed. The presence of an excessive amount of a protein low in tryptophan (e.g., ossein) in a purified, nicotinic-acid low ration produced nicotinic acid deficiency which led within three weeks to complete failure of any eggs to hatch. Following the addition of 50 mg. of nicotinic acid to each 100 g. feed hatchability improved rapidly. Hansborough (1947) reported that an excess of nicotinic acid, supplied by injection into the albumen of eggs, led to the occurrence of abnormalities in the nervous and vascular systems of chicken embryos, but it remains to be determined whether or not these defects were specific responses. On the other hand, it was shown by Ackermann and Taylor (1948) that injection into the yolk sac at 96 hours of incubation of 3-acetylpyridine, a niacin antagonist, was responsible for hypoplasia of the skeletal musculature, sometimes accompanied by shortening of the upper beak, and generalized edema. When nicotinamide was injected together with 3-acetylpyridine, the embryos developed normally. It is interesting that another niacin antagonist, 6-amino- nicotinamide, has quite different teratological effects (Landauer, 1957 d). Injection at 24 hours is responsible for a high incidence of rumplessness; treatment at 96 hours produces embryos with micromelia and parrot beak. As in the case of 3-acetylpyridine, supplementary nicotinamide provides complete protection against the teratogenic action of 6-amino- nicotinamide. Moreover, the effects of both 3-acetylpyridine and 6-amino- nicotinamide can be forestalled nearly completely by the simultaneous injection of either 3-hydroxyanthranilic acid or tryptophan.

A deficiency of the feed in vitamin B₆ (in different forms known as pyridoxal, pyridoxamine and pyridoxine) has, according to Gravens, Sebesta, Halpin and Hart (1943, 1946), a much more adverse effect on egg production than on hatchability, and its influence on the latter is for this reason not easily tested by the usual methods. It has been shown, however, by Gravens and Snell (1949 a and b) that early embryonic development of the chick is inhibited by desoxypyridoxine, a metabolic antagonist of vitamin B₆, and that this inhibition can be prevented by simultaneously injecting into the eggs adequate amounts of vitamin B₆. These conclusions have been confirmed by Karnofsky, Stock, Ridgway and Patterson (1950) on the basis of tests with methoxypyridoxine.
Studies by Taylor (1947) first indicated that folic acid (pteroylglutamic acid) was indispensable for good hatchability. This is supported by the earlier observations of Cravens, Sebesta, Halpin and Hart (1942 b) concerning the effect on hatchability of the so-called Lactobacillus casei factor, now known to be identical with synthetic folic acid. The quantitative requirements of dietary folic acid appear, however, to be very slight (Schweigert, German, Pearson and Sherwood, 1948). On an unsupplemented diet hatchability dropped to zero by the end of the sixth week, but returned to a normal level when 0.1 to 0.8 mg. of the vitamin were added to each kilogram of feed (Couch, German and Pearson, 1949: Couch and German, 1950). Similar results were obtained by Sunde, Cravens, Bruins, Elvehjem and Halpin (1950), whereas slightly lower estimates of the critical level of folic acid needs were made by Lillie, Combs and Briggs (1950). Bends in the tibiotarsus, syndactylism, parrot beak and other beak defects have been described as morphological symptoms of folic acid deficiency. The majority of deficient embryos, however, died towards the end of the incubation period without showing gross defects. The time of death varies with the degree of deficiency. The appearance of deficiency symptoms can be prevented by injecting folic acid into the eggs (Sunde, Cravens, Elvehjem and Halpin, 1950 b). Folic acid antagonists produce a general stunting of embryo growth and the occurrence of developmental abnormalities (Wagley and Morgan, 1948; Karnofsky, Patterson and Ridgway, 1949; Snell and Cravens, 1950).

Biotin is of great importance for hatchability (Cravens, Sebesta, Halpin and Hart, 1942 a; Couch, Cravens, Elvehjem and Halpin, 1947). When biotin concentrate was added to a basal diet which had led to the death of nearly all embryos, the hatching quality of eggs rose to 80 per cent in the course of three weeks. In eggs produced on a biotin-deficient diet peaks of excessive embryo mortality were found on the third day of development and toward the end of incubation. The occurrence of a micromelia, similar in appearance to and probably identical with sporadic chondrodystrophy (which will be discussed later), seems to be a characteristic feature of biotin deficiency (Cravens, McGibbon and Sebesta, 1944; Couch, Cravens, Elvehjem and Halpin, 1948 a). Normal hatchability of eggs produced on a biotin-deficient diet can be restored by injecting into the albumen approximately 10 γ of crystalline biotin. This must be done at the beginning of incubation, the effectiveness decreasing to zero by 120 hours of development (Couch, Cravens, Elvehjem and Halpin, 1949).

On a synthetic diet containing sucrose as the source of carbohydrate, hatchability fell to zero within three weeks. There was a simultaneous reduction of biotin in the yolk from 510 to 48 micrograms and in the albumen from 65 to less than 15 micrograms per gram of substance. When biotin was added to this diet (200 γ per kg.) hatchability returned to a normal level. With dextrin instead of sucrose as the carbohydrate, hatchability and biotin content of the eggs declined less drastically. These
results suggest that the occurrence or non-occurrence of intestinal biotin synthesis depends on the available dietary carbohydrates (Cravens and Couch, 1947; Couch, Cravens, Eilertsen and Halpin, 1948 b).


Vitamin B<sub>12</sub> appears to be identical with the previously unidentified hatchability factor in fish meal (Lindstrom, Petersen, Wiese and Moore, 1949) and other animal proteins, including that in cow manure (Lillie, Olsen and Bird, 1949), to be discussed below (p. 110). It has, in fact, now been shown that an all-vegetable protein ration, when properly supplemented with a source of vitamin B<sub>12</sub>, will support very satisfactory hatchability (Skinner, Quisenberry and Couch, 1951). Hill, McConachie, Cartley and Brandon (1950) observed that on a diet deficient in vitamin B<sub>12</sub> the maximum embryo mortality occurred between 8 and 14 days of incubation. The principal deficiency symptoms were edema about the eyes, shortening of the beak, curled toes and poor leg muscle development. Olcese, Couch, Quisenberry and Pearson (1950) reported that the peak of embryo mortality on a vitamin B<sub>12</sub>-deficient diet occurred between the sixteenth and eighteenth day of development and that myoatrophy of the legs and hemorrhages were the principal gross symptoms. There is marked dwarfing and edema (Ferguson, Rigdon and Couch, 1955). The thyroid is enlarged, the walls of the digestive tract are thin, and about half of the B<sub>12</sub>-deficient embryos had a fatty liver and a dilated, irregularly-shaped heart (Ferguson and Couch, 1954 a, b). Liver, brain and spinal cord contained focal areas of necrosis and the amount of fat was increased in the parenchymatous tissues (Ferguson, Rigdon and Couch, 1955). In the spinal cord of B<sub>12</sub>-deficient embryos the number of myelinated fibers was markedly reduced, as was the size and number of multipolar cells in the ganglia of the spinal cord and the sympathetic trunk (Ferguson, Alexander and Couch, 1956). With eggs produced on B<sub>12</sub>-deficient diets hatchability can be improved by injecting vitamin B<sub>12</sub> into the yolk sac: injection into the albumen has no effect (Källai, Aros, Biskup and Krlovánszky, 1955). Analogous to vitamin B<sub>12</sub> interferes with normal development (Coates, Davies and Harrison, 1960).

Experiments conducted by Peeler, Miller, Carlson, Norris and Heuser (1951) demonstrate, however, that after prolonged vitamin B<sub>12</sub> deficiency of laying hens, embryo mortality may occur so early as to simulate infertility. Vitamin B<sub>12</sub>-deficiency is responsible for a marked decrease in
phospholipids, especially cephalin and sphingomyelin, in the embryo (Yesair, MrOsher and Daniel, 1959), and the level of vitamin \( B_{12} \)-intake affects the storage of folic acid in the yolk of eggs (Welch, Perreti, Clements and Couch, 1954). On a vitamin \( B_{12} \)-free diet the addition of penicillin raised hatchability from zero to 39 percent (Elam, Gee and Couch, 1951; Elam, Jacobs and Couch, 1953; also Müller, 1958). Sizemore, Lillie and Bird (1952), Sizemore, Lillie, Denton and Bird (1953) as well as Havermann and Wegner (1958) and Gerrets (1960) reported similar results after using aureomycin supplements in the vitamin \( B_{12} \)-deficient diet of growing chicks and Mariakulaidai, Myint and McGinnis (1952) obtained an improvement of hatchability with terramycin supplements, but other experiments with added antibiotics led to negative results (Lillie and Bird, 1952) or to inconsistent effects (Bentley and Hershberger, 1954). The advantage derived from aureomycin supplements given to growing chicks may persist in the hatching results of the second laying year (Sizemore, Lillie, Bird and Denton, 1955). On complete rations, supplements of antibiotics had no effect on hatchability (Smith, Delaplane and Wiley, 1952; Waibel, Sunde and Cravens, 1952; Sherwood and Milby, 1954; Gordon, Chubb and Stacey, 1954; Heywang, 1956, 1959; Thornton and Moreng, 1958; Carlson, 1959; Saxena and Kumar, 1959). The beneficial effects of antibiotics in combination with vitamin \( B_{12} \)-deficient diets are presumably the result of changes in the intestinal flora and a consequent stimulation of vitamin \( B_{12} \)-synthesis.

Studies by Yacowitz, Miller, Norris and Heuser (1952) led to the conclusion that on an all-vegetable diet containing 25 percent protein the vitamin \( B_{12} \) requirement for good hatchability is about 0.2 \( \gamma \) per 100 grams of feed, and that the embryos needed approximately 2.5 \( \gamma \) per gram of yolk. On the basis of tests with New Hampshires Milligan, Arscott and Combs (1952) reported similarly that the requirement for normal hatchability is about or slightly more than 2.2 \( \gamma \)/kg. feed, but Mariakulaidai and McGinnis (1953) estimated the need as not over 1 \( \gamma \)/kg. As might be expected, the requirements vary with different methods of management. Petersen, Wiese, Milne and Lampman (1953) found, for instance, that on built-up litter about 1.7 \( \gamma \)/kg. vitamin \( B_{12} \) are required, but that in laying cages or on raised wire floors as much as 3.3 to 4.4 \( \gamma \)/kg. may be needed. On a vegetable diet Johnson (1954) found that 1 to 2 \( \gamma \)/kg. added vitamin \( B_{12} \) sufficed. Chin, Anderson, Miller, Norris and Heuser (1958) reported for White Leghorns that in the presence of adequate amounts of riboflavin the \( B_{12} \) requirement was 0.5 to 1 \( \gamma \)/kg. feed, but as much as 2 to 4 \( \gamma \)/kg. if the available riboflavin was inadequate. There were great (genetic?) differences between hens in the amounts of vitamin \( B_{12} \) which they deposited in their eggs.

Dehydrated alfalfa leaf meal was reported by Jacobs, Elam, Quisenberry and Couch (1953) to contain an unidentified factor promoting hatchability. Jensen and McGinnis (1957) suggested that vitamin K was the responsible agent, but no experimental evidence is yet available in
Table 26

<table>
<thead>
<tr>
<th>U.S.P. units of vitamin D fed per 100 g. of feed</th>
<th>10</th>
<th>19</th>
<th>39</th>
<th>58</th>
<th>78</th>
<th>116</th>
<th>155</th>
<th>0 (range)</th>
<th>39 (range)</th>
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</thead>
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<tr>
<td>Average weight of eggs in g.</td>
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<td></td>
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<tr>
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<td>51.7</td>
<td>52.7</td>
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<td>Average blood serum calcium of laying hens.</td>
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<td>Calcium in mg. per 100 cc. blood serum.</td>
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<td>21.4</td>
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<td>Average shell weight in % of total egg weight</td>
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<td>8.9</td>
<td>8.8</td>
<td>9.1</td>
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<tr>
<td>Average ash content of egg shell in %</td>
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<tr>
<td>1932-1933</td>
<td>52.1</td>
<td>52.4</td>
<td>52.0</td>
<td>52.3</td>
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<td>54.7</td>
<td>52.6</td>
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<td>53.4</td>
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<tr>
<td>1934-1935</td>
<td>41</td>
<td>111</td>
<td>191</td>
<td>290</td>
<td>247</td>
<td>300</td>
<td>300</td>
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<tr>
<td>Average % hatch of fertile eggs</td>
<td></td>
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<tr>
<td>1932-1933</td>
<td>56.4</td>
<td>44.5</td>
<td>74.6</td>
<td>84.5</td>
<td>84.0</td>
<td>88.1</td>
<td>87.8</td>
<td>91.0</td>
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<td>79.6</td>
<td>74.2</td>
<td>86.5</td>
<td>77.1</td>
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</table>
support of the conclusion that vitamin K influences embryo survival and hatching.

The presence of vitamin D in eggs is necessary for normal hatching ability, and in order to be deposited in the eggs in sufficient quantities, vitamin D or its precursor must be supplied to laying hens through the feed, or the hens must be exposed to direct sunlight or to ultraviolet radiation. Out of the many publications bearing on these questions, reference is here made only to the work of Hughes, Payne and Latshaw (1924-1925), Hart, Steenbock, Lepkovsky, Kletzen, Halpin and Johnson (1925), Holmes, Brown, Smith, Treadwell and Whitelock (1925-1926), Martin and Insko, Jr. (1929), Martin, Erikson and Insko, Jr. (1930), Graham, Smith and McFarlane (1931), Martin and Insko, Jr. (1933), Payne and Hughes (1933), Murphy, Hunter and Knandell (1934), Carver, Robertson, Braze, Johnson and St. John (1934), and Insko, Jr. and Lyons (1936). Further literature will be found in these publications.

Nestler (1937) reported that the addition of 2 percent cod liver oil to an otherwise complete all-mash ration, or the exposure of the confined laying hens to ultraviolet irradiation for 15 minutes daily (carbon arc, distance 3 feet, intensity 3400 to 4000 Angstrom units) gave comparable hatching results. Hens appear to require somewhat higher amounts of vitamin D than pullets for equal hatchability of their eggs (Couch, James and Sherwood, 1947).

In laying hens which receive inadequate supplies of vitamin D the blood calcium falls below the normal level. Such hens lay small eggs with shells which are reduced in total relative weight as well as in ash content (calcium); hatchability of these eggs is decreased. All this is illustrated by the data of Table 26, giving the results of Murphy, Hunter and Knandell (1936) from two years’ experimentation with White Leghorn females which had been kept on diets with varying vitamin D content.

It was demonstrated that embryos developing in eggs which had been produced on diets deficient in vitamin D were unable to obtain the normal amounts of calcium and phosphorus (Insko, Jr. and Lyons, 1936). This is shown by the data in Table 27. The experimental birds were confined to a chick house with the sunshine filtered through window glass. One group received no cod liver oil, while 2 percent of cod liver oil was added to the feed of the other group. As incubation proceeded, the embryos in the D-deficient group fell increasingly behind the normal ones in calcium and phosphorus content. The apparent recovery at the end of the incubation period is unquestionably explained by the fact that the embryos most deficient in the two substances had died by then, since according to Insko and Lyons the peak of mortality fell on the eighteenth and nineteenth day. During the first two weeks of incubation vitamin D deficiency apparently does not cause an increase in embryonic death rate, but during the last week mortality is much greater than normal (Figure 24).
Factors other than shell quality and calcium metabolism may affect the hatching quality of eggs as a consequence of vitamin D deficiency. Heuser (1927), with reference to feeding experiments with cod liver oil and yeast, raised the question whether or not increased hatchability, following the addition of one or the other of these substances to the diet, is due to a definite vitamin or to an improved general physiological condition of the birds. He found that eggs from hens which at the time were gaining in body weight showed 71.6 percent hatchability; those from hens with a constant weight had 66.2 percent hatchability, and those from hens which were losing weight hatched only 61.2 percent.
While these relationships are interesting, they hardly offer a basis for conclusions since effects of vitamin deficiency may well be reflected simultaneously in the physical condition of the hens and the hatching quality of their eggs.

Dmitrieva (1935) reported that irradiated yeast was a more effective supplement for D-deficient diets than cod liver oil. She observed that birds on a D-deficient ration laid many abnormally shaped eggs, and also that the incidence of “chondrodystrophy” was much increased. With regard to the latter statement, it is likely that some other form of micro-melia had occurred, possibly the one that is brought on by manganese deficiency.

The fact that the presence of the Creeper trait causes an earlier appearance and more severe expression of the symptoms of vitamin D deficiency in growing chicks (Landauer, 1934) suggests that the vitamin D needs for the production of eggs with high hatching quality may vary with the presence or absence of certain genetic factors.

An excess of vitamin D in the diet leads to a decline of hatchability, with a drop to zero in case of extreme overdosage (Brannon and Smith, 1932; Titus and Nestler, 1935; Heywang, 1944 a).

With regard to what is known concerning the importance of vitamin D for hatchability, it is interesting to inquire if exposure of eggs either to direct sunlight or to ultraviolet radiation will affect their hatching quality. Fronda and Belo (1928) obtained a significant improvement of hatchability by exposing eggs to direct sunlight before they were put into the incubator and either every day or every third day thereafter until the eighteenth day of incubation. A number of studies have been made concerning the effect of ultraviolet radiation on the hatching quality of eggs. Hart, Steenboch, Lipkovsky, Kletzien, Halpin and Johnson (1925), Boyd (1928), and Kuêma (1928, 1929) failed to observe a beneficial effect of irradiating eggs, but Iguchi and Mitamura (1928), Cholevčuk (1929), and Sheard and Higgins (1928/1929, 1930) found that hatchability increased somewhat when eggs were exposed to ultraviolet radiation. According to Sheard and Higgins treatment was especially effective when incubation conditions were unfavorable on account of high humidity. Romanoff and Ludlam (1943) found that repeated exposure of incubating eggs to ultraviolet radiation failed to improve hatchability, but it produced an acceleration of development, resulting in somewhat earlier emergence of the chicks from the shells.

Experiments which were carried out at the Storrs Agricultural Experiment Station sustained the conclusion that ultraviolet treatment of hatching eggs during the incubation period may increase hatchability to a certain extent (Landauer, 1932 b). This is shown by the data in Table 28 which were obtained with eggs from inter se matings of Creeper fowl. The experiments represented by groups I and II were run simultaneously.
with stock of the same ancestry; the difference in hatchability of the eggs of these two groups amounted to $12.9 \pm 1.91$ percent in favor of the irradiated lot. Groups III and IV are one and the same mating, first used as control (III) and subsequently for irradiation of the eggs (IV); the difference in hatchability between groups I and IV was $8.5 \pm 1.87$ percent, again in favor of the group in which the eggs had been irradiated. There can be no doubt about the statistical significance of these differences. The generally low hatchability in these experiments is explained by the fact that we are dealing with birds carrying a lethal mutation, and that mortality of the lethal embryos was not affected by the ultraviolet treatment. The increase in hatchability was shared in similar proportions by the heterozygous Creeper and normal embryos which were segregating in these matings.

### Table 28

<table>
<thead>
<tr>
<th>Group</th>
<th>Treatment</th>
<th>Number of fertile eggs</th>
<th>Fertile eggs hatched %</th>
</tr>
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<tbody>
<tr>
<td>I</td>
<td>none</td>
<td>793</td>
<td>47.4 ± 1.48</td>
</tr>
<tr>
<td>II</td>
<td>Repeated irradiation of eggs with Cooper Hewitt lamp</td>
<td>875</td>
<td>60.3 ± 1.21</td>
</tr>
<tr>
<td>III</td>
<td>Parents treated with sunlamp: eggs not irradiated</td>
<td>471</td>
<td>49.6 ± 3.64</td>
</tr>
<tr>
<td>IV</td>
<td>Repeated irradiation of eggs with sunlamp</td>
<td>345</td>
<td>55.9 ± 1.15</td>
</tr>
</tbody>
</table>

In still other experiments it was shown that the hatchability of eggs of Frizzle fowl was not improved by ultraviolet treatment. To this we shall refer later. In general, it may be concluded that, at least with the eggs of some stocks, ultraviolet treatment during the incubation period will improve the hatching quality of eggs. It is also true, however, that this improvement is relatively slight in extent. This may be due to the fact that only small quantities of ultraviolet energy penetrate through the egg shell. There is reason to believe that ultraviolet irradiation of eggs does not serve as a source of vitamin D for the embryo, but that its beneficial results are due to a more general effect on metabolism and growth. More recent observations in Russia and Hungary tend to confirm the conclusion that small, but significant improvements of hatching may be obtained by pre-incubation exposure of eggs to ultraviolet rays (Kodinecz and Lacza, 1954; Kodinecz, 1955; Gudkin, Nurnisze and Smirnov, 1959). The feeding of a gamma-irradiated diet, on the other hand, may be responsible for a rise in embryo mortality during the last week of incubation, probably on account of the destruction of vitamin D (Burns, Brownell and Eckstein, 1956).

The presence of vitamin E is also necessary in eggs in order to obtain normal hatching results, and this vitamin must be supplied to the laying hens with the feed so as to enable the birds to deposit the needed amounts in their eggs (Card, 1928-1929; Card, Mitchell and Hamilton, 1930;
In the experiments of Card, Mitchell and Hamilton Rhode Island Red pullets, after they had reached the age of eight weeks, were raised on a diet in which vitamin E had been destroyed by treatment with ferric chloride. These females later on were used for matings; the males in the matings were supplied with vitamin E. Out of 317 fertile eggs, only 41 developed beyond the ninth day of incubation, and none hatched.

During the latter part of the hatching season only nine embryos among 192 fertile eggs survived the sixth day and these died at later stages. When vitamin E, in the form of wheat germ oil, was administered, hatchability in successive settings became 32.6, 61.7, 61.7, and 69.4 percent, respectively. When vitamin E was discontinued once more, the hatching quality of the eggs declined at once and, within two weeks, dropped to almost zero. It was found that the embryo mortality caused by vitamin E deficiency has its peak between 84 and 96 hours of incubation. As early as 24 hours after the starting of incubation the embryos showed retarded development, both in growth and in differentiation. Hemorrhages and other disturbances in the circulatory system seem to be the principal direct cause of death (Adamstone, 1931), though the early developmental retardations may in turn be responsible for these symptoms. It should be noted, however, that, when an otherwise complete ration is fed to laying hens, the addition of wheat germ oil may not improve hatchability significantly (Dols, 1937).

According to a report by Heyn (1951) certain preparations of vitamin T improve hatchability. This is a vitamin which Goetsch first found in extracts from termites. Heyn's data are not very convincing and his techniques leave much to be desired, especially in regard to the basal diets used. Further observations must be awaited, and one hopes that the possible relationship of vitamin T to members of the B-group will be studied.

It has been claimed that the feeding of follicular hormone to laying hens materially increases the hatching quality of eggs (Koch, 1935, 1936, 1937; Westermayer, 1936). Extensive tests by Prüfer (1936) and by Ebbell (1938) failed, however, to substantiate any such effect of follicular hormone. Simon (1939) found that the feeding of follicular hormone improved hatchability in some instances, but that in the majority of cases no such response was obtained. Negative results were also recorded by Adams, McGibbon and Casida (1951). Subcutaneous implantation of a single pellet (12 or 15 mg.) of diethylstilbestrol at the age of eight or nine weeks had no effect on the hatchability of eggs laid subsequently (Fraps, Sohn and Olsen, 1956; Talmadge, 1959), but multiple pellets affected hatchability adversely to at least 180 days after implantation. Stefani (1936) reported that the injection into eggs of small amounts of prostate, follicular or testis extracts did not alter the length of the incubation period.
Proteins and fatty acids

Various experiments have been made with regard to the effect of proteins of different origin on hatchability. It is difficult, however, to evaluate the available evidence, since in many cases it may only be a question of how good a source a particular animal protein is for vitamin B₁₂ or other vitamins. Reservations of a similar nature seem to apply to much of the experimentation in this field. A proper balance of proteins and other nutrients is unquestionably important for the production of eggs with good hatching quality (e.g. Sherwood, 1957). An excessive amount of protein in the feed may, according to Sergeev and Kudriavtsev (1941), lead to the production of eggs without shells. For a general review of earlier work see Heuser (1911). Fat-free diets do not prevent the production of hatchable eggs (Reiser, Gibson, Carr and Lamp, 1951).

In using buttermilk powder, fish meal, tankage or meat meal as protein supplements to the diet McFarlane, Fulmer and Jukes (1930) obtained wide variations in the hatching quality of eggs and in the stage of development at which the highest mortality occurred. But chemical analysis did not reveal significant differences between the eggs of high and low hatching groups with regard to the relative amounts of total nitrogen, total amino-nitrogen, tyrosine, tryptophan and cystine in the egg contents. The source of origin or methods of manufacture appear to play a considerable role with regard to the value (for hatchability) of protein supplements. Thus, in the experiments to which reference was just made, tankage as a protein supplement produced a very low hatching quality, while this was not true in experiments carried out by Francisco, Chan and Fronda (1934). Similar experiences were recorded by Byerly and his associates. Ingram, Graves, Elvehjem and Hatpin (1950) found that on diets deficient in lysine and tryptophan no changes occurred in the tryptophan, lysine, cystine or methionine content of the eggs and hatchability was not altered.

Titus, Byerly, Ellis and Nestler (1936) found definite differences in the value for hatchability of different types of beef products; for example, ground and dried lean meat or blood meal were inferior to all-beef scrap. Call and Wilcke (1939), comparing the effect of different grains in feeding rations, reported best hatching results with wheat, less satisfactory ones with oats, and still lower hatches with corn, but even rations with high wheat content are inadequate for good hatching results, presumably on account of riboflavin deficiency (McGlymont and Hart, 1947). According to J. B. Smith (1934) there is a difference in the degree to which sunshine (via the body of laying hens) improves the hatching quality of eggs, depending on the kind of protein supplement used in the feed. Hammond (1942) reported on the value of milo and hegari (types of sorghum) for the production of hatching eggs. Olsen (1942) found that laying hens fed on acorns of white oaks produced eggs with olive-colored yolks and the hatchability of such eggs appeared to
be reduced. The hatching power of eggs suffers also greatly by the addition to the diet of beta-aminopropionitrile, a compound found in the seeds of the sweet pea, Lathyrus odoratus, of the chick-pea, Cicer arietinum, and of certain other vetches (Barnett, Riechey and Morgan, 1957). Rosenberg (1957) found that this compound is responsible for the appearance of malformations if injected into developing eggs on the fourth or seventh day of incubation. The toxicity of beta-aminopropionitrile can be partially reversed with supplementary calcium pantothenate (Naber and Dunn, 1959).

Lupine seed is reported by Skuratov (1957) to contain an ingredient that reduces hatchability when the seed is added to the feed of laying hens.

The investigations of Ringrose, Morgan and Lease (1941) and of Naber and Morgan (1957) have shown that cottonseed oil contains certain fatty acids which reduce hatchability when the oil is used as a supplement to otherwise satisfactory feed mixtures. An addition of 3.6 percent of cottonseed oil to the ration produced a decline in hatchability from 80 percent to less than 30 percent. Excessive amounts of cottonseed meal (20 to 30 percent) or of cottonseed (3 3/4 percent) in the diet of laying hens have an adverse effect on hatchability, apparently on account of the toxic action of gossypol (Heywang, Denton and Bird, 1949; Heywang, Bird and Altschul, 1950). It is not entirely clear whether or not the noxious principles in cottonseed oil and cottonseed meal are actually separate entities. Moreover, cottonseed meal is probably deficient in vitamin B₁₂ and lysine (Heywang and Bird, 1950; Heywang, Bird and Kupperman, 1952).

Contradictory results have been reported for the effect of soybean oil meal on hatchability. Wilgus and Gassner (1941), Wilgus and Zander (1944) and Bird, Rubin, Whitson and Haynes (1946) observed a lowering of hatchability when soybean meal was added to the diet of laying hens. Carver, McGinnis, McClary and Evans (1946) found similarly that soybean oil meal, when used as the only protein supplement, had a detrimental effect on the hatching quality of eggs. On the other hand, Card (1942), Heywang (1942), Heuser and Norris (1944), and Clark and Cunningham (1945) observed no lowering of hatchability as a consequence of feeding soybean meal supplements. These discrepancies may possibly find an explanation in peculiarities of the residual diets which were used in the various experiments. There is no doubt, at any rate, that raw soybeans (all varieties) contain a growth-inhibiting substance (Klose, Hill and Fervold, 1946; Potter and Kummerow, 1954). Furthermore, soybean oil meal was found to be deficient in a hatchability factor which is present in meat scraps, menhaden fish meal and, in lesser amounts, in dried skim milk, casein and dehydrated alfalfa meal (Bethke, Record, Kennard and Chamberlin, 1946; Pensaek, Bethke and Kennard, 1949) and which is, at least in part, now identified as vitamin B₁₂.
The harmful effects on hatchability of large amounts of soybean meal in a diet which does not contain animal protein can be counteracted by adding 5 to 8 percent of dried cow (or steer) manure to the feed (Whitson, Titus and Bird, 1946 a and b; Bird, Rubin, Whitson and Haynes, 1946). Experiments with an acid precipitate of a water extract of cow manure suggested that the same dietary factor in cow manure influences hatchability as well as growth of chicks (Bird, Rubin and Groschke, 1947; Rubin, Groschke and Bird, 1947). As a practical application of these observations Kennard, Bethke and Chamberlin (1948) have reported that built-up floor litter is a potent source of these dietary factors. More recent observations by Lillie, Olsen and Bird (1949) have shown that vitamin B\textsubscript{12} is the effective ingredient in cow manure.

Certain fats, if added to the diet, produce a disease in which hydropericardium and other edematous symptoms are particularly obvious. The toxic constituent of such fats is located in the nonsaponifiable fraction of the ether extract. In laying birds toxic fats will reduce hatchability of their eggs (Edgar, Bond, Melius and Ingram, 1958; Naber, Bletner and Touchburn, 1958; Dunahoo, Edwards, Schmittle and Fuller, 1959).

Dietary choline deficiency, by some included among the B-avitaminoses, may, according to Jukes (1940) and Hogan, Richardson, Patrick and Kempster (1941), be responsible for skeletal abnormalities of the embryo similar to those resulting from manganese deficiency (see below). Lucas, Norris and Heuser (1946) found, however, that laying hens apparently can synthesize adequate amounts of choline. According to Balloun (1956) the choline requirement of breeding hens does not exceed 500 mg./lb. of diet. Further information will be needed to clarify whether or not dietary choline deficiency has an appreciable effect on the hatching quality of eggs. Diets which were deficient in leucine and either tryptophan or methionine reduced egg production drastically, but had no effect on hatchability. It appears that, as long as eggs are produced at all, they are supplied with these amino acids (Cravens, 1948). Yet, Mehring, Titus and Waddell (1954) observed some beneficial effect of methionine on hatchability when the amino acid was used as a supplement to a corn-soybean diet. The existence of hereditary differences in methionine utilization (McDonald, 1957, 1958) may provide interesting material for further studies.

Youngner, Ward and Salk (1950) from observations that cannot be discussed in detail, are led to believe that chicken embryos require guanine (an amino purine of nucleic acids) and that they may be unable to synthesize it. An unidentified factor promoting hatchability has been reported repeatedly (e.g., Kurnick, Soucha, Reid and Couch, 1956) from experiments in which a synthetic diet was supplemented with liver preparations, fish solubles or fermentation products. But it has also been observed that certain samples of fish meal have a depressing effect on
hatching (Coles, 1956 a). Supplementation of feed with the antimicrobial compound N-(5-nitro-2-furfurylidene)-3-amino-2-oxazolidone (Furazolidone) had no effect on hatchability (Francis and Shaffner, 1955; Dean and Stephenson, 1958).

**Minerals**

The importance of calcium in feed as a factor in hatchability has already been discussed in connection with the role which the egg shell plays in hatchability and in relation to the importance of vitamin D. It should here be added, however, that Titus, Byerly, Ellis and Nestler (1937) observed a decrease of hatchability when the calcium level of the diet was high. The increase in embryonic mortality concerned chiefly the last three days of incubation. The detrimental effect of a high calcium level appeared to be more pronounced when the phosphorus intake amounted to 0.9 instead of 1.2 percent. These authors found also that calcium carbonate led to more satisfactory hatchability than calcium sulphate. Calcites of different origin and containing varying amounts of impurities may differ significantly in regard to their effect on hatchability (Little and Thompson, 1947). Experiments reported by O'Rourke, Bird, Phillips and Cravens (1954 a, b) have demonstrated that an intake of 0.19 percent phosphorus is inadequate for maintaining normal hatchability. When sufficient Ca HPO₄ • 2H₂O was added to the ration to raise the level of phosphorus to 0.30 or 0.35 percent, hatchability returned to a normal level. Traces of zinc in the maternal diet are probably necessary for good hatchability (Blumberg, Blackwood, Supplee and Combs, 1960; Yates and Schaible, 1960).

The importance of manganese for development of the chicken embryo was discovered by Lyons and Insko (1937). Laying hens which consumed insufficient amounts of manganese produced eggs with very low hatchability. The peak of embryo mortality occurred just before the end of the incubation period. Those embryos which survived the tenth day of development were characterized by very short extremities, an abnormal conformation of head and beak, retarded growth of the body as a whole and abnormally-formed down feathers. In many cases edema was present. Addition of manganese to the diet or injection of manganese into the egg albumen, previous to incubation, prevented the occurrence of abnormal embryos.

The detrimental effect of manganese deficiency on hatchability was confirmed by Gallup and Norris (1937, 1939) and by Caskey, Norris and Heuser (1941). The latter authors observed a congenital ataxia, in addition to micromelia, in chicks hatched from eggs that had been produced during manganese deficiency of the maternal diet. A general review of the subject was given by Wilgus, Norris and Heuser (1939). A developmental abnormality obviously identical with that described by Lyons and Insko, had been reported previously by Byerly, Titus and Ellis (1933 a and b) and by Byerly, Titus, Ellis and Landauer (1935). A histological study of the bones of abnormal embryos of this type was carried out at Storrs. Extensive disturbances in structure and formation of the shaft of the
long bones were found (Landauer, 1936). The histological features sharply differentiate this nutritional micromelia from chondrodystrophy, though grossly the two types of abnormalities are practically identical.

For equal hatching results the requirements of dietary manganese appear to be somewhat greater in hens than in pullets (Couch, James and Sherwood, 1947). The occurrence of breed or strain differences in manganese requirements, as far as hatchability is concerned, was demonstrated by Golding, Schaible and Davidson (1940). In a comparison of Barred Plymouth Rocks and White Leghorns these authors found that, in order to give good hatching results, their Barred Plymouth Rock stock needed significantly greater manganese supplements than did their Leghorn stock. Chubb (1954) obtained discordant results in work with Barred Rock and Brown Leghorn fowl. He reported that hatchability was reduced by a low dietary level of manganese, but he failed to find either micromelia among the embryos that had died in late stages of development or ataxia among the hatched chicks. The explanation of this discrepancy has not been made clear.

Christiansen, Halpin and Hart (1939) observed the peculiar fact that low hatchability due to manganese deficiency may be improved considerably by exposure of the laying hens to longer hours of direct sunlight.

A number of studies have been made relative to the importance of iodine for hatchability. Scharrer and Schropp (1932) and Zajtay (1934) reported that the addition of small amounts of potassium iodide to the feed of hens increased the hatching quality of their eggs. Johnson, Pilkey and Edson (1935), like the former authors working in a goitre district, and Pfaunder (1940) did not obtain beneficial effects. It seems possible that the results of such experiments depend to a certain extent on whether or not the grain used in the feed of the experimental birds had been grown in an iodine deficient region. Rogler (1958) observed that hens which had been raised and maintained for an extended period (more than 2 years) on an iodine-deficient diet produced eggs in which hatching was delayed and its percentage reduced. The injection of 20 micrograms of iodine, as potassium iodide, into the air space of such eggs, between 12 and 20 days of incubation, led to a dramatic improvement of their hatching quality. Rogler found, on the other hand, that in hens which had been on an adequate diet, hatchability of their eggs remained unaffected even after a period of 35 weeks on an iodine-deficient diet. A further account of this work was given by Rogler, Parker, Andrews and Carrick (1959). Extensive observations at the Colorado Agricultural Experiment Station led to the conclusion that a level of 0.1 mg./lb. iodine in the feed satisfies the requirements of normal hatchability, and also that levels of 22.7 mg./lb. or more will interfere with normal hatching (Wilgus, Gassner, Patton and Harshfield, 1953). The latter is probably the result of interference with thyroid activity. Investigations by Grossowicz (1946), Wheeler and Hoffmann (1948), McCartney and Shaffner
(1949), Savage, Turner, Kempster and Hogan (1952), Rogler (1958), Rogler, Parker, Andrews and Carrick (1959, b) and Sinha, Ringer, Coleman and Zindel (1959) have shown that chicken embryos respond to such substances as thiourea and thyroprotein with enlarged and poorly functioning thyroid glands and delayed hatching.

Certain mineral substances ingested with the feed may be deposited in eggs and may affect hatchability. Franke and Tully (1935, 1936) demonstrated that this is the case with selenium as it is found in grain grown on certain soils in areas of the north-central Great Plains. Thus two lots of eggs from a South Dakota farm on which such grain was used for chicken feed gave only 3.9 and 11.8 percent hatches out of 127 and 136 fertile eggs, respectively. The great majority of embryos (70 to 74 percent) died during the last days of incubation or were still alive at the end of the incubation period but were unable to hatch. Many of these embryos showed striking malformations of the head, wings and legs. Similar abnormalities were obtained by injecting selenium solutions into eggs (Franke, Moxon, Pol ey and Tully, 1936).

Poley, Moxon and Franke (1937) reported that on a balanced ration containing 15.15 parts per million of selenium no normal chicks hatched after seven days of feeding and after 13 days hatchability dropped to zero. Six days of feeding a ration free of selenium restored development and hatching to normal. A laying ration containing 25 parts per million of selenium did not appreciably affect hatchability; with a content of 5 parts per million hatchability was slightly reduced; with 10 parts per million no chicks hatched (Poley and Moxon, 1938). A summary of most of the selenium work has been given by Moxon (1937).

The detrimental action of feeding selenium-containing grain, with regard to embryonic mortality and the origin of developmental abnormalities, was confirmed by Landauer (1940). In this work at Storrs a comparison was made of the effect which feeding of toxic grain has on eggs laid by Creeper hens and by their genetically normal sisters. It was found that the presence of the Creeper mutation exaggerates the selenium effect (earlier average mortality, more extreme abnormalities). Westfall (1938) observed that the simultaneous injection of sodium selenite and of glutathione or sodium monosulfide into eggs prior to the beginning of incubation reduced mortality and the incidence of deformed embryos. This protective action of certain sulphur compounds is probably related to some basic cellular or metabolic activity.

More recently Moxon and Wilson (1944) found that arsenic counteracts to a certain extent the toxic effects of selenium. Sufficient seleniferous wheat was used in their experimental ration to give a concentration of ten parts per million. Either 2.5 or 5 parts per million of sodium arsenite were added to the drinking water. The results for an experimental period of eight weeks are shown in Table 29. Tests during an-
other year gave similar results. Arsenic at the level of five parts per million was more effective than the low concentration, but did not completely restore normal hatchability. The lesser toxicity of selenium alone, in comparison to earlier tests, was not explained. Gruenewald (1958) made a histological study of embryos whose mothers had received a diet containing 8 p.p. million of selenium. He found in 2½ to 5-day embryos a remarkably constant pattern of tissue necrosis. This occurred regularly in certain well-defined areas of the brain and spinal cord, in the optic cups and lens vesicles, in the mesenchyme of the limb buds and, to a slight degree, in somites of the tail region. These necrotic events presumably are responsible for the gross malformations seen in older embryos.

Table 29

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Number of fertile eggs</th>
<th>Hatch %</th>
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<tbody>
<tr>
<td>Control</td>
<td>409</td>
<td>72.3</td>
</tr>
<tr>
<td>Selenium</td>
<td>509</td>
<td>49.6</td>
</tr>
<tr>
<td>Selenium + arsenic</td>
<td>419</td>
<td>69.2</td>
</tr>
</tbody>
</table>

AGE AND REPRODUCTIVE ACTIVITY OF PARENT STOCK
AS FACTORS IN HATCHABILITY

Age

Much attention has been paid to the question whether there is a difference in the hatching quality of eggs which are laid during the first or during the second laying year of chickens. The most extensive data were obtained by Axelsson (1932 a). These are shown in Table 30. Within each of his six groups the eggs produced during the first laying year hatched better than those laid during the second year. For the whole material the difference in hatchability between the two years amounted to 4.6 ± 1.49 percent. In view of the consistent behavior of all groups, this must be considered as the expression of a significant, though small, difference in hatchability in favor of the eggs laid during the pullet year. If the comparison is based on eggs from the same hens, laid during the first and second year, the average hatchability for the first year amounted to 68.3 ± 3.21 percent, and for the second year it was 46.8 ± 4.52 percent, with a difference of 21.5 ± 5.54 percent between the two years.

These data confirm the earlier results of Hays and Sanborn (1924) who, in a comparison of the hatching records of 253 Rhode Island Red females as pullets and as hens, had found an average hatchability of 56.8 ± 1.68 percent for the pullet year and of 47.9 ± 1.93 percent for the second laying year, with a difference of 8.87 ± 2.55 percent in favor of the pullet year. This difference is also statistically significant. A similar
trend was indicated by the observations of Warren (1934), Funk (1934a), Full (1935), Insko, Lowry and Caldwell (1951) and Goodwin, Lamoreux and Dickerson (1960). On the whole, there can be no doubt that the hatching quality of eggs laid during the first laying year is to a slight but significant degree superior to the hatching quality of those produced during the second laying year. Since the differences are small and since hatchability varies considerably, it is not surprising that some authors were unable to verify these results.

Does this downward trend of hatchability with age continue after the second laying year? Observations by Hyre and Hall (1932) and Greenwood (1932) demonstrate that it does. On three groups of White Leghorns Hyre and Hall collected the observations shown in Table 31. For 34 females hatching records were available through the sixth laying year, and for this group the figures for hatchability in consecutive years, beginning with the second year, were as follows: 64.8, 57.5, 57.6, 56.4, and 47.8 percent. It appears further from these observations that variability of the hatching quality of eggs increased with age of the mother. Martin and Insko (1934), working also with White Leghorns, obtained different results. Their data are given in Table 32. In this case the figures for hatchability represent the results obtained with a steadily decreasing

### Table 30

<table>
<thead>
<tr>
<th>Breed or cross</th>
<th>First laying year</th>
<th>Second laying year</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. of eggs</td>
<td>Fertile eggs hatched %</td>
</tr>
<tr>
<td>Rhode Island Red</td>
<td>931</td>
<td>76.0 ± 1.40</td>
</tr>
<tr>
<td>Barnevelder</td>
<td>796</td>
<td>61.4 ± 1.73</td>
</tr>
<tr>
<td>White Leghorn</td>
<td>868</td>
<td>60.8 ± 1.66</td>
</tr>
<tr>
<td>Wh. Leghn. x R.I.R.</td>
<td>713</td>
<td>60.6 ± 1.83</td>
</tr>
<tr>
<td>Wh. Leghn. x Barnev.</td>
<td>212</td>
<td>55.2 ± 3.41</td>
</tr>
<tr>
<td>R.I.R. x Barnev.</td>
<td>871</td>
<td>54.4 ± 2.59</td>
</tr>
<tr>
<td>Total</td>
<td>3891</td>
<td>63.6 ± 0.77</td>
</tr>
</tbody>
</table>

### Table 31

<table>
<thead>
<tr>
<th>Number of females</th>
<th>2nd year</th>
<th>3rd year</th>
<th>4th year</th>
<th>5th year</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>633</td>
<td>61.4 ± 0.09</td>
<td>58.2 ± 0.07</td>
<td></td>
</tr>
<tr>
<td>II</td>
<td>219</td>
<td>62.1 ± 1.22</td>
<td>54.8 ± 1.35</td>
<td>46.3 ± 0.18</td>
</tr>
<tr>
<td>III</td>
<td>85</td>
<td>62.0 ± 2.37</td>
<td>59.0 ± 2.33</td>
<td>57.9 ± 2.56</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>62.0 ± 3.01</td>
<td>59.6 ± 3.13</td>
<td>57.9 ± 3.62</td>
</tr>
</tbody>
</table>
number of hens. Such a procedure of comparison is of doubtful validity. It would lack justification, for instance, if there should be a positive correlation between longevity of individual hens and hatchability of their eggs. The same is true for data reported by Neel (1942). The actual existence of such a relationship has been demonstrated by Insko, Steele and Wightman (1947). With reference to the relation between life expectancy and hatchability these authors made the following interesting statement: “Hens capable of qualifying for several years gave to their eggs in their early years of life something which hens able to qualify for shorter periods did not give to their eggs. This is apparent in considering embryonic mortality in pullet eggs for each of the respective age-groups. First-year embryonic mortality was definitely lower for pullets progressively older age-groups. A similar relationship was observed for embryonic mortality in the second year in the progressive age groups; and likewise in the third year, and in the fourth year. Essentially the same relationships pertain for mortality in any one week for the respective years.” In more general terms Insko, Steele and Wightman confirmed that hatchability decreases progressively with increasing maternal age. Additional evidence for this conclusion was published by Hays and Talmadge (1949), Lerner (1950), Tinhaye (1956), Meireles de Miranda (1956) and Baranovskaya (1957), but the further claim of Hays and Talmadge that “males used in successive years exhibit some decline in hatchability” (see also Hays, 1927-1928) is not critically supported by their own data. Baranovskaya failed to detect any direct relationship between age of sires and hatchability of their mates’ eggs.

The first eggs laid by pullets produce, according to Tut (1907), a high incidence of malformed embryos. These findings deserve further study. In experiments with White Leghorn pullets and cockerels Sunde and Bird (1959) demonstrated that fertility and hatchability of the eggs laid at the beginning of production were low, but reached a normal level within about six weeks. The evidence of Sunde and Bird, unfortunately, does not discriminate critically between the ages of the pullets and the cockerels as the responsible source of variation. For the occurrence of some malformations, on the other hand, increasing age of the mother may be a predisposing factor. This is suggested, though not critically proven, by the observation that the incidence of various types

### Table 32

<table>
<thead>
<tr>
<th>Age in years</th>
<th>Number of hens</th>
<th>No. of eggs set</th>
<th>Fertile eggs hatched %</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>159</td>
<td>5892</td>
<td>65.8</td>
</tr>
<tr>
<td>3</td>
<td>99</td>
<td>3408</td>
<td>58.5</td>
</tr>
<tr>
<td>4</td>
<td>84</td>
<td>2292</td>
<td>60.1</td>
</tr>
<tr>
<td>5</td>
<td>60</td>
<td>1097</td>
<td>68.2</td>
</tr>
<tr>
<td>6</td>
<td>39</td>
<td>707</td>
<td>74.0</td>
</tr>
<tr>
<td>7</td>
<td>11</td>
<td>220</td>
<td>70.0</td>
</tr>
<tr>
<td>8</td>
<td>3</td>
<td>43</td>
<td>81.5</td>
</tr>
</tbody>
</table>
of body duplications tends to rise in the course of the laying year (Landauer, 1943). More direct evidence for a rising rate of malformations with advancing maternal age was presented by Meirelles de Miranda (1956).

**Antecedent and current egg production**

It is of considerable interest to know whether the intensity of egg production previous to the time when eggs are used for incubation has an effect on hatchability. It seems that this question was first studied in some detail by Lamson and Card (1920), working at the Storrs Agricultural Experiment Station. They found that there was no significant correlation between number of eggs laid by White Leghorns during one year and hatching quality of the eggs of the same birds during the following spring, the coefficients for two successive trials being $-0.117 \pm 0.095$ and $-0.208 \pm 0.128$, respectively. Similarly, winter egg production as well as production during a period of 90 days immediately preceding the hatching period failed to show a significant correlation with hatchability. Comparable results were later obtained by Knox (1927) with White Plymouth Rocks, by Jull (1927-1928) with Barred Plymouth Rocks, Rhode Island Reds and White Leghorns, by Bronkhorst (1933) with White Leghorns, and by Funk (1934a) with White and Barred Plymouth Rocks, Rhode Island Reds and White Leghorns.

An early record by Pearl and Surface (1909) suggesting the possible existence of a slight negative correlation between winter egg production and hatchability during the following spring was plausibly explained by Funk on the basis of the unsatisfactory housing and feeding at that time which may have led to a vitamin D depletion of the body of the layers with heaviest winter production and, subsequently, impaired hatching quality of their eggs. Data which are somewhat at variance with those discussed above were presented by Warren (1934), who found in Rhode Island Red pullets a correlation coefficient of $0.332 \pm 0.068$ between the number of eggs laid previous to the incubation period and hatching quality of the eggs laid subsequently, suggesting the existence of a slight relationship. He did not find a similar association, however, for White Leghorn pullets, nor for hens of either breed.

Between the length of period of production (first egg to March 1) and hatching quality of the eggs laid later, Warren obtained the following correlation coefficients: White Leghorn pullets $-0.229 \pm 0.087$, Rhode Island Red pullets $0.248 \pm 0.086$, White Leghorn hens $-0.209 \pm 0.064$, and Rhode Island Red hens $0.031 \pm 0.095$. The inconsistent nature of these relationships makes it appear likely that all the reported associations are spurious. On the other hand Warren's material suggests that a pause in production previous to the hatching season may improve hatchability (Table 33). Among the White Leghorns as well as among the Rhode Island Reds statistically significant differences existed between pausing and non-pausing pullets. No significant correlation was found,
however, between the length of the pause and the mean percentage hatchability.

### Table 33

<table>
<thead>
<tr>
<th>Breed</th>
<th>Hatchability %</th>
<th>Mean current egg production per pen of group showing hatchability above mean percentage hatchability of the females of each pen</th>
<th>Mean current egg production per pen of group showing hatchability below mean percentage hatchability of the females of each pen</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>White Leghorn</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pausing pullets</td>
<td>72.48 ± 1.30</td>
<td>23.5 ± 1.0</td>
<td>21.7 ± 0.9</td>
<td>1.8 ± 1.3</td>
</tr>
<tr>
<td>non-pausing pullets</td>
<td>66.37 ± 1.90</td>
<td>25.0 ± 0.4</td>
<td>23.6 ± 0.4</td>
<td>1.4 ± 0.6</td>
</tr>
<tr>
<td>Rhode Island Red</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pausing pullets</td>
<td>66.15 ± 2.08</td>
<td>25.9 ± 0.4</td>
<td>24.4 ± 0.4</td>
<td>1.5 ± 0.6</td>
</tr>
<tr>
<td>non-pausing pullets</td>
<td>54.34 ± 1.67</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

If antecedent egg production does not have any influence upon hatching quality, there is convincing evidence that current egg production does influence it in such a fashion that with increasing intensity of production (during the hatching season) the average percentage of hatchability tends to improve to a slight but significant extent. Evidence bearing on this problem was presented by Jull (1930-1931), Byerly, Titus and Ellis (1933 a), and Funk (1934 a). In a comparison of the mean current egg production in relation to hatchability, above and below the mean respectively, of the females of each pen (the data being based on the number of eggs laid during each of the six years' breeding seasons of 50 days each), Jull obtained the results shown in Table 34. Among the Rhode Island Reds and White Leghorns the differences, though slight, appear to be significant.

### Table 34

<table>
<thead>
<tr>
<th>Breed</th>
<th>Mean current egg production per pen of group showing hatchability above mean percentage hatchability of the females of each pen</th>
<th>Mean current egg production per pen of group showing hatchability below mean percentage hatchability of the females of each pen</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barred Plymouth Rocks</td>
<td>23.5 ± 1.0</td>
<td>21.7 ± 0.9</td>
<td>1.8 ± 1.3</td>
</tr>
<tr>
<td>Rhode Island Reds</td>
<td>25.0 ± 0.4</td>
<td>23.6 ± 0.4</td>
<td>1.4 ± 0.6</td>
</tr>
<tr>
<td>White Leghorns</td>
<td>25.9 ± 0.4</td>
<td>24.4 ± 0.4</td>
<td>1.5 ± 0.6</td>
</tr>
</tbody>
</table>

Similarly, Byerly, Titus and Ellis (1933 a) compared the relationship between intensity of egg production during the months of March and April and the hatching quality of eggs during the same period, and found a correlation of 0.30 ± 0.061. The authors concluded 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.” Coles and Underwood (1954 b) have reported evidence of the same nature.
Funk recorded the correlation coefficients shown in Table 35. The “heavy” breeds were White and Barred Plymouth Rocks and Rhode Island Reds. As in the material of Jull and of Byerly, Titus and Ellis, the data secured by Funk suggest the existence of a slight, but significant, correlation between current (spring) egg production and hatchability. Again, similar to previous investigations, no correlation was found between antecedent (winter) egg production and hatchability. Between annual egg production and hatchability the coefficients were not significant for the two Leghorn groups, but suggest the existence of a slight correlation in the heavy breeds. Hays (1943), however, did not find a significant correlation between annual persistency (during the first laying year) and subsequent hatchability in a flock of Rhode Island Red fowl.

In an analysis of the relation between current egg production and hatchability in White Leghorn matings, Bernier (1947) and Bernier, Taylor and Guns (1951) obtained for one year a significantly higher hatchability in the group with production above the median as compared with the low producers, but this relationship did not hold in another year. Such correlations, if and when they exist, may reflect the effect of agencies which act simultaneously on production and hatchability, but they may also be the result of other factors, such perhaps as a tendency of cocks to mate more often with high than with low-producing females with a consequent difference between the two groups in age of sperm cells at fertilization (see below). A trend of declining hatchability toward the end of the first year of production was reported by Hays and Talmadge (1949) and Tomhave (1956, 1958) and may be correlated with a similar trend in production.

<table>
<thead>
<tr>
<th>Stock used</th>
<th>Number of birds</th>
<th>Spring egg production (March to June)</th>
<th>Annual egg production and hatchability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leghorn hens</td>
<td>120</td>
<td>0.19 ± 0.09</td>
<td>0.09 ± 0.09</td>
</tr>
<tr>
<td>Leghorn pullets</td>
<td>72</td>
<td>0.22 ± 0.12</td>
<td>0.18 ± 0.12</td>
</tr>
<tr>
<td>Heavy hens</td>
<td>169</td>
<td>0.21 ± 0.07</td>
<td>0.20 ± 0.07</td>
</tr>
<tr>
<td>Heavy pullets</td>
<td>246</td>
<td>0.13 ± 0.06</td>
<td>0.20 ± 0.06</td>
</tr>
</tbody>
</table>

The time of day when eggs are laid

An interesting question was brought into the discussion of hatchability problems when Hutt and Pilkey (1929-1930) reported that the hatching quality of eggs laid during the afternoon was somewhat poorer than that of eggs laid before 9 a.m. In the data which the authors analyzed, this difference was greatest in March, and was not found after the middle of April. The trend of the relation between time of laying and hatchability was similar in data obtained from two different sources. The combined results are shown in Table 36. There were statistically significant group differences as follows: C−A = 4.69±1.30; D−A = 3.14±1.28;
\[(C + D) - (A + B) = 2.95 \pm 0.87; \text{ and } (C + D) - A = 3.89 \pm 1.10. \] Furthermore, it was observed that the incidence of malformed embryos was higher in eggs laid during the afternoon than in those laid during the early morning or forenoon.

\[
\begin{align*}
(C + D) - (A + B) &= 2.95 \pm 0.87; \\
(C + D) - A &= 3.89 \pm 1.10.
\end{align*}
\]

Table 36

<table>
<thead>
<tr>
<th>Group</th>
<th>Hours of laying</th>
<th>Number of fertile eggs</th>
<th>Embryonic mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>To 9 a.m.</td>
<td>3108</td>
<td>32.00 (\pm) 0.83</td>
</tr>
<tr>
<td>B</td>
<td>9:05 a.m. to 12 m.</td>
<td>5942</td>
<td>33.71 (\pm) 0.67</td>
</tr>
<tr>
<td>C</td>
<td>12:05 p.m. to 2 p.m.</td>
<td>2221</td>
<td>36.69 (\pm) 1.02</td>
</tr>
<tr>
<td>D</td>
<td>After 2 p.m.</td>
<td>2362</td>
<td>35.14 (\pm) 0.98</td>
</tr>
</tbody>
</table>

Results very similar to those of Hutt and Pilkey have been reported by Pritsher (1940 a). His data are shown in Table 37. Among eggs produced during March and April those which had been laid before noon hatched better than those which had been laid between noon and four o'clock in the afternoon. No comparable difference was found among eggs laid during August. Pritsher did not give a statistical analysis of his material, but stated that the two seasonal groups consisted of three settings each, and that, within the seasonal groups, the trend of hatchability was the same in each setting.

Table 37

<table>
<thead>
<tr>
<th>Season</th>
<th>Hours of laying</th>
<th>Total no. of eggs</th>
<th>Infertile %</th>
<th>Mortality during incubation days in %</th>
<th>Fertile eggs hatched %</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1-6</td>
<td>7-14</td>
</tr>
<tr>
<td>March and April</td>
<td>To 10 a.m.</td>
<td>1385</td>
<td>4.7</td>
<td>2.8</td>
<td>2.5</td>
</tr>
<tr>
<td></td>
<td>10-12</td>
<td>1385</td>
<td>5.2</td>
<td>1.8</td>
<td>2.9</td>
</tr>
<tr>
<td></td>
<td>12-2</td>
<td>1386</td>
<td>5.2</td>
<td>2.9</td>
<td>2.7</td>
</tr>
<tr>
<td></td>
<td>2-4</td>
<td>1367</td>
<td>5.1</td>
<td>2.4</td>
<td>2.3</td>
</tr>
<tr>
<td></td>
<td>10 a.m.</td>
<td>923</td>
<td>5.7</td>
<td>2.5</td>
<td>2.1</td>
</tr>
<tr>
<td></td>
<td>10-12</td>
<td>873</td>
<td>7.1</td>
<td>2.3</td>
<td>1.0</td>
</tr>
<tr>
<td>August</td>
<td>12-2</td>
<td>715</td>
<td>3.5</td>
<td>2.1</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>2-4</td>
<td>736</td>
<td>4.1</td>
<td>2.2</td>
<td>2.0</td>
</tr>
</tbody>
</table>

Other investigations failed to yield results similar to those recorded by Hutt and Pilkey and by Pritsher. Nicolaides (1933) found a mean embryonic mortality for afternoon eggs of 27.87 \(\pm\) 5.87 percent and for morning eggs of 22.42 \(\pm\) 3.88 percent, with a difference of 5.45 \(\pm\) 7.04 percent. This difference is not statistically significant. Nicolaides further observed that eggs laid between 7 and 9 a.m. gave a somewhat higher mean embryonic mortality than those laid between 9:05 a.m. and 12 m.

Bernier (1947) and Bernier, Taylor and Gunns (1951) arrived at results very similar to those of Nicolaides. They found that eggs laid between 9 a.m. and 2 p.m. gave better hatching results than those laid either earlier or later. The differences were statistically significant when
the analysis was based either on eggs of all clutch positions \( (N = 819) \) or on those laid subsequent to the first egg of each clutch \( (N = 640) \). Eggs produced before 8 a.m. had a poorer hatchability than those laid at any other time of the day.

Careful observations relating to these problems were made by Funk (1934 b). His results for 1931 are given in Table 38. Data for two more years gave closely similar results as is shown by the averages for the entire season of each of these years (Table 39). The chi-square test applied to the hatchability of eggs laid in the morning and in the afternoon for the combined data of 1932 and 1933 gave a value of 11.396, where 6.635 was significant, the afternoon eggs showing a somewhat higher hatchability. In another summary of his observations Funk (1934 a) made a comparison

<table>
<thead>
<tr>
<th>Season of laying</th>
<th>Time of day of laying</th>
<th>Number of eggs set</th>
<th>Infertile %</th>
<th>Fertile eggs hatched %</th>
</tr>
</thead>
<tbody>
<tr>
<td>January 15 to February 7</td>
<td>Before 9 a.m.</td>
<td>605</td>
<td>22.0</td>
<td>76.9</td>
</tr>
<tr>
<td></td>
<td>9 a.m. to 12 m.</td>
<td>382</td>
<td>23.9</td>
<td>72.8</td>
</tr>
<tr>
<td></td>
<td>12 m. to 2 p.m.</td>
<td>432</td>
<td>22.7</td>
<td>79.4</td>
</tr>
<tr>
<td></td>
<td>After 2 p.m.</td>
<td>180</td>
<td>28.9</td>
<td>76.6</td>
</tr>
<tr>
<td>February 8 to February 28</td>
<td>Before 9 a.m.</td>
<td>775</td>
<td>15.1</td>
<td>79.9</td>
</tr>
<tr>
<td></td>
<td>9 a.m. to 12 m.</td>
<td>448</td>
<td>18.5</td>
<td>80.8</td>
</tr>
<tr>
<td></td>
<td>12 m. to 2 p.m.</td>
<td>485</td>
<td>17.9</td>
<td>82.9</td>
</tr>
<tr>
<td></td>
<td>After 2 p.m.</td>
<td>225</td>
<td>15.6</td>
<td>76.9</td>
</tr>
<tr>
<td>March 1 to March 21</td>
<td>Before 9 a.m.</td>
<td>753</td>
<td>15.7</td>
<td>69.4</td>
</tr>
<tr>
<td></td>
<td>9 a.m. to 12 m.</td>
<td>509</td>
<td>17.5</td>
<td>72.1</td>
</tr>
<tr>
<td></td>
<td>12 m. to 2 p.m.</td>
<td>447</td>
<td>16.1</td>
<td>77.3</td>
</tr>
<tr>
<td></td>
<td>After 2 p.m.</td>
<td>192</td>
<td>20.3</td>
<td>75.2</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Date set</th>
<th>Eggs laid before 9 a.m.</th>
<th>Eggs laid from 9 a.m. to 12 m.</th>
<th>Eggs laid from 12 m. to 2 p.m.</th>
<th>Eggs laid after 2 p.m.</th>
</tr>
</thead>
<tbody>
<tr>
<td>January 15 to March 18, 1932</td>
<td>72.3</td>
<td>71.4</td>
<td>75.7</td>
<td>77.3</td>
</tr>
<tr>
<td>January 13 to March 4, 1933</td>
<td>74.2</td>
<td>73.3</td>
<td>76.6</td>
<td>76.8</td>
</tr>
</tbody>
</table>

of the hatching quality of morning versus afternoon eggs for four different seasons (Table 40). These figures were, in part, based on the same material as that of the two previous tables. The author concluded that eggs laid in the afternoon hatched slightly better than eggs laid in the morning. This is the opposite of the findings by Hutt and Pilkey and by Pritsker.
Table 40

<table>
<thead>
<tr>
<th>Year</th>
<th>Morning eggs</th>
<th>Afternoon eggs</th>
<th>Difference in favor of afternoon eggs %</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of eggs set</td>
<td>Fertile eggs hatched %</td>
<td>Number of eggs set</td>
</tr>
<tr>
<td>1931</td>
<td>3472</td>
<td>75.7</td>
<td>1961</td>
</tr>
<tr>
<td>1932</td>
<td>4106</td>
<td>74.5</td>
<td>2326</td>
</tr>
<tr>
<td>1933</td>
<td>2589</td>
<td>73.8</td>
<td>2383</td>
</tr>
<tr>
<td>1934</td>
<td>3204</td>
<td>68.0</td>
<td>2093</td>
</tr>
</tbody>
</table>

Hays (1937) found that in his material embryonic mortality and hatchability were independent of the hour of the day at which the eggs had been laid. Kumanov (1948), similarly, obtained negative results with White Leghorn eggs.

Hutt and Pilkey made the assumption that embryonic abnormalities and lowered hatching quality result from an arrest of development when embryos are chilled at a critical period of ontogeny, viz., prior to gastrulation or early in that process. They made the further assumption that such arrests are less likely to occur in eggs laid early in the morning since many of these eggs supposedly were held in the mother's body for a prolonged period during the night, with the consequence that the embryos were past the danger period at the time of laying. The authors saw further support for this explanation in the observation that the difference in hatching quality of morning and afternoon eggs decreased in their material with advancing spring and finally disappeared entirely, presumably parallel with the lessening of the degree of chilling of the eggs at the time of laying because of higher air temperatures.

This explanation meets with difficulties inherent in the original data. For, it was reported by Hutt and Pilkey as well as by Pritsher that eggs laid during the late forenoon showed the same hatching quality as those laid early in the morning. A direct attempt to test experimentally the hypothesis advanced by Hutt and Pilkey was made by Funk (1934 b). Eggs which had been collected immediately after being laid at 11 a.m. were held at 101°F (38.3°C) for six hours. The eggs were then cooled and held in storage until put into the incubator. Out of 764 fertile eggs thus pre-incubated 77.2 percent hatched, while out of 255 fertile control eggs 74.9 percent hatched. The difference between the two lots was not statistically significant. Finally, it was demonstrated by Scott and Warren (1936) that the break in a laying cycle and the initiation of a new clutch are not associated with the holding of an egg in the oviduct, but are chiefly due to a delay of ovulation. It should be noted, however, that Scott and Warren's data do suggest the existence of a slight prolongation of the period of formation of the first egg in a clutch as compared with later ones. These first eggs of a clutch are generally laid in the early morning. They tend to be larger than succeeding ones. The average weight of early morning eggs consequently exceeds that of those laid later.
in the day (Atwood, 1926-1927; Funk and Kempster, 1934). In a personal communication Dr. F. B. Hutt has suggested that excessive size of early morning eggs may account for the poor hatching results which these eggs showed in the experiments of some investigators. This view is supported by the observations of Bernier, Taylor and Gunn (1951) on the relations between time of laying and blastoderm size in newly-laid eggs, and, in particular, by the finding of the latter authors that in eggs laid before 8 a.m. (predominantly first eggs of a clutch) blastoderm size is more variable than it is in eggs laid at other hours of the day.

Further observations which have a bearing on the problem of the relation between time of laying and hatchability were made by McNally and Byerly (1936). They studied the relation between the time of the day eggs had been laid and the stage of embryo development, as expressed by somite numbers, after 48 hours of incubation; and, on the other hand, they made observations on the hatching quality of eggs according to the time of day they had been laid (Figure 25). It was found that the average somite number, in general, was smaller when the eggs were laid later in the day, an especially rapid decrease occurring from 8 to 9 a.m. As in the data presented by Funk, eggs laid in the afternoon showed a slight trend toward improvement in hatchability over those laid in the morning. McNally and Byerly, grouping hens according to
the average number of somites shown by embryos after 48 hours of incubation, found that the hatching quality of eggs gradually increases to an optimum (average of 20 somites after 48 hours of incubation) and rapidly decreases for the eggs of those hens which show higher average somite counts at that time (Figure 26).

These observations, together with information relative to the effect of the time interval between laying of eggs on developmental stage at time of laying, and on hatchability (to be discussed below), seem to justify the authors' conclusion that "if the egg is only 21 or 25 hours in the oviduct, the embryo is too young to stand the variations in environment it must undergo," and "if the egg is held over 27 hours its hatchability is reduced." This implies that the developmental stage after two days of incubation is an indication of the degree of development at the time of laying, and that the embryonic stage reached at laying is a function of the time which the egg spent in the body of the hen.

![Figure 26](image-url)

**Figure 26**

Relationship between percentage hatchability and degree of development (number of somites) after 48 hours of incubation (From McNally and Byerly, 1936).

Scott and Warren (1936) found that clutch position (to be further discussed below) has no bearing on somite number after 38 hours of incubation; but they observed also that, irrespective of clutch position, the
degree of embryonic development tended to vary with the time interval between laying, i.e., for intervals of 24 to 30 hours between laying, the eggs which had been laid after a longer interval generally showed more advanced development when incubated for 38 hours. According to Bernier (1947) and Bernier, Taylor and Guns (1951), however, blastoderm size at laying and number of somites after 38 hours of incubation are significantly greater in eggs of the first and second clutch positions than in later ones and the coefficients of variability are higher. Further reference to these observations will be made below.

It is impossible at present to give a satisfactory explanation for the conflicting results which are on record with regard to the relationship between time of laying and hatchability. It seems likely that the time interval between laying has an influence on the hatching quality of eggs, and that this time interval, in turn, is influenced (in regard to clutch position) by methods of management. Such an explanation is in harmony with the observation of Funk (1934 b) that the use of all-night lights in the pens, with a consequently longer period of activity and of food consumption, tends to minimize the differences in hatchability which exist between eggs laid at different hours of the day.

**Time interval between laying of eggs. Position of egg in clutch.**

McNally and Byerly (1936) studied the relationship of time interval between successive eggs of a clutch to average somite number of the embryos after 48 hours of incubation. They found (Figure 27) that if the time interval between eggs was from 24 to 27 hours the average somite number of the embryos after two days of incubation increased with length of interval, but that a slight decrease occurred if the time interval was more than 27 hours. A relationship of a similar nature was observed for

![Figure 27](image)

**Figure 27**

Relationship (o) between degree of development (number of somites) after 48 hours of incubation and time interval between laying of eggs; and relationship (x) between percent hatchability and time interval between laying of eggs (From McNally and Byerly, 1936).
the time interval between the laying of eggs and hatching quality. Hatchability increased up to the 27-hour interval and decreased thereafter (Figure 27). Hays (1936) reported most satisfactory results for the eggs of hens which laid at mean time intervals of from 25 to 26.5 hours, whereas individuals with mean laying rates above, and possibly also below this interval produced eggs with poorer hatchability.

Observations by Bernier (1947), Bernier, Taylor and Gunn (1951) and Moore (1959) are in essential agreement with those of McNally and Byerly and of Hays. That the degree of development after a short period of incubation, and presumably already at the time of laying, is influenced by the time interval between successive eggs was confirmed by Scott and Warren (1936). In a study of eggs, all of which were second in the clutch, and which had been incubated for 38 hours, the authors obtained the data shown in Table 41. It can be seen that there is a definite trend for the eggs laid after a longer interval to show a more advanced stage of development.

<table>
<thead>
<tr>
<th>Time interval in hours between successive eggs</th>
<th>24</th>
<th>25</th>
<th>26</th>
<th>27</th>
<th>28</th>
<th>29</th>
<th>30</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of eggs in class</td>
<td>5</td>
<td>10</td>
<td>29</td>
<td>19</td>
<td>34</td>
<td>29</td>
<td>3</td>
</tr>
<tr>
<td>Mean somite number</td>
<td>6.0</td>
<td>7.4</td>
<td>7.7</td>
<td>7.6</td>
<td>9.0</td>
<td>8.9</td>
<td>10</td>
</tr>
</tbody>
</table>

On the whole, there can be little doubt that developmental stage at the time of laying is influenced by the time interval between the laying of eggs. In unincubated eggs these differences probably are difficult to establish, but they can be observed relatively easily after a short period of incubation.

Funk (1939) found that eggs laid as one-egg clutches do not hatch as well as eggs laid in two- to six-egg clutches. Again, significantly better hatching results were obtained from eggs belonging to four- to six-egg clutches as compared with eggs from two-egg clutches. This has been confirmed by Lamoreux (1940). On the other hand, the position of an egg within a given clutch did not influence the hatching result. This agrees well with the observations by Scott and Warren (1936) to which reference has been made above. Funk's and Lamoreux's observation that eggs from one-egg clutches appear to have a lower fertility than those laid in multiple egg clutches is of interest with regard to the relationship between fertility and hatchability to be discussed below. Contrary to Funk's results, Bernier (1947) and Bernier, Taylor and Gunn (1951) found that eggs occupying a clutch position intermediate between the first and last egg, hatched significantly better than the last eggs and this relationship was apparently independent of the rate of egg production.

In an analysis of winter eggs laid by 47 Rhode Island Red pullets Hays (1938) obtained the data shown in Table 42 for time interval between clutches as related to hatchability of the eggs.
These observations suggest that "birds producing clutches of eggs at frequent intervals are likely to produce eggs of high hatchability," and that with lengthening of the interval between clutches there was a tendency for hatchability to decline. The data, however, admittedly need verification. It is likely, moreover, that some of the results on time interval between clutches, as affecting hatchability, are merely another expression of the relation between intensity of current egg production and hatchability, discussed earlier.

Table 42

<table>
<thead>
<tr>
<th>Time between clutches (hours)</th>
<th>Number of birds</th>
<th>Hatchability of fertile eggs in %</th>
</tr>
</thead>
<tbody>
<tr>
<td>41.5</td>
<td>5</td>
<td>59.5</td>
</tr>
<tr>
<td>44.5</td>
<td>15</td>
<td>61.9</td>
</tr>
<tr>
<td>47.5</td>
<td>8</td>
<td>49.9</td>
</tr>
<tr>
<td>50.5</td>
<td>8</td>
<td>47.8</td>
</tr>
<tr>
<td>53.5</td>
<td>7</td>
<td>56.9</td>
</tr>
<tr>
<td>56.5</td>
<td>2</td>
<td>35.5</td>
</tr>
<tr>
<td>65.5</td>
<td>2</td>
<td>27.8</td>
</tr>
</tbody>
</table>

Fertility and age of sperm cells

Several investigators have studied the question of the influence of fertility on hatchability. The results are summarized in Table 43. Monte­mayor (1936) has presented data for White Leghorns, Rhode Island Reds and Cantonese fowl which suggest that some relation between fertility and hatchability may exist in these breeds during certain parts of the year. No statistical analysis was made.

Table 43

<table>
<thead>
<tr>
<th>Author</th>
<th>Material</th>
<th>Coefficient of correlation between fertility and hatchability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pearl and Surface (1909)</td>
<td>Barred Plymouth Rock 110 pullets (1908)</td>
<td>0.417±0.053</td>
</tr>
<tr>
<td>Hays and Sanborn (1924)</td>
<td>Rhode Island Red 758 pullets</td>
<td>0.142±0.055</td>
</tr>
<tr>
<td>Knox (1926-1927)</td>
<td>White Plymouth Rock 92 pullets</td>
<td>0.067±0.024</td>
</tr>
<tr>
<td>Full (1927-1928)</td>
<td>Barred Plymouth Rock 92 pullets</td>
<td>0.59±0.06</td>
</tr>
<tr>
<td>Hyre and Hall (1932)</td>
<td>White Leghorn 801 hens</td>
<td>0.056±0.024</td>
</tr>
<tr>
<td>Munro and Kosin (1945)</td>
<td>Barred Plymouth Rock 848 hens</td>
<td>0.332</td>
</tr>
<tr>
<td>Hays (1951 b)</td>
<td>White Leghorn 848 hens</td>
<td>0.202±0.022</td>
</tr>
</tbody>
</table>

1Significant at 1% level; 2Significant at 5% level.
In a small group of Brown Leghorn fowl Blyth (1915) could show that both infertility and embryonic mortality rose towards the end of the laying season. "There was a strong and significant correlation between the monthly means of the two conditions and a lesser but still significant correlation between the bird means."

The most plausible explanation for the occurrence of correlations between fertility and hatchability may be seen in an influence of age of the sperm cells at the time of fertilization on the chances of eggs to produce hatched chicks. For, with a reduced frequency of matings, an increase in average age of the spermatozoa at the time of fertilization and a decrease in fertility of the eggs will occur simultaneously.

An effect of excessive age of sperm on viability of the embryo was already suggested by observations of Lau (1894), Barfurth (1895), Gilbert (1904, 1905), Philips (1917-1918) and Crew (1926), but only studies by Nalbandov and Card (1943) have established this beyond doubt. In fact, even apparently contradictory data (Dunn, 1927 a; Warren and Kilpatrick, 1928-1929) now seem to fall in line with this conclusion.

Nalbandov and Card gathered their data by removing cocks from pens of hens and recording the hatchability of eggs laid during subsequent five-day periods. A summary of their results is given in Table 44. The three different ways in which the eggs were handled prior to incubation had no significant effect on hatchability and will not be considered here. The data show clearly that later than two weeks after mating the chances decline rapidly that spermatozoa will produce viable zygotes. Not a single chick hatched from 41 eggs which had been fertilized 21 or more days after mating. Furthermore, it was found that there was a definite relationship between the age of sperm at fertilization and the age at which embryos died, the average age at death declining rapidly beyond the tenth day after mating. This is shown by the figures in Table 45. No relationship was observed between age of sperm and incidence of malformations (but see below).

Confirmatory evidence for the influence of sperm age on embryo viability was reported by Kosin (1947) and Cooper and Rowell (1958). Genetic variability appears not to have any effect on the relationship between fertility and hatchability (Bernier, Taylor and Guns, 1951).

The causes of high mortality after fertilization of eggs by stale sperm were studied by Dharmarajan (1950). He confirmed the findings of earlier investigators (on lower animals) in regard to the rising incidence of malformations with increasing age of the sperm. Dharmarajan found that defects of the head end are most common in such embryos, abnormalities of the tail end being next in frequency. Malformations of the nervous system manifested themselves as irregular swellings of the wall of the brain and spinal cord, irregular foldings of the brain, overgrowth and faulty (or even lack of) union of the neural folds. Hypertrophy of the embryonic blood vessels and heart and hemorrhages are other fea-
Table 44

**Relation of age of sperm to hatchability**

<table>
<thead>
<tr>
<th>Number of days after removal of male from females</th>
<th>1-5</th>
<th>6-10</th>
<th>11-15</th>
<th>16-20</th>
<th>21-25</th>
<th>26-30</th>
<th>31-35</th>
</tr>
</thead>
</table>

Eggs warmed to 100°F. for one hour daily during storage for seven days at 55°-60°F.

<table>
<thead>
<tr>
<th></th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>24</td>
<td>58.3</td>
<td>24</td>
<td>75.0</td>
<td>12</td>
<td>30.0</td>
<td>7</td>
<td>14.3</td>
</tr>
<tr>
<td>b</td>
<td>2</td>
<td>0</td>
<td>7</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
</tbody>
</table>

Eggs set daily

<table>
<thead>
<tr>
<th></th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>66</td>
<td>78.8</td>
<td>65</td>
<td>71.4</td>
<td>31</td>
<td>32.3</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>b</td>
<td>6</td>
<td>0</td>
<td>10</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Eggs set after seven days storage at 55°-60°F.

<table>
<thead>
<tr>
<th></th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>60</td>
<td>78.8</td>
<td>50</td>
<td>68.0</td>
<td>42</td>
<td>23.8</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>b</td>
<td></td>
<td></td>
<td>6</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
<th>Number fertile eggs</th>
<th>Hatched %</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>104</td>
<td>49.0</td>
<td>81</td>
<td>54.3</td>
<td>58</td>
<td>60.3</td>
<td>9</td>
<td>77.8</td>
</tr>
<tr>
<td>b</td>
<td></td>
<td></td>
<td>1</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 45

<table>
<thead>
<tr>
<th>Number of days after removal of cocks</th>
<th>1-5</th>
<th>6-10</th>
<th>11-15</th>
<th>16-20</th>
<th>21-25</th>
<th>26-30</th>
<th>31-35</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean age at death</td>
<td>12.4</td>
<td>11.0</td>
<td>5.5</td>
<td>3.5</td>
<td>1.6</td>
<td>1.0</td>
<td>1.0</td>
</tr>
</tbody>
</table>

tures of such embryos. Dharamarajan believed that “sperm, by its sojourn in the genital tract of the female before fertilization, becomes toxic to the zygote.” This conclusion is somewhat hazardous unless the word “toxic” is not used in its pharmacological connotation, but simply as signifying a noxious influence. Furthermore, in view of recent observations of Sjodin (1957) it appears likely that at least some of the abnormalities reported by Dharamarajan were in reality post-mortem changes. Allen and Champion (1955) found a correlation of 0.72 ± 0.018 between motility rating of spermatozoa and hatchability. Kamar (1960) confirmed this and, in addition, reported significant positive correlations between sperm concentration and hatchability and between ejaculatory responsiveness and hatchability. All of these various conditions may become effective by affecting mean age of the spermatozoa at the time of fertilization.

Observations by Parker (1945, 1950) suggest the possibility that environmental factors, acting on the sperm cells, may influence the hatching quality of eggs. Parker artificially inseminated groups of Rhode Island Red pullets at different times of the day (morning, noon and afternoon), using semen of the same males for the different groups. Hatchability was determined for the eggs laid between the second and fourteenth day after insemination. The following hatching percentages were found for the three groups (weighted means): 79.9% after morning insemination, 79.8% following noon insemination, and 91.7% in the group which had been inseminated during the afternoon. The differences between the last and the first two groups were statistically significant. No physiological explanation of these peculiar observations is available. The author believes that it is possible to increase hatchability “by restricting the mating of chickens to the afternoon.” Such an application of Parker’s results should, however, await their verification by further tests.

Gowe and Howes (1956) made experiments in which thyroxin was added to semen prior to artificial insemination. They believed that in a group of Broad Breasted White fowl that had shown relatively low fertility, hatchability was improved by this procedure during the first week after insemination. The statistical significance of the differences between control and treated groups was, however, not established beyond doubt.
There is a possibility that conditions of the egg as well as of the sperm may be implicated in correlative changes of fertility and hatchability. An analysis of Wyandotte records led Munro (1916) to the conclusion that a parallel trend of fertility and hatchability may be brought about by such nutritional factors as the depletion of the body of laying hens in an essential metabolite, e.g., vitamin B₂. No evidence was presented, however, which would exclude the possibility that the nutritional regime had an effect on the frequency of matings and, therefore, on age of sperm cells at fertilization. No correlation seems to exist between preovipositional and later embryonic mortality (Bernier, Taylor and Gunns, 1951). Interesting data on a correlation between fertility and early embryonic growth rate in inbred lines of Brown Leghorn fowl are due to Krzanowska (1959).

THE METABOLISM OF LAYING HENS

AS A FACTOR IN HATCHABILITY

An interesting effect on hatchability caused by disturbances of metabolism has been observed in Frizzle fowl. Due to an incompletely dominant mutation, chickens belonging to this breed have wavy (heterozygous) or curly (homozygous) feathers (Landauer and Dunn, 1930 b; Hutt, 1930). The feathers break off easily, leaving the body bare. A detailed study of the physiology of Frizzle chickens was made at the Storrs Agricultural Experiment Station. It was shown that such birds, on account of their defective plumage, lose much more body heat than normal fowl, and that as a consequence metabolism is much increased (Benedict, Landauer and Fox, 1932).

This initial alteration in the economy of the body is followed by complex adjustments and rearrangements in the structure and function of different organs and systems (Landauer and Upham, 1936; Landauer, 1942 b). The less pronounced plumage abnormality of heterozygous Frizzle fowl causes less loss of body heat than the more extreme disturbance of protection in homozygous Frizzles, and consequently all changes are less extreme in the heterozygous animals. Frizzle fowl responded favorably to any changes in the environment (temperature) or in feeding (caloric value) which promote the preservation of body heat. With regard to hatchability in Frizzle matings, it was found that the hatching quality of eggs laid by homozygous Frizzle hens, even if bred to normal males, is much reduced, and that, to a lesser degree, the same is true of eggs from heterozygous Frizzle hens, whereas hatchability seemed to be normal in the reciprocal matings (Landauer and Dunn, 1930 b). Hutt (1930) did not observe reduced hatchability in eggs from heterozygous Frizzle females, but subsequent work at Storrs tended to confirm the earlier findings (Landauer, 1932 b). The fact that differences in hatchability were obtained in reciprocal crosses, for example, 42.7 percent in a cross of homozygous Frizzle hens by a normal cock, but 75.3 percent in a
mating of normal hens with a pure Frizzle male, suggests that the differences are due to peculiarities of maternal physiology.

In view of the evidence as a whole, it seems most likely that because of the excessive loss of body heat and the resulting disturbances of temperature regulation and of metabolism (associated with abnormal thyroid activity) Frizzle hens cannot always deposit in their eggs all substances necessary for normal embryonic development, and that this in turn leads to increased embryo mortality. Somewhat similar observations have been recorded by Abbott and Asmundson (1957) on eggs of the almost bare chickens which are homozygous for the "scaleless" mutation and by Smyth (1954) for eggs laid by turkeys with the "hairy" plumage defect. It has not yet been determined whether eggs laid by Frizzle hens are deficient chiefly in one substance, possibly iodine, or whether their abnormal composition involves several substances. Similar events, viz., metab-
olic effects mediated via the thyroid, were presumably at work in the lowering of hatchability by about 25 percent, observed by McCartney and Shaffner (1949, 1950) after feeding thiouracil to New Hampshire hens at a level of 0.3 percent and for four weeks.

Since the effect of frizzled plumage on the hatching quality of eggs obviously is not directly determined by the Frizzle gene, but is only a secondary consequence of excessive loss of body heat associated with frizzling, it may be expected that any other agency producing similar heat loss will also lead to a decline in hatchability. It seems likely that observations by Lewis and Thompson (1915), Mussell and Bancroft (1924-1925), Warren (1934) Funk (1934a) and Vickers (1936), concerning the effect of periods of very low environmental temperature on hatchability, are instances of this kind. Figure 28 shows the effect of a sudden drop of outside temperature on hatchability as found by Funk in the records of a commercial hatchery during four consecutive years. Hatchability in this case was based on the number of all eggs set. Similar observations, but with hatchability calculated on the basis of the number of fertile eggs, were reported by Warren as shown in Figure 29. It is evident from both sets of observations that periods of severe cold led to a decline of hatchability, and that there was a tendency for the maximum loss in hatching quality to occur in those eggs which were laid a short time after the minimum temperature had been reached.

Infertility, due to depressed mating habits, is excluded as a possible cause since Warren showed that curves with closely similar trends were obtained when hatchability was based on the number of fertile eggs or on the total of all eggs put in the incubator. Chilling of the eggs also seems to be ruled out as a possible explanation; not only because we know that eggs can be exposed for relatively long periods to low temperatures without harm to their hatching quality, but especially because, in both sets of data, the maximum effect of low temperature appears to lag behind the occurrence of the minimum temperature. Thus, the plausible explanation, already considered by Warren as a possible cause, appears to be the effect of extremely low temperature on the body of the laying hens (excessive heat loss). The resulting disturbances of temperature regulation and metabolism may be assumed to be essentially the same as those found in Frizzle fowl, with a similar mechanism leading in both instances to reduced hatching quality of the eggs. On the basis of this explanation it is not surprising that some data will not show an effect of low outside temperature on hatchability, since it may be expected that adequate protection of the layers (insulation or heating of pens, caloric value of feed, etc.) will minimize or prevent the occurrence of disturbances in body temperature regulation, and hence of reduced hatchability. According to Melendy, Ogasawara and Wilson (1959) induced, transitory hyperthermy of laying hens has no obvious effect on hatchability, but a critical study of this problem, taking into account possible response
The effect of sudden drops in outside temperature on hatching results. Data from White Leghorns and Rhode Island Reds. Comparison of hatchability based on the total of all eggs incubated with hatchability based on the number of fertile eggs (From Warren, 1934, modified).

differences during the passage of eggs through the reproductive tract, is lacking.

The possible existence of another type of metabolic effect on hatchability is perhaps indicated by data on blood sugar which Bronkhorst (1933) and Bronkhorst and Hall (1935 a) reported. In comparing two groups of White Leghorns, one consisting of hens with an average individual hatchability of their eggs below 50 percent, the other one with individual hatching averages above 75 percent, they found that hens of the low hatching group had a mean blood glucose content of 155.03 ± 2.46 mg., while the hens of the high hatching group had 148.13 ± 2.42 mg. glucose per 100 cc. of blood. The difference amounts to 6.90 ± 3.44 mg. The authors rightly doubt if this difference is significant since no adequate period of starvation had preceded the time when the tests were made. Yet, a further study of this and similar problems would be of interest.

Payne and Ingram (1926-1927) believed that frost injury to the comb of mated cocks led to a temporary drop in hatchability of the eggs fertilized by them. This conclusion, however, is open to serious doubt since the experimental procedure was complicated by the feeding of deficient
diets to most groups; another complicating factor is the likelihood of increased sperm age on account of a lowered frequency of mating.

Intestinal toxins, circulating in the body of laying hens, can probably act as a cause of abnormal embryonic development and of low hatchability. This conclusion is suggested by observations made at the Storms Agricultural Experiment Station, and of which a short account will be given here (Landauer, unpublished). In a Barred Plymouth Rock chick (♀ 6765) with posterior duplication, the accessory legs were removed at hatching time and the bird was raised to maturity. The anatomical features of this case, as is most common in such instances, consisted of two extra legs, partial duplication of the pelvis, two cloaca and three coeca. The V-shaped colon opened into the two cloaca. Throughout its life ♀ 6765 experienced frequent periods of physical unfitness which seemed to be brought on by accumulations of large masses of feces in the abnormally-shaped colon. A lowering or cessation of egg production usually coincided with these periods of ill health. During her first laying year this hen was inseminated with sperm from an unrelated Creeper cock. The results of incubation were as follows:

<table>
<thead>
<tr>
<th>Mortality during incubation days in %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fertile eggs</td>
</tr>
<tr>
<td>1-6</td>
</tr>
<tr>
<td>7-13</td>
</tr>
<tr>
<td>14-16</td>
</tr>
<tr>
<td>17-22</td>
</tr>
<tr>
<td>Hatched</td>
</tr>
<tr>
<td>23</td>
</tr>
<tr>
<td>17.4</td>
</tr>
<tr>
<td>60.9</td>
</tr>
<tr>
<td>4.3</td>
</tr>
<tr>
<td>17.4</td>
</tr>
<tr>
<td>0</td>
</tr>
</tbody>
</table>

Out of 23 fertile eggs none hatched. Many of the embryos showed an extreme shortening of the wings and legs and abnormally small eyes.

During her second laying year ♀ 6765 was inseminated with sperm of two Leghorn cocks. The resulting incubation data were as follows:

<table>
<thead>
<tr>
<th>Mortality during incubation days in %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fertile eggs</td>
</tr>
<tr>
<td>1-6</td>
</tr>
<tr>
<td>7-13</td>
</tr>
<tr>
<td>14-16</td>
</tr>
<tr>
<td>17-22</td>
</tr>
<tr>
<td>Hatched</td>
</tr>
<tr>
<td>36</td>
</tr>
<tr>
<td>27.8</td>
</tr>
<tr>
<td>8.3</td>
</tr>
<tr>
<td>11.1</td>
</tr>
<tr>
<td>27.8</td>
</tr>
<tr>
<td>25.0</td>
</tr>
</tbody>
</table>

Only 25 percent of the 36 fertile eggs produced hatched chicks. During the two years of her life ♀ 6765 layed 59 fertile eggs, and of these only 15.3% hatched. No cases of posterior duplication occurred either in the F₁ generation or in three generations of subsequent inbreeding. Hatchability was quite satisfactory in all matings of the (normal) descendants of this female. It was observed that complete loss of hatchability occurred at those times when ♀ 6765 was in poor condition (con-
gestion of colon) and egg production was low; conversely, the few eggs which hatched were laid at times when the hen was in good condition and laid relatively many eggs.

When a cock with a (low grade) posterior duplication (δ 703; accessory legs removed at hatching time; single cloaca, no duplication of colon) was mated to normal hens, hatchability was satisfactory (73.3% out of 304 fertile eggs). All these observations point to the conclusion that in δ 6765 toxic substances were resorbed from the intestinal canal during the periods of congestion of the colon, and that these toxic substances were responsible for ill health, low fecundity, abnormal embryonic development and very poor hatchability.

Hays (1941) published some data which suggest that length of the incubation period may be slightly shorter early in the breeding season (first half of March) than later (middle of March to late April). These observations need verification and further analysis. Metabolic factors may be involved.

For the control of coccidiosis in growing chicks Nicarbazin has found wide use. Nicarbazin is a complex of 4,4’-dinitrocarbanilide and 2-hydroxy-4,6-dimethylpyrimidine. When this drug was added to the feed of laying fowl, hatchability of their eggs dropped (Ott, Kuna, Porter, Cuckler and Fogg, 1955, 1956; Sherwood, Milby and Witz, 1956; Lucas, 1958). With a dosage of 0.005 to 0.0125 percent the loss in hatchability was about 50 percent, and a slight adverse effect was noticeable with as little as 0.0006 percent. High mortality during the first week of incubation was the principal cause of reduced hatchability. Within two weeks of omitting the drug from the feed, hatchability returned to its normal level. Appearance and composition of the yolk were especially affected by feeding of Nicarbazin (Baker, Hill, van Tienhoven and Bruckner, 1957). No unfavorable effect was observed on the reproductive functions of cocks (van Tienhoven, Crawford and Duchaine, 1957). The evidence, mainly negative, concerning the influence of glandular preparations or of chemicals with effects on endocrine activity has been reviewed before (p. 107).
GENETIC FACTORS AFFECTING HATCHABILITY

Lethals and other harmful genetic factors

Lethal mutations, that is, hereditary factors causing death of the developing chick before the end of the incubation period, probably are of widespread occurrence among various breeds of fowl.

The first lethal mutation in poultry was found by Dunn (1923 a) at the Storrs Agricultural Experiment Station. It was discovered on account of its close or complete linkage with the gene for recessive white plumage in Wyandottes. In a cross of White Wyandotte females with a Pull Game male all the F₁ offspring were colored, as expected. But when some of the F₁ males were crossed each to his own mother, abnormal segregation with regard to plumage color occurred in two sibships. One of these cocks \((\delta 104)\) was bred to all his available female relatives. The results of these matings are shown in Table 46. The upper part of the table gives the results of matings between \(\delta 104\), heterozygous for the gene for recessive white, and a daughter, a half-sister and a niece. Sufficient offspring was obtained from every one of these females to make it probable that normal segregation occurred with regard to plumage color.

<table>
<thead>
<tr>
<th></th>
<th>Genotype</th>
<th>Colored</th>
<th>White</th>
<th>Total</th>
<th>Colored</th>
<th>White</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daughter 254</td>
<td>Cc</td>
<td>18</td>
<td>5</td>
<td>23</td>
<td>17.3</td>
<td>5.7</td>
</tr>
<tr>
<td>Half-sister 44</td>
<td>Cc</td>
<td>20</td>
<td>5</td>
<td>34</td>
<td>25.5</td>
<td>8.5</td>
</tr>
<tr>
<td>Niece 199</td>
<td>cc</td>
<td>10</td>
<td>10</td>
<td>20</td>
<td>10.0</td>
<td>10.0</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>57</td>
<td>20</td>
<td>77</td>
<td>52.8</td>
<td>24.2</td>
</tr>
</tbody>
</table>

Table 46

The lower part of the table shows the result of matings of this cock to his mother as well as to all other available relatives. These latter were all pure Wyandottes, belonging to the mother's family. It is evident that there is a marked deficiency in recessive white offspring. If a recessive lethal gene was present, closely or completely linked with white, for which both the male and the females were heterozygous, the expectation in these matings would be two colored to one white offspring. The actual data \((58:32)\) agree very well with this interpretation.

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Support for the assumption that a lethal gene was present in the stock may be seen in the fact that embryo mortality was excessive in the Wyandotte family which was used in the experiment (average hatchability about 30 percent), while in outcrosses hatchability was high (92 percent). The ratio of colored to white chicks among embryos dying after the sixteenth day of incubation was similar to that found at hatching time, indicating that death of the missing white chicks occurred relatively early in development. The stock became extinct before further studies could be made.

Some additional evidence on probably the same lethal was obtained by Warren (1933). With regard to his own and Dunn’s observations on this Wyandotte lethal, Warren points out that they are of “special interest since this variety of fowl is in somewhat ill repute for the hatching quality of its eggs.” The poor reproductive capacity of White Wyandottes, however, seems to be due, in part at least, to low fertility (Hutt, 1940; Cochez, 1951). Claims by Ponsignon (1951) for the existence of a lethal factor in White Wyandottes, linked to the gene for Rose comb, are unconvincing.

The second lethal mutation in poultry was found in the breed known as Creeper fowl. The characteristic external trait of Creeper chickens is the shortness of their extremities. The histological features of the long bones indicate that the Creeper condition belongs to the category of skeletal abnormalities known as chondrodystrophy. Cutler (1925) observed that Creeper fowl are always heterozygous for their characteristic breed features and suspected lethality of the homozygotes. In extensive studies, conducted at the Storrs Agricultural Experiment Station, it was confirmed that the offspring of Creeper matings always show segregation for the Creeper and normal traits (Dunn and Landauer, 1926; Landauer and Dunn, 1930 a). True-breeding Creeper chickens do not exist. This was a strong indication that the Creeper mutation is lethal when homozygous. Though outcrosses to normal stock showed that the Creeper traits are due to a dominant mutation, inter se matings of Creepers produced Creeper and normal offspring in the ratio of 2:1 (actual data 1197:567), instead of the expected 3:1, suggesting that the class of homozygous Creepers is lacking. Confirmation of this conclusion was obtained from the records of embryonic mortality and hatchability (Table 47).

<table>
<thead>
<tr>
<th>Table 47</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mating</strong></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Creeper x normal</td>
</tr>
<tr>
<td>Creeper x Creeper (same lines)</td>
</tr>
<tr>
<td>Creeper x Creeper (different lines)</td>
</tr>
</tbody>
</table>
It can be seen from these data that in crosses of Creeper by Creeper, hatchability is much lower than in crosses of Creeper by normal. It is also evident that in Creeper by Creeper matings a peak of mortality, not present in outcrosses, occurs during the first week of incubation.

Observations on early embryonic development showed that most of the homozygous Creeper embryos die after three days of incubation (Landauer, 1932 a.) In comparison with normal embryos of the same age, they are much retarded, especially in the region of the head and of the limb buds (Figure 30).

A few of the homozygous Creeper embryos continue development beyond this early critical stage, and die towards the end of the incubation period; none ever hatch. The late homozygous Creeper embryos (Figure 31) show extensive abnormalities of the eyes, the head generally, and especially the extremities (Landauer, 1933).

Whereas in matings of ordinary Creeper fowl homozygous embryos survive to late developmental stages only on rare occasions, survival of the lethal embryos to such late stages occurs much more commonly in eggs of Japanese Bantam fowl, a breed which carries the Creeper mutation (Landauer, 1938, 1942 a). In addition to its lethal effect on all homozygous embryos, the Creeper mutation is also responsible for an increased embryonic mortality of the heterozygotes. This is shown by the data in Table 48. In outcrosses as well as in inter se matings there is close agreement of actual and expected figures if the total of hatched chicks and of classifiable dead embryos is taken into consideration. But if these two
groups are studied separately, it is found that there are too few Creepers among the hatched chicks and too many among the embryos which died towards the end of incubation. It follows that the mortality of heterozygous Creeper embryos is somewhat greater than that of normal embryos from the same matings.
A comparison of the results of reciprocal matings between sibs of Creeper and normal fowl furnished proof that the presence of the Creeper mutation affects the chances of embryo survival in still another way. In eggs produced by Creeper females, embryo mortality during the last stages of development is slightly, but significantly, higher than in eggs laid by their normal sisters (Landauer and Bliss, 1943). The causes of this "maternal" effect of the Creeper mutation have not been definitely established, but are probably to be found in abnormalities of egg shell formation which, in turn, find their explanation in the skeletal defects (inadequate calcium deposits). Maternal effects on egg shell formation had earlier been demonstrated by Taylor and Lerner (1939) in White Leghorn stock.

Finally, unusual malformations sometimes occur in the Creeper stock which may involve heterozygous Creeper as well as genetically normal embryos (Landauer, 1935 a).

A third lethal mutation was found at the Storrs Agricultural Experiment Station in Dark Cornish fowl (Landauer, 1935 b). Similar to the Creeper mutation, the Cornish lethal in heterozygous condition has a shortening effect on the long bones of the extremities. The homozygous embryos die during the last days of incubation or are alive within the shell at hatching time, but are unable to hatch. These lethal embryos have markedly shortened extremities and a quite abnormal, short and broad head with bulging eyes (Figure 32). Table 49, combining the results of several matings, gives the data of embryonic mortality, hatchability, and incidence of abnormal embryos for hens which did (group I) or did not (group II) produce deformed embryos when mated to roosters which were heterozygous for the mutation.

Figure 32
A lethal embryo from Dark Cornish fowl. Age 21 days.
The frequency of occurrence of deformed embryos in group I is sufficiently close to 25 percent to justify the conclusion that we are dealing with a recessive lethal mutation produced by a single factor difference. In the largest of the several matings, summarized in group I, 25.4 percent deformed embryos occurred (456 fertile eggs). Hatchability in group II was also relatively low. From available evidence it seems unlikely that this is, to any large extent, accounted for by a heterozygous lethal effect of the mutation in question. It seems more likely that still other genes, detrimental to survival of the embryo, have been accumulated in the Cornish stock. When cocks heterozygous for the Cornish lethal were outcrossed to unrelated normal females (Leghorn, etc.), the average hatchability rose to 83.2 percent (631 fertile eggs). The Creeper and Cornish lethals, though in many ways similar in expression, were found to be independent of each other genetically: four matings between Creeper and Cornish fowl, with a total of 902 fertile eggs, gave hatches of 81.1, 87.9, 88.3 and 89.0 percent, respectively, and no deformed embryos occurred. The Cornish chickens used in these matings were known to carry the Cornish lethal.

The occurrence of a sex-linked lethal in a flock of White Leghorn fowl was reported by Uppe (1934 and Uppe and Waters (1935), but the evidence is scarcely sufficient to support this claim.

A fourth lethal mutation in poultry was found by Asmundson (1936). It occurred in an inbred strain of White Leghorns. The lethal-type embryos showed abnormal maxillae. The maxillae were absent or much reduced in size, while the pre-maxillae were present, though at times somewhat smaller than normal (Figure 33). In some cases the nasal bones also were smaller. The upper beak was frequently bent to one side. Other facial bones may be affected and the eyes appeared to be slightly smaller than normal in some of the lethal embryos.

These deformities did not seem to reduce the viability of the embryos appreciably, but hatching occurred only in one instance. This chick, as well as seven others which had been helped out of the shell, died within one week. The abnormal embryos occurred among the progeny of one hen mated to a son, and among the progeny of some daughters of this hen bred to the same male, their full brother. The breeding data indicate that we are dealing with a recessive mutation due to a single gene difference (Table 50). Sex has no influence on the occurrence of the malformed embryos. In the whole material there were

<table>
<thead>
<tr>
<th>Table 49</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Group</strong></td>
</tr>
<tr>
<td>----------</td>
</tr>
<tr>
<td>I</td>
</tr>
<tr>
<td>II</td>
</tr>
</tbody>
</table>

142
173 normal and 58 abnormal embryos, with an expectation of 173.25:57.75 for a 3:1 segregation.

### Table 50

<table>
<thead>
<tr>
<th>Female No.</th>
<th>Normal upper mandible</th>
<th>Abnormal upper mandible</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>I 13</td>
<td>14</td>
<td>17</td>
</tr>
<tr>
<td>K 12</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>K 36</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>K 46</td>
<td>28</td>
<td>18</td>
</tr>
<tr>
<td>K 68</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>K 91</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>K 100</td>
<td>17</td>
<td>20</td>
</tr>
<tr>
<td>Total</td>
<td>78</td>
<td>84</td>
</tr>
</tbody>
</table>

The data on embryonic mortality and hatchability for the eight heterozygous hens (group I) and for five other hens which produced only normal progeny (group II) are shown in Table 51. Group I includes 14 embryos which died too early to be classified. It is evident that the chief difference in mortality occurred at the end of the incubation period (failure to hatch). Hatchability in the control group was also low, probably on account of inbreeding. Malformed embryos of the same type have been observed in the material of the Storrs Experiment Station and elsewhere (Waters, 1945), suggesting that this lethal mutation has a wide distribution among flocks of White Leghorn fowl.

In White Leghorn stock Cole (1939, 1942) discovered the fifth, so-called "talpid", lethal of fowl (Figure 34). The distinguishing features of this mutation are an extreme form of polydactylyism, involving both pairs of extremities, a marked reduction in length of the proximal long bones of legs and wings, ectopia viscera and abnormalities of the face, especially the mandible. The feet of such embryos may have as many as nine or ten digits which are very poorly differentiated and fused with each other or webbed. The wings also show multiple digit primordia. The entire vertebral column is shortened. There is subcutaneous edema, often resulting in large blebs over the thigh region and on head and neck. Development of the feather papillae is retarded. The talpid embryos generally die at the age of eight to ten days, but one was found alive at 17 days of incubation. The abnormalities are recognizable on the fourth day of development.
The talpid syndrome owes its appearance to a single autosomal, recessive gene substitution. In matings of heterozygous animals in which the number of unclassifiable embryos did not exceed 5 percent, the incidence of talpid embryos was 23.6 percent (98 out of 415), a result which agrees satisfactorily with the expected 25 percent. It is true, however, that the records of all matings of heterozygous parents showed an incidence of only 16.6 percent of the lethal-type embryos. This deficient ratio is presumably an indication of preferential mortality of the recessive homozygotes before they become classifiable. A study by Inman (1946) of homozygous talpid embryos revealed additional and extraordinary abnormalities. Rathke's pouch, the primordium of the pituitary, is either missing altogether or involved in the formation of supernumerary ectopic lenses; no normal pituitary is formed. In almost all talpid embryos epiphysis-like evaginations of the roof of the forebrain were observed and in some of them there were, in addition, diverticula of the hypothalamus. In about half of the talpid embryos Inman found that the tail bud had split in an early stage, leading to the formation of two axial structures, one of which was in the normal position of the tail, whereas the other one protruded into the cloacal cavity. There was evidence of necrotic degeneration in certain areas of the body wall, the mid-gut region and the cloacal lining, and Inman believes that a lesser amount of such de-
generation can also be observed in embryos which are heterozygous for talpid.

The sixth lethal mutation of chickens was found at the Storrs Agricultural Experiment Station in stock of Houdan crossbred ancestry (Landauer, 1941a). This mutation produces a variable reduction in

![A 17 day embryo with lethal polydactyly (From Cole, 1942).](image)

length of the upper beak (Figure 35) and a shortening of the long bones of the extremities. The reduction in length affects the bones of the legs to a higher degree than those of the wings. The majority of “short upper beak” embryos die during the last days of incubation, but in the original material about 13 percent of them hatched, suggesting the presence of modifying factors.

The multiple characters of this mutation are brought on by a single, autosomal, recessive factor. This is shown by the data in Table 52. When one of the parents in the matings was genetically normal, hatchability was high and no “short upper beak” embryos occurred; when both parents were heterozygous for the trait, 25.5 percent of all embryos surviving the eighteenth day of incubation were “short upper beak” \( (N=652) \); when
heterozygous females were mated to a homozygous "short upper beak" male 47.6 percent of the embryos which reached the end of the eighteenth day had the "short upper beak" characteristics (N=119). Subsequent studies (Landauer, 1946) adduced proof that in the absence of modifiers the "short upper beak" mutation is completely lethal. It was also shown that by continued selection the morphological features of the mutation as well as its lethal effect can be suppressed to a large extent. Unpublished observations have shown that the combined presence of the Cornish and "short upper beak" lethals has no cumulative effect on either morphological expression or viability.

Hereditary chondrodystrophy, as described by Lamoreux (1941, 1942), represents the seventh lethal mutation of fowl. The mutation was found
<table>
<thead>
<tr>
<th>Type of mating</th>
<th>Number of fertile eggs</th>
<th>Embryo mortality during incubation days in %</th>
<th>Hatched</th>
<th>Dead embryos (19-22 days)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1-6</td>
<td>7-18</td>
<td>19-22</td>
</tr>
<tr>
<td>Normal ♀ ♀ × heterozygous ♂</td>
<td>675</td>
<td>5.0</td>
<td>4.6</td>
<td>14.5</td>
</tr>
<tr>
<td>Heterozygous inter se</td>
<td>742</td>
<td>7.1</td>
<td>5.0</td>
<td>33.3</td>
</tr>
<tr>
<td>Normal ♀ ♀ × homozygous ♂</td>
<td>78</td>
<td>9.6</td>
<td>5.6</td>
<td>6.8</td>
</tr>
<tr>
<td>Heterozygous ♀ ♀ × homozygous ♂</td>
<td>294</td>
<td>6.5</td>
<td>8.5</td>
<td>46.3</td>
</tr>
</tbody>
</table>

Table 52

Note: The table presents the number of fertile eggs and the mortality rates of embryos during incubation days, along with the hatched percentages and the percentage of dead embryos (19-22 days). The data are categorized by type of mating, with different combinations of normal and heterozygous individuals.
in an inbred strain of White Leghorns. Its phenotype is variable. In its most abnormal form of expression the external appearance of such embryos and the histological structure of their long bones bear close resemblance to sporadic chondrodystrophy (see p. 194). The beak is parrot-like and the extremities are shortened (Figure 36). The long bones of the legs are more reduced in length than those of the wings; some of the bones are bent. According to Lamoreux the abnormalities frequently are less pronounced, however, and may be so slight as to be barely distinguishable. These “modified” chondrodystrophic embryos and the extreme ones were reported to belong to two distinct groups. Chondrodystrophic embryos of the sporadic type regularly die prior to the end of the incubation period. In the hereditary form of chondrodystrophy, as described by Lamoreux, the abnormal embryos frequently are still alive on the twenty-second day of development and even some of the extreme variants may hatch on occasion (Figure 37).
The following segregation data (Table 53) were obtained, for embryos of more than ten days incubation, from heterozygous parents which had produced progeny with the extreme form of chondrodystrophy. The total incidence of chondrodystrophic embryos amounted to 22.5 percent.

Table 53

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of mothers</th>
<th>Number of offspring</th>
<th>Normal %</th>
<th>Extreme %</th>
<th>Modified %</th>
<th>Total %</th>
</tr>
</thead>
<tbody>
<tr>
<td>1936</td>
<td>1</td>
<td>38</td>
<td>84.2</td>
<td>10.5</td>
<td>5.3</td>
<td>15.8</td>
</tr>
<tr>
<td>1937</td>
<td>8</td>
<td>253</td>
<td>77.9</td>
<td>15.4</td>
<td>6.7</td>
<td>22.1</td>
</tr>
<tr>
<td>1938</td>
<td>15</td>
<td>382</td>
<td>76.2</td>
<td>17.3</td>
<td>6.5</td>
<td>23.8</td>
</tr>
<tr>
<td>1939</td>
<td>9</td>
<td>217</td>
<td>74.7</td>
<td>11.5</td>
<td>13.8</td>
<td>25.3</td>
</tr>
<tr>
<td>1940</td>
<td>33</td>
<td>823</td>
<td>78.4</td>
<td>14.0</td>
<td>7.6</td>
<td>21.6</td>
</tr>
<tr>
<td>Total</td>
<td>66</td>
<td>1713</td>
<td>77.5</td>
<td>14.5</td>
<td>8.0</td>
<td>22.5</td>
</tr>
</tbody>
</table>

Figure 37
Chondrodystrophy of the extreme type in a newly-hatched chick (From Lamoreux, 1942).
Lamoreux concluded from his data that the trait is transmitted as a single recessive gene substitution. This has been confirmed by (unpublished) observations at the Storrs Agricultural Experiment Station where selection experiments are in progress relative to the nature of the modifying genes that affect the expression of hereditary chondrodystrophy. Lamoreux could also demonstrate that the "sporadic" type of chondrodystrophy (to be discussed later) is independent of his mutant form.

Figure 38
Micromelia, parrot beak and deformed mandible produced by two recessive genes (From Asmundson, 1942 a).

Asmundson (1939, 1942) observed a lethal micromelia which appears to be the homozygous expression of two recessive genes. The phenotype of this eighth lethal of fowl is marked by very short extremities, a short and curved upper beak and a defective lower beak (Figure 38). The great majority of these embryos survive to the third week of incubation, but none ever hatch. The mutation was found in White Leghorn stock. Segregating families gave 716 normal embryos and chicks and 47 embryos of the micromelic type. The data are in good agreement with the 15:1 expectation for dihybrid segregation. The sex ratio of the micromelic embryos was normal.

Waters and Bywaters (1941, 1943) described the ninth lethal mutation of fowl which they designated as "wingless." It occurred in White Leghorns. The mutation leads to the following syndrome of abnormali-
Figure 39
A wingless embryo (left) and one with wing vestiges (right). Courtesy of Dr. Edgar Zwilling.

cies. The wings are generally entirely lacking, but in rare instances wing vestiges are found on one or both sides (Figure 39). In the hind limbs, toes may be missing or duplicated, the first toe is misplaced, the scales are missing from shanks and toes, the third and fourth toe, if present, are syndactylyous, the tibiotarsometatarsal joint is ankylosed. The primary bronchi end in a blind pouch, the lungs proper being absent. There are no air-sacs. Islands of metanephrogenous tissue were found in some cases, but the metanephros proper (i.e. the definitive kidney) is always missing. The down is regularly in the “clubbed” condition. Many of these “wingless” embryos survive to the end of the incubation period: they never hatch. The whole syndrome is brought about in the presence of one recessive gene substitution. A progeny of 141 individuals from heterozygous parents included 30 embryos of the lethal type. The early embryology of this lethal condition has been studied by Zwilling (1949 a).

The most important result of his observations was that absence of the wings and abnormalities of the legs are related to corresponding defects in the apical epidermal ridges of the buds of the extremities. This is of great interest because these epidermal ridges are known to play an inductive role in development of the extremities. A lethal mutation very similar to that reported by Waters and Bywaters was found at Storrs in matings with Leghorn-crossbred ancestry. The defects of the extremities, especially the legs, tended to be more extreme, but the lungs were present (Zwilling, 1956). Since the original “wingless” mutation had become extinct, it could not be ascertained whether the new variant was a repeat mutation, and the phenotypic differences brought about by dissimilarities
of residual heredity, or whether the mutation was independent of the original one.

In a family of Rhode Island Red fowl Hays (1944) found a hereditary micromelia which he designated as chondrodystrophy. This represents the tenth lethal of fowl. The principal phenotypic traits are very short (but straight) long bones of legs and wings and a shortened beak. Matings of seven heterozygous females to a heterozygous cock gave 172 normal and 54 micromelic progeny. This result is in good agreement with the expectation (169.5:56.5) for segregation in a single gene difference, micromelia being recessive. Hays found that on rare occasions a micromelic chick hatched, but none survived more than a few days. Ob-

![Figure 40](image)

An adult Rhode Island Red male with hereditary micromelia.

servations at the Storrs Agricultural Experiment Station suggest that the hatching of such micromelic chicks tends to occur in late (rather than early) spring. One chick of this type was raised to maturity (Figure 40).

The eleventh lethal mutation of fowl was described by Marble, Ham-mers and Harper (1942) and by Marble, Harper and Hammers (1944). It occurred in White Leghorn stock. The mutation interferes with development of the head. Cerebral hernia is one of the regular features, though varying in degree. Both maxillae are abnormal: the lower one usually is only a vestige; the upper one is much reduced in size and pointing upward (Figure 41). The eyes are generally abnormal and other facial parts are reduced in size. The syndrome is inherited as an autosomal recessive. Among a progeny of 512 individuals from matings of heterozygous parents 378 were normal and 134 showed the lethal syndrome (expectation 384:128). The sex ratio of the lethal embryos was normal. Among the normal progeny two-thirds were heterozygous, one-third did not carry the mutation.
In a flock of New Hampshires Asmundson (1945) observed a syndrome of abnormalities which represents the twelfth lethal mutation of fowl. The phenotype of this mutation has the following principal features (Figure 42). The upper beak is slightly shortened; the neck is twisted, thereby seeming short; the sternum is reduced in size and its keel and lateral processes are lacking; the breast muscles are absent or very poorly formed; the muscles of the legs are also underdeveloped; the long bones of the legs are slightly reduced in length. The embryos are below normal weight as early as the tenth day of development and this dwarfing becomes very marked towards the end of the incubation period. Death occurs on the twentieth or twenty-first day. Progenies of heterozygous parents contained 103 lethal-type embryos among a total of 400 embryos and chicks. The syndrome is, therefore, brought about by a recessive gene substitution. The occurrence of muscular degeneration was demonstrated in embryos of this type (Rosenberg, 1947). Another feature of this lethal syndrome is, according to Pun (1954), atresia of the esophagus which prevents the embryos from ingesting amniotic fluid, and which may thereby be responsible for symptoms of starvation and for hydramnion.
A dwarf embryo (left) and a normal one (right). Observe that in the dwarf embryo the upper beak is shortened and the leg muscles are atrophic
(From Asmundson, 1945).

McGibbon (1946) observed in White Leghorns the thirteenth lethal mutation. It is expressed as a shortening of the mandible and inherited as an autosomal recessive trait. The reduction in size of the lower beak acts as a semi-lethal, about half of the homozygous embryos dying prior to the end of the incubation period and the majority of those which emerge from the shells perishing soon thereafter.

The fourteenth lethal mutation of fowl was described by Taylor and Gunns (1947). The variation was found in White Leghorn stock. Polydactylism and shortening of the upper beak are the principal phenotypic features of the mutation. The morphological expression of polydactyly differs in these so-called „diplopod” embryos from Cole’s polydactylous lethal as well as from the two viable forms of hereditary polydactylism of fowl. A group of three toes is generally found in place of the first digit of the foot, the two inner ones being much smaller than the lateral one. The metatarsal bones frequently are doubled.

There are, however, many variations in expression. In 97 percent of these embryos supernumerary digits are also found in the wings. The long bones of both pairs of extremities tend to be shortened. The upper
Figure 43
Embryo with diplopodia. Note shortening of upper beak and polydactylism of wings and legs (From Taylor and Gunns, 1947).

Figure 44
An embryo with Micromelia VII (Courtesy of Dr. Paul E. Bernier).
beak is reduced in length in over 80 percent of the diplopod embryos. One of the more extreme variants of this lethal is illustrated in Figure 43. About 98 percent of the diplopod embryos died before the end of the incubation period, and the few which hatched survived for only brief periods. In matings of heterozygous fowl a progeny of 1531 yielded a segregation of 1183 normals and 348 diplopod. The slight deficiency in diplopod embryos (22.7 percent instead of 25 percent) may be due to a somewhat disproportionate mortality prior to the time when their morphological features can be recognized by gross inspection. After outcrossing this family to another stock of White Leghorn fowl Taylor, Abbott and Gunn (1959) succeeded in establishing by selection three lines with significantly differing phenotypic segregation ratios. In their line I the segregation data agreed with a 3:1 expectation; in line III the number of visibly diplopod embryos was grossly deficient, some individual matings producing as little as only 1 to 3 percent of diplopod phenotypes; line II was intermediate between lines I and III. The results of these breeding tests demonstrate clearly the existence of multiple modifying genes by the accumulation of which the penetrance of diplopodia can be progressively reduced. Abbott (1959 a, b) found that early cartilage differentiation and osteogenesis are retarded in homozygous diplopod embryos, with differences of expression between the selection lines. She observed also that the lowering of the penetrance of diplopodia by selection was attended by correlated reduction in expressivity of the various features of the diplopodia syndrome.

A fifteenth lethal condition was described by Bernier (1951 and personal communication) as Micromelia VII. Such embryos live to the end of the incubation period, they resorb the yolk sac completely into the body cavity, but they fail to hatch. The legs are extremely short; the tibiotarsus is bent; the wing bones are, as in other forms of micromelia, less shortened than those of the legs. Differing from other types of micromelia, the beak is normal; but the eyes are always microphthalmic. An embryo of this kind is shown in Fig. 44. A total of 165 individual matings produced, in a progeny of 1464, a segregation into 1090 normal and 374 micromelic chicks. This is a quite insignificant deviation from the 1098:366 ratio, expected on the assumption that the abnormality is brought about by a single, recessive gene substitution.

The sixteenth lethal mutation of fowl was found in the Barnevelder breed by Broekhuizen and van Albada (1953). The typical phenotypic expression of this mutant consists of an upward curling of the maxilla (normal in length) and a downward curling of the usually shortened mandible (Fig. 45). The deformation of the maxilla may involve all of the upper beak or only its tip. Instead of being curled downward, the mandible is in some instances only shortened or bent toward one side. The abnormality can be recognized in 10-day embryos. The majority of embryos of this type die during the last days of incubation; a few were
helped out of the shell, and one such chick lived to the age of 7½ weeks (Fig. 46). These “curled beak” abnormalities were found in seventeen matings of phenotypically normal parents. Among a total progeny of 327 embryos and chicks 252 were normal, 65 had the “curled beak”, and in 10 the diagnosis was doubtful. If the latter group is added to the abnormalities, the resulting ratio of 252:75 does not differ significantly from that expected for an autosomal, recessive gene substitution, and such the authors conclude it to be. They assigned the symbol dck to the mutant gene.

The seventeenth lethal mutation of chickens was discovered at the Storrs Agricultural Experiment Station in a flock of Black Minorca fowl (Landauer, 1956 a). The phenotype of this mutant is a close mimic of the diplopodia lethal of White Leghorns described by Taylor and Gunns (1947). As in the latter variant, the principal features of the Minorca lethal are polydactylism of hands and feet, reduction in length of the long bones and shortening of the upper beak (Fig. 47), but there are...
minor differences in morphological expression which are possibly accounted for by dissimilarities of residual heredity. In *inter se* matings of heterozygous parents progenies totalling 828 survivors of the thirteenth day of incubation yielded a segregation ratio of 650 normal and 178 diplopod embryos and chicks. This is an insignificant deviation from the 621:207 ratio expected on the assumption of a single, recessive gene substitution. It was found that the Leghorn (dp-1) and Minorca (dp-2) genes for diplopondia are discrete and non-allelic, the double heterozygotes having a normal phenotype. The majority of homozygous Minorca diplopod embryos died during the last few days of incubation and were small in size; none hatched.

The eighteenth lethal mutation of fowl is represented by malformations of the head which, in their whole range of expression, have been described as perocephaly (*Landauer*, 1956 b). The phenotype of this mutant condition varies from a very poorly developed upper beak, associated with blindness, to microcephaly; its most common manifesta-
tions are synophthalmia and cyclopia (Fig. 48). The perocephaly mutant was found at the Storr's Agricultural Experiment Station in F₂ and later generations of crosses between recessive-rumpless fowl and representatives of the following three breeds: Silver Gray Dorking, Rhode Island Red and Jungle fowl. The initial incidence of perocephalic embryos was only between 2 and 3 percent, but rose to 13 percent when the genotypes of all sources of origin were combined. The breeding history showed clearly that the gene or genes for perocephaly had been present in the recessive-rumpless stock (and likely in the White Leghorn family from which the rumpless mutant was derived), but had been prevented from expression by protective modifiers. The incidence rose pari passu with the removal or dilution of these protective (stabilizing) genes, but it appeared that even in later generations many of the perocephaly homoygotes had a normal phenotype (normal overlaps). Chicks with low-grade perocephaly hatched on rare occasions, but were inviable (Fig. 49). The incidence of perocephaly showed in three out of four breeding seasons a highly significant trend, the frequency of segregating abnormal embryos rising from early spring toward summer. Experiment-
al evidence suggests that this trend is caused by parallel changes (lowering) in the oxygen tension of the surrounding air (Landauer, 1957 a). Similar conditions probably play a role in producing the seasonal trends in the incidence of sporadic eye defects (p. 195-196).

A nineteenth lethal mutation has been discovered recently at the Storrs Agricultural Experiment Station in Silver Gray Dorking stock (Landauer, 1959). The principal gross symptoms are shortness of the neck and beak (Fig. 50); more posterior sections of the vertebral column may also be involved: interference with some, as yet undetermined, vital function presumably accounts for death of the embryos which occurs during the ninth day of incubation. The segregation data agree well with the assumption that a simple, recessive mutation is present in the stock.

Figure 48
Forms of expression of the perocephaly lethal. Upper left, rudimentary upper beak; upper right, synophthalmia; lower left, cyclopia; lower right, lack of oral cavity, central pigment spot on ventral side in place of eyes, otocephaly.
A brief report by \textit{Abbott, Taylor and Abplanalp} \textit{(1959)} describes a twentieth lethal mutation of fowl. It was found in White Leghorn stock and bears a close resemblance to the talpid-lethal described by \textit{Cole} which has already been discussed. Hence the new lethal is designated as \textit{talpid}$^2$ (\textit{ta}$^2$). Each foot of these embryos has 7 or 8 syndactylous and poorly differentiated digits; in the wings 4 or 5 fingers are fused into a hand-like structure. The \textit{talpid}$^2$ embryos usually die at 13 days of age. Segregation agrees well with expectation for a recessive, autosomal gene substitution. It is of particular interest that the apical ectodermal ridge,

\textbf{Figure 49} \hspace{1cm}

A blind ptercephalic chick at the age of 3 months, raised by forced feeding.

the structure that plays such an important role in determining events in the differentiating extremities, is enlarged in embryos that are homozygous for the \textit{ta}$^2$ gene.

A twenty-first lethal of fowl was discovered by \textit{Rosenblatt, Kreutziger and Taylor} \textit{(1959)}, also in the White Leghorn stock of the University
of California. It is represented by yet another form of polydactylysm. The condition which bears some similarity to the phenotype of diplopodia has been given the name eudiplopodia. Eudiplopod embryos have a variable number of replicated toes (total up to 9 for each foot) and in the more severely affected cases there is also replication of one or more tarsometatarsals. The wings are relatively rarely involved. The eudiplopod embryos die at the end of the incubation period. Matings of heterozygous animals to each other produced 464 normal and 151 abnormal embryos and chicks, the close fit to expectation indicating segregation for a single autosomal, recessive mutant gene. Test crosses have shown that eudiplopodia is not allelic to the diplopodia of White Leghorn fowl.

Kawahara (1956) has briefly reported on a lethal mutation in White Leghorn fowl. As phenotypic traits he noted micromelia, shortening of the upper beak, poor skeletal calcification and highly viscous amniotic and allantoic fluids. Death occurred at the end of the incubation period.
Matings of heterozygous parents produced 339 normal and 99 micromelic embryos, with a normal sex ratio in both classes. The mutation, therefore, appears to be autosomal and recessive. It is of particular interest that the bones of the micromelic embryos contained little calcium but an abnormally high percentage of magnesium.

Reference has been made earlier (p. 97) to the reports by Mauw and his associates on a recessive mutation in White Leghorn fowl which in homozygous condition interferes with the transfer of riboflavin to the eggs of laying hens. The mutation creates an egg environment that is lethal even if the embryos themselves are genetically normal (heterozygous).

The possibility of the existence of sex-linked genes with an effect on hatchability is suggested by observations of Gredina (1936). This author studied hatchability in matings between rapid and slow-feathering Rhode Island fowl. Her results are shown in Table 54. The author concluded from her data that embryos with the phenotype for rapid feathering hatch better than those with the phenotype for slow feathering. The difference in hatchability between the first two matings amounted to 16.0 ± 4.7 percent.

Hutt (1949, 1951) found in progenies from crosses of Barred Plymouth Rock ♀♀ x Rhode Island Red ♂♂ a deficiency of females among the newly-hatched chicks and an excess among the embryos that had died during the last days of incubation. About 1 percent of the hatched female chicks showed bare spots on the back and a shortening of the down plumules, but these chicks subsequently developed normally. In about 3.5 percent of the female embryos, however, the down defects were sufficiently severe to prevent hatching. It is evident that this condition can be a source of appreciable losses in such Rock-Red crosses. The incidence of defective embryos and chicks was greater in the progenies of dams that had themselves been defective at the time of hatching, than among the progenies of dams that had been normal, indicating the existence of multiple modifying factors. These down defects are associated with the presence of extended black plumage pigmentation; they occur only very seldom in barred chicks and for this reason the males from the crosses under discussion, with rare exceptions, escape damage.

The physiological basis of these down defects has been clarified by the observation of Bernier and Cooney (1954) that embryos with a black down require greater amounts of riboflavin during development than do non-black embryos. They found that in progenies segregating for down color the incidence of symptoms of riboflavin deficiency was higher among black than among non-black embryos. It appeared, furthermore, that in the presence of genetic modifiers of the gene (E) for extended black pigmentation the requirement of embryos for riboflavin was reduced in proportion to restriction of the area of black down color, with
a corresponding increase in survival and hatching. Bernier and Cooney suggested that their observations may provide the explanation for the excessive mortality of female embryos in matings involving sex-linked factors for plumage pigmentation, such as the crosses of Barred Plymouth Rock $\varnothing \times$ Rhode Island Red $\varnothing \varnothing$ referred to above, in which the females are the sex with greater intensity of pigmentation. The additional observation by Hutt that embryo mortality due to such down defects is eliminated in chicks which are homozygous for the genes for rapid feathering (kk) presumably constitutes confirmation of the report by Gredina, discussed above.

New evidence relating to an influence of the genotype for plumage pigmentation on embryo viability was brought forward in extensive tests by Collins and Hubbard (1958). In the authors' own words: "When the proportion of dominant white to colored progeny from backcross matings to New Hampshires of parents heterozygous for dominant white, I, and extended black, E, was compared with the ratio of offspring from the backcross mating of parents heterozygous for dominant white but homozygous for restricted black, e, the number of dominant white chicks from the former mating was significantly reduced. This is interpreted as being due to lower viability of the embryo resulting from interaction of the I and E genes."

Quisenberry and Atkinson (1956) have reported on experiments in which young White Leghorn cockerels were exposed to whole-body X-ray irradiation. When such males were later used in breeding tests, it was found that overall hatchability of the eggs fertilized by them was not adversely affected. An interesting relation was, however, observed between the dosage of X-rays with which these cockerels had been treated and the sex ratio of those embryos in their progenies that died during the last week of incubation. The higher had been the X-ray dosage (between 50 and 700 r) the greater was the percentage of females among the late-dying embryos. The authors conclude that sex-linked lethal mutations had been induced in proportion to the dosage of X-rays. Reference has been made earlier (p. 55) to experiments by Sandvik with gamma rays of cobalt and to tests by Samoletov, Kostin and Salgannik with radiation from salts of uranium and thorium.

In addition to the large number of well-established genetic lethal conditions that have just been reviewed, there are various reports which are incomplete or of a doubtful nature, but which must be briefly reviewed.

In inter se matings of the progenies of crosses between Barred Plymouth Rock and Rhode Island Red fowl Byerly and Jull (1932) found abnormal embryos which were reduced in size, had very soft (poorly calcified or uncalcified) bones, and showed edema of varying extent. Most of these embryos died during the last days of incubation; none hatched.
<table>
<thead>
<tr>
<th>No.</th>
<th>Females</th>
<th>Males</th>
<th>Number of fertile eggs</th>
<th>Mortality during incubation periods</th>
<th>Hatch %</th>
<th>Phenotype of embryos</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>rapid</td>
<td>rapid</td>
<td>134</td>
<td>2-6-14-22</td>
<td>61</td>
<td>all rapid</td>
</tr>
<tr>
<td>2</td>
<td>rapid</td>
<td>slow</td>
<td>577</td>
<td>2-6-14-22</td>
<td>45</td>
<td>all slow</td>
</tr>
<tr>
<td>3</td>
<td>slow</td>
<td>rapid</td>
<td>301</td>
<td>5-15-15-22</td>
<td>54</td>
<td>50% rapid, 50% slow</td>
</tr>
</tbody>
</table>
Because the amniotic and allantoic fluids were unusually viscous, the condition was called “stickiness.” The authors concluded from their data that they were dealing with a recessive (or partially dominant) lethal mutation. They noted that in eggs containing such abnormal embryos practically no calcium was withdrawn from the shell. Ogorodniy and Penion-schkevitsch (1939) believe that “stickiness” is caused by a vitamin B₂ deficiency. Although the identity of the condition described by them with that reported by Byerly and Jull is not established, the chances that their suggestion meets the situation have been strengthened by the observations of Bernier and Gooney (1954) to which reference has been made above (p. 163-164).

Interesting observations are reported by Bernier (1953) in a brief, preliminary paper. He found that in a mating of 12 White Leghorn pullets and one particular White Leghorn male early embryo mortality amounted to 45.9 percent among 146 fertile eggs. When these pullets were mated to another cock the mortality during the same period was only 6.5 percent (186 fertile eggs), but rose once again to 46.4 percent when the original male was returned to the pen (250 fertile eggs). Early mortality was similarly high when this cock was mated with Cornish hens. The data suggest that a dominant lethal mutation had occurred in the testes of the male in question. Bernier (1960) suggests that a chromosome aberration, probably a translocation, had occurred. Observations by Hays (1926) on a Rhode Island Red cock, open to a similar interpretation, will be referred to subsequently (p. 183).

Many mutant conditions, without being lethal, reduce the viability of chicken embryos. Hutt and Sturkie (1938) reported on a mutation, “naked”, which interferes with normal formation of the down plumage. At hatching time the expression of the trait varies from nearly complete to partial nakedness. Up to 18 days of development the viability of “naked” embryos is normal, but during the last few days of incubation about half of the homozygous “naked” chicks die. No difference in expression of the trait was found between the chicks which died before hatching and those which hatched. The mutation is recessive and sex-linked.

Incomplete data on a somewhat similar variation had been presented earlier by Serebrowsky and Petroff (1929). In an inbred strain of chickens they observed three fully formed embryos, two of which were entirely downless, while the third was only sparsely covered with incompletely developed down. All three embryos showed poor development of the scales on shanks and toes. Two of these embryos occurred in a progeny of 14, the third in a progeny of 15 chicks. All were closely related to each other. The fact that all three embryos appeared in one inbred strain, and that none were found in other stocks, suggests that the condition was hereditary, though probably not in a monofactorial way. Warren (1930) has called attention to the fact, however, that downlessness may also appear as a non-hereditary trait. In yet another “naked” mutation embryo mortality is not increased (Sturkie, 1941, 1942).
The dominant "flightless" mutation probably has a partial lethal effect. In the heterozygous condition the flight feathers tend to break off near their base. In progenies of heterozygous flightless fowl some individuals show retarded body growth and plumage development as well as defective beaks and toe nails. These are believed to be the homozygous "flightless" birds. They remain almost entirely bare, do not become sexually mature and generally die early. Warren (1937) believes that many of the homozygous "flightless" segregates die early, possibly prior to the end of the incubation period. Conclusive evidence is wanting.

The presence of a lethal mutation in a stock of Australorps in which changes of plumage color from black to white occurred in a number of females was claimed by Gericke (1934), but his evidence is unconvincing.

A recessive mutation leading to bilateral microphthalmia was found by Jeffrey (1941) in an inbred strain of Barred Plymouth Rock fowl. The abnormality was frequently associated with thickening and doubling of the posterior part of the comb. Embryo mortality was much increased in the presence of this mutation. The morphogenesis of this eye abnormality was studied by Gruenwald (1941). He found that during development cysts and folds, with subsequent degenerative processes, occurred in the retina. Abnormal folding was also found in the iris and ciliary body. The pecten was rudimentary and the scleral cartilage thickened. The formation of cysts and of abnormal growth centers in the retina appears to be the primary abnormality.

Finally, reference should be made to observations of Kondyrev (1925), who ascribed the occurrence of malformations of the legs in the F₂ of a cross between Bantams and Minorcas to disharmonies incident to segregation after a cross between a small and a large breed. Confirming evidence is lacking, although several other investigators have made crosses between breeds of widely different body size. There are several mutations which cause death of the chicks some time after hatching, but since they do not seem to interfere with hatchability, they will not be considered here.

High embryonic mortality is the rule when genus crosses are made. Thus, a mortality of 43 percent occurred during the first week of incubation in a cross of pheasant ♀ ♂ x chicken ♂ (Sandnes and Landauer, 1938). Similar observations have been recorded by Yamashima (1942), Shaklee and Knox (1954), Sandnes (1957) and Asmundson and Lorenz (1957). In reciprocal crosses of turkeys and chickens 85 percent of the hybrid embryos died on the first day of incubation and most of the remaining ones during the second and third day (Quinn, Burrows and Byerly, 1937; Warren and Scott, 1935; Kondo, 1947; Suschka, 1956). When, however, the turkey parent came from a strain in which parthenogenetic development occurred with appreciable frequency, viability of hybrid embryos was greatly enhanced and some of the hybrids even hatched (Olsen, 1960). Owen (1941) found that in crosses of chicken
females and guinea fowl males all hybrid embryos died early, approximately half of their number at the primitive streak stage (prior to the appearance of blood islands), the remainder shortly before or during the fourth day (after the establishment of blood circulation). In the reciprocal cross embryo mortality was also very high, but did not occur within such a brief period, more embryos surviving to late stages. Similar observations on the latter cross had been made earlier by Marchlewski (1936). In eggs of quail (Coturnix coturnix japonica) inseminated with fowl sperm the embryos survived for 9 to 10 days at most (Mitsumoto, 1959). The influence that serological properties may have on viability of embryos derived from genus crosses has been investigated by Ryle (1957).

Such crosses of distantly related forms may also lead to the appearance of various developmental abnormalities among the progeny. The hybrid embryos from the pheasant-chicken cross, for instance, showed a high incidence of cerebral hernia (Sandnes, 1937; G. Smith, 1912-1913). Gross structural defects of the head region have also been observed in guinea-chicken hybrids (Marchlewski, 1936; Owen, 1941).

The results of species crosses within the genus Gallus are of still greater interest. Steiner (1945) made observations on crosses between Gallus gallus, the domestic fowl, and Gallus varius, the so-called Black Jungle fowl. Among 12 F₂ embryos from this cross none survived the seventh day of incubation. In a cross of domestic hens to an F₁ cock only 7 out of 51 fertile eggs produced chicks, and in a mating of one such backcross female to an F₁ cock all 8 resulting embryos died during the first two days of incubation. The great majority of embryos from all these crosses showed morphological abnormalities, especially lordoses.

Much more extensive, but in their results similar, unpublished data for the cross of Gallus gallus and Gallus sonnerati, the Gray Jungle fowl, have been kindly put at the writer’s disposal by Mr. Elliot Kimball. Both kinds of Jungle fowl used in Mr. Kimball’s important and interesting experiments were of feral origin. In the first crosses of the two species (F₁ embryos) fertility and hatchability were satisfactory. The results of inter se matings between F₁ hybrids (F₂ embryos), obtained from reciprocal crosses, and of backcrosses of F₁ animals to Gallus gallus are summarized in Table 55. None of the more than 1200 F₂ embryos survived to hatching, the majority dying during the second week of incubation and many of them being grossly malformed. In the backcross progenies the results were similar, but these matings produced a few viable chicks. In crosses of Gallus sonnerati to domestic varieties of Gallus gallus or to Jungle Gallus gallus with presumed admixture of domestic stock Mr. Kimball found also a high embryo mortality in F₂, but a few chicks hatched. Experiments by Danforth (1958 and personal communication) produced similar results. In the cross of (domestic ♀ x sonnerati ♂) F₁ ♀ x (domestic ♀ x gallus ♂) F₁ ♂ Mr. Kimball found that none of 23 fertile eggs produced a hatched chick. In contradistinction to these failures and near-failures, feral Gallus gallus bred to domestic breeds led to normal viability in F₂ and later generations.
The results of these species crosses tend to bear out the contention of Federley (1932) that in crosses of nearly related species the presence of complete ancestral genomes (in F₁) permits normal development and unimpaired viability, but that chromosomal segregation (in F₂) is attended by incompatibilities and failure of embryos to develop normally and to survive (hybrid breakdown). It appears unlikely, from the foregoing evidence, that either the Gray or the Black Jungle fowl contributed to the origin of our domestic chickens. In crosses between domestic chickens and Gallus lafayetti, the last of the four wild species of fowl, fertile F₁ animals seem to occur (Devaniyagala 1953, 1956), but little is known about their breeding behavior. Newton (1893-96) had reported them as sterile.

<table>
<thead>
<tr>
<th>Cross</th>
<th>Number of fertile eggs</th>
<th>Results of incubation</th>
</tr>
</thead>
<tbody>
<tr>
<td>(G. sonnerati ♀ x G. gallus ♂) F₁ inter se</td>
<td>47</td>
<td>All dead by end of second week</td>
</tr>
<tr>
<td>(G. gallus ♀ x G. sonnerati ♂) F₁ inter se</td>
<td>1162</td>
<td>Principal period of mortality between 11th and 15th day. None hatched. Many malformed.</td>
</tr>
<tr>
<td>(G. gallus ♀ x G. sonnerati ♂) x G. gallus ♂</td>
<td>88</td>
<td>None hatched</td>
</tr>
<tr>
<td>One ♀ of preceding group x another G. gallus ♂</td>
<td>13</td>
<td>11 viable chicks</td>
</tr>
<tr>
<td>(G. gallus ♀ x F₁ ♂) (G. gallus ♀ x G. sonnerati ♂)</td>
<td>116</td>
<td>5 viable chicks</td>
</tr>
</tbody>
</table>

The fact that in poultry such large numbers of genetic factors are detrimental to embryo viability, raises interesting questions which cannot, however, be answered satisfactorily at present. Is heterozygosity for recessive lethal genes disadvantageous to their bearers? If this is true, such genes should gradually disappear from the flocks in which they had occurred, and the relatively frequent encounter of mutant genes of this kind (if looked for) would presumably point to their repeated origin by mutation. It is possible, on the other hand, that heterozygosity for recessive genes with homozygous lethal effect confers an advantage on their bearers and that on this account such genes become widely disseminated. That this may be so is suggested by the fact that in some instances even homozygosity for a lethal gene, completely hidden from expression by genetic modifiers, appeared to be widespread in particular stocks.

If breeders favor the presence of a lethal gene in their flock because of desirable dominance effects in the heterozygotes, they must, of course, pay the price in reduced hatching results. This situation presumably
obtained in regard to the lethal of Dark Cornish fowl and holds true for the Creeper and Japanese Bantam breeds. In the absence of such conscious propagation of lethal mutations, or of enhanced viability of the heterozygotes, natural selection will ordinarily, on account of the reduced size of individual progenies, lead to a rapid decline in the number of heterozygous parents. Hence it may be said with regard to such lethals that it is "the wisest procedure for a breeder simply to ignore them" (Lerner, 1958).

Sex of embryos

Do male and female embryos have the same chances to survive and to hatch, or does sex of the embryo have an effect on hatchability?

Landauer and Landauer (1931) found among data from various sources 48.77 ± 0.13 percent males among 67,993 sexed baby chicks. Provided that the primary sex ratio was equality which may be assumed from data provided by Hays (1945), this would seem to indicate that in this material more males than females had died before hatching. Crew (1938), on the other hand, observed in chicks of several breeds a tendency toward a slight excess of males at hatching time. Dudley and Hindhaugh (1938-1939) found at hatching an excess of males in some and of females in other stocks.

These conflicting results tend to bear out the suggestion made by Byerly and Jull (1935) that breed and stock differences exist with regard to the proportions of the two sexes at hatching time. The latter authors, summarizing the data available in the literature, reported that among a total of 6,864 dead embryos there were 3,335 or 48.59 percent males. In sex records obtained by these authors themselves there were 8,556 males or 47.56 percent among 17,989 embryos which had died after the ninth day of incubation. The differences from 50 percent were 1.41 ± 0.61 percent and 2.44 ± 0.37 percent, respectively, and for the combined data the deviation from 50 percent amounted to 2.15 ± 0.31 percent. These differences must be accepted as significant, proving that in this embryo material female mortality had exceeded male mortality. Strain differences were also reported by Champion (1960).

A similar situation was reported by Landauer (1943), Thornton (1944) and Hutt (1951) for observations relating to crosses of Barred Plymouth Rock females and Rhode Island Red males, and by Hays (1949, 1952 b, 1954) and Hays and Spear (1950) for Rhode Island Red progenies. Asmundson (1941) found excessive female mortality during the last days of incubation, but a trend in the opposite direction earlier. Hays (1954) claimed that with increasing age of sires the rate of mortality of female embryos among their progenies tended to rise; he did not provide details or a statistical analysis in support of this statement.

It is impossible at present to interpret all of these observations satisfactorily. However, it seems justifiable to conclude that in general sex-linked lethal factors (discussed previously) do not play an important role
in the embryonic mortality of fowl. This conclusion is supported by observations of Hazel and Lamoreux (1946). We do not know how the differences in the secondary sex ratio of various breeds and stocks are brought about. The sex incidence among embryos which die early, and for which no data are available, may play a role in this respect. Data reported by Asmundson (1941) suggest, but do not critically prove, such an interpretation. More critical evidence for the conclusion that mortality of the two sexes is not evenly distributed throughout the incubation period has been provided by Ivanov (1955 a). He collected data on mortality of White Leghorn, New Hampshire Red and Australorp embryos according to sex and three periods of incubation. A summary of his results is shown by the following figures:

<table>
<thead>
<tr>
<th>Days of incubation</th>
<th>Number of dead embryos</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td>9-11</td>
<td>176</td>
<td>50.0±3.79</td>
</tr>
<tr>
<td>12-18</td>
<td>948</td>
<td>61.6±1.58</td>
</tr>
<tr>
<td>19-21</td>
<td>1589</td>
<td>40.9±1.26</td>
</tr>
</tbody>
</table>

The deviations from equality are highly significant in the last two groups (χ² = 25.88 and 25.91, respectively, with a probability in each instance of less than 0.001), indicating a change from high male mortality during the middle part of incubation to high female mortality at the end.

Coles (1956 c) assumed that deviations from equality may occur in the primary sex ratio of some stocks of fowl. The acceptance of such an hypothesis is discouraged by data on the primary sex ratio which are free from the complications of "infertility" (including death during segmentation) and mortality (Hays, 1945; Landauer, 1957 b), and by observations such as those of Ivanov, discussed above. It has been brought to light, in addition, that environmental agencies may produce a differential effect on mortality of the two sexes during development, thereby creating a complex and variable situation. Thus, it appears from observations by Ivanov (1955 b) that eggs that had been stored for 6 to 19 days prior to incubation produced more male chicks (i.e. had a higher mortality of female embryos) than did eggs that had been set at once after they had been laid. Coles (1956 c) reported that in eggs that had been produced on a poor diet, the relative mortality of female embryos was higher than in eggs produced on a better ration.

Observations by Dove (1935 b), Hays (1941) and Godfrey, Williams and Thompson (1952) indicate that females tend to outnumber males among the chicks which are the first ones to emerge from the shell, and that, conversely, males are numerically in excess among those hatching late. Similar results, on the margin of statistical significance, have been reported by Henderson (1956).

Carne and Waterhouse (1958) observed a Black Orpington pullet which, early in her second year, assumed male characteristics. The ani-
mal was first mated to a pen of Black Orpington females and subsequently to three Australorp pullets. Fertility was low and embryo mortality high. Among 50 offspring, sufficiently developed for sexing, all were males. The theoretical expectation in this type of mating is 2 females: 1 male, and a 25% mortality of the yy zygotes: the actual results remain unexplained.

**Inbreeding and heterosis**

A number of studies concerning the effects of close inbreeding in fowl have brought to light some interesting information on problems of hatchability. Cole and Halpin (1916) found that during three generations of brother-sister matings in a flock of Rhode Island Reds hatchability declined from 67 to 18 percent. In this first experiment matings were arranged without special selection methods, but in a second test Cole and Halpin (1922) selected their breeding stock for high viability, hatchability and fecundity. Although some effect of this selection was apparent, hatchability again declined in successive generations and the inbred family soon became extinct. No detailed account of these experiments has been published.

Extensive inbreeding experiments with White Leghorns have been made by Dunn (1923 b; 1928) at the Storrs Agricultural Experiment Station. No direct selection was practiced in these experiments, but by limiting matings in each generation and line to the offspring of that hen which had the largest number of daughters surviving at nearly one year of age, a premium was placed on all characteristics concerned in determining the number of surviving daughters; namely, fecundity of the mother during the mating season, fertility and hatching quality of her eggs, disease resistance, and so on.

The results, with regard to hatchability of the four families which gave the greatest amount of information, are shown in Table 56. All data refer to eggs laid during the pullet year and incubated between April 15 and May 15.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Family IV</th>
<th></th>
<th>Family II</th>
<th></th>
<th>Family VI</th>
<th></th>
<th>Family VII</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of fertile eggs</td>
<td>Hatch %</td>
<td>Number of fertile eggs</td>
<td>Hatch %</td>
<td>Number of fertile eggs</td>
<td>Hatch %</td>
<td>Number of fertile eggs</td>
</tr>
<tr>
<td>P_1</td>
<td>29</td>
<td>70.4</td>
<td>25</td>
<td>95.8</td>
<td>27</td>
<td>85.2</td>
<td>28</td>
</tr>
<tr>
<td>F_1</td>
<td>50</td>
<td>56.0</td>
<td>220</td>
<td>60.0</td>
<td>383</td>
<td>51.4</td>
<td>214</td>
</tr>
<tr>
<td>F_2</td>
<td>182</td>
<td>44.5</td>
<td>605</td>
<td>57.2</td>
<td>703</td>
<td>49.8</td>
<td>383</td>
</tr>
<tr>
<td>F_3</td>
<td>294</td>
<td>29.6</td>
<td>286</td>
<td>45.8</td>
<td>94</td>
<td>19.1</td>
<td>107</td>
</tr>
<tr>
<td>F_4</td>
<td>180</td>
<td>50.0</td>
<td>11</td>
<td>18.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F_5</td>
<td>65</td>
<td>41.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Two conclusions follow quite clearly from this material: (1) that hatchability declined in all the inbred families; and (2) that this decline
took place at different rates in the several families. Family IV maintained a relatively high percentage of hatchability. It was the general experience in this work that families in which hatchability dropped below 25 to 30 percent tended to become extinct. The results for all families combined are given in Table 57. The outbred stock did not show any definite trend of hatchability. In the inbred stock there was a decline both of families surviving and of hatchability. The apparent rise of hatchability in the fourth and fifth generations was due to the survival of one family (IV) with a relatively high rate of hatch.

### Table 57

<table>
<thead>
<tr>
<th>Generation</th>
<th>Number of families</th>
<th>Number of fertile eggs</th>
<th>Hatch %</th>
<th>Number of fertile eggs</th>
<th>Hatch %</th>
</tr>
</thead>
<tbody>
<tr>
<td>P, 8</td>
<td>204</td>
<td>75.0</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>F, 8</td>
<td>1304</td>
<td>50.5</td>
<td>520</td>
<td>49.8</td>
<td>49.8</td>
</tr>
<tr>
<td>F, 2</td>
<td>2269</td>
<td>46.7</td>
<td>492</td>
<td>67.5</td>
<td>67.5</td>
</tr>
<tr>
<td>F, 3</td>
<td>932</td>
<td>34.3</td>
<td>531</td>
<td>60.8</td>
<td>60.8</td>
</tr>
<tr>
<td>F, 4</td>
<td>141</td>
<td>46.8</td>
<td>581</td>
<td>60.1</td>
<td>60.1</td>
</tr>
<tr>
<td>F, 5</td>
<td>65</td>
<td>41.5</td>
<td>742</td>
<td>59.2</td>
<td>59.2</td>
</tr>
</tbody>
</table>

Crossees were made between different inbred lines, and the results, as far as hatchability is concerned, are shown in Table 58 (Dunn, 1928; supplemented by unpublished data). These results afford a comparison between inbreeding and crossbreeding. The same females of family I- and family I- first were crossed with their own brothers to produce inbred progeny, and later to a male from another inbred family. Both male and female parents, when inbred, gave a low or mediocre hatchability, but substitution of another equally inbred male for the own brother led to a considerable increase in hatchability (47 to 85 percent, and 56 to 73 percent, respectively). The maternal inheritance in the two cases is the same. An immediate effect of the more distantly related sperm on the viability of the embryo is shown. The amount of this heterosis in regard to hatchability differed in the various crosses, some combinations producing a greater improvement than others, so that there is evidence not only of a general heterosis but also of specific genetic differences between the families which were crossed.

New inbreeding of the progeny of these crosses between inbred lines again resulted in decline of hatchability, but there were definite differences between individual sibships with regard to the amount of loss of hatchability. Since the embryos in these matings represent the F, generation, it may be assumed that segregation in factors affecting embryo survival had taken place. Double crosses between the new inbred lines gave the results shown in Table 59. No further effect of heterosis was
Table 58

<table>
<thead>
<tr>
<th>Family and type of mating</th>
<th>Number of fertile eggs</th>
<th>Hatch %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inbreeding: $I_2 \frac{\varnothing \varnothing}{\varnothing} \times$ brother</td>
<td>174</td>
<td>47.4</td>
</tr>
<tr>
<td>$I_4 \frac{\varnothing \varnothing}{\varnothing} \times$ brother</td>
<td>140</td>
<td>53.0</td>
</tr>
<tr>
<td>Cross: $I_3 \frac{\varnothing \varnothing}{\varnothing} \times I_4 \frac{\varnothing \varnothing}{\varnothing}$</td>
<td>151</td>
<td>85.0</td>
</tr>
<tr>
<td>New inbreeding: $I_{24} F_1$ mating a, brother-sister</td>
<td>245</td>
<td>69.0</td>
</tr>
<tr>
<td>&quot; b, brother-sister</td>
<td>97</td>
<td>49.5</td>
</tr>
<tr>
<td>&quot; b, half-brother-sister</td>
<td>87</td>
<td>49.4</td>
</tr>
<tr>
<td>&quot; c, brother-sister</td>
<td>81</td>
<td>51.9</td>
</tr>
<tr>
<td>&quot; c, half-brother-sister</td>
<td>103</td>
<td>56.3</td>
</tr>
<tr>
<td>&quot; d, brother-sister</td>
<td>187</td>
<td>70.1</td>
</tr>
<tr>
<td>$I_{24} F_2$ descendants of $F_1$, a brother-sister</td>
<td>91</td>
<td>41.2</td>
</tr>
<tr>
<td>&quot; b, half-brother-sister</td>
<td>68</td>
<td>39.7</td>
</tr>
<tr>
<td>descendants of $F_1$, d brother-sister</td>
<td>98</td>
<td>64.3</td>
</tr>
<tr>
<td>&quot; b, half-brother-sister</td>
<td>124</td>
<td>72.6</td>
</tr>
<tr>
<td>&quot; brother-sister</td>
<td>64</td>
<td>67.2</td>
</tr>
<tr>
<td>$I_{24} F_3$</td>
<td>136</td>
<td>56.3</td>
</tr>
<tr>
<td>Inbreeding: $I_6 \frac{\varnothing \varnothing}{\varnothing} \times$ brother</td>
<td>174</td>
<td>47.4</td>
</tr>
<tr>
<td>$I_2 \frac{\varnothing \varnothing}{\varnothing} \times$ brother</td>
<td>127</td>
<td>73.4</td>
</tr>
<tr>
<td>New inbreeding: $I_{82} F_1$ mating a, brother-sister</td>
<td>284</td>
<td>52.5</td>
</tr>
<tr>
<td>&quot; b, half-brother-sister</td>
<td>55</td>
<td>41.8</td>
</tr>
<tr>
<td>&quot; a, brother-sister</td>
<td>87</td>
<td>51.7</td>
</tr>
<tr>
<td>&quot; b, brother-sister</td>
<td>106</td>
<td>30.4</td>
</tr>
<tr>
<td>&quot; b, half-brother-sister</td>
<td>106</td>
<td>28.0</td>
</tr>
<tr>
<td>$I_{82} F_3$</td>
<td>198</td>
<td>39.4</td>
</tr>
</tbody>
</table>

visible in these crosses. This, however, may be due to the fact that family II was common to both parental groups, thus involving a certain measure of inbreeding. Between various inbred lines Dunn found differences in the time at which peaks of embryo mortality occurred; Krzanowska (1959) made similar observations.

Table 59

<table>
<thead>
<tr>
<th>Mating</th>
<th>Number of fertile eggs</th>
<th>Hatch %</th>
</tr>
</thead>
<tbody>
<tr>
<td>$I_{24} \frac{\varnothing \varnothing}{\varnothing} \times I_{82} \frac{\varnothing}{\varnothing}$ mating a</td>
<td>268</td>
<td>63.1</td>
</tr>
<tr>
<td>mating b</td>
<td>168</td>
<td>55.4</td>
</tr>
<tr>
<td>$I_{82} \frac{\varnothing \varnothing}{\varnothing} \times I_{24} \frac{\varnothing}{\varnothing}$</td>
<td>198</td>
<td>65.2</td>
</tr>
</tbody>
</table>

On the whole, these experiments demonstrate that the heredity of the embryo plays an important role in hatchability, and they show further that many genetic factors are at work since the responses, both to inbreeding and to crossing, indicate segregation into various classes. In the experience of Knox (1946) the most favorable effect on hatchability resulted from crossing inbred stocks of different breeds.

Very similar results were obtained in subsequent inbreeding and crossbreeding experiments conducted by Warren (1927-1928, 1934), Full (1928-1929 a and b; 1929-1930), Dumon (1931, 1938), Dunkerly (1931), the Northern Sub-Committee of the National Poultry Institute (1934), Funk

Jull (1928-1929 b) gave some interesting illustrations for the relation between degree of inbreeding and hatchability. Thus, in one line of inbred White Leghorns the data shown in Table 60 were found. In this table the half-brother-and-sister matings are given first for each year, and the full-brother-and-sister matings second. The percentage of hatchability decreased with rising coefficient of inbreeding. The greatest loss of hatchability occurred with the first step of inbreeding. The effect on hatchability was the same whether a certain coefficient of inbreeding was reached in one or in two years. Experiments with Barred Plymouth Rocks gave the same results. From data for various breeds and lines Shoffner (1948 b) calculated that the regression of hatchability on inbreeding was $-0.436 \pm 0.132$, indicating that for each 10 percent increase in coefficient of inbreeding there was an average decrease of 4.4 percent in hatchability. Blow and Glazener (1953) calculated a similar coefficient of regression $(-0.37 \pm 0.111)$. Such regression coefficients are of doubtful value, however, in view of the observation by earlier authors, confirmed by Bernier, Taylor and Gunn (1951), that the relationship between inbreeding and hatchability is non-linear, the greatest increase in embryonic mortality being produced by the initial steps of inbreeding.

Borisenko (1945) observed certain physical changes in the eggs of an inbred stock of White Leghorn fowl. The relative amount of thin

<table>
<thead>
<tr>
<th>Year of inbreeding</th>
<th>Number of families</th>
<th>Coefficient of inbreeding</th>
<th>Hatchability %</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>10</td>
<td>0</td>
<td>81.04 ± 2.42</td>
</tr>
<tr>
<td>First</td>
<td>6</td>
<td>12.50</td>
<td>69.90 ± 2.85</td>
</tr>
<tr>
<td>Second</td>
<td>5</td>
<td>25.00</td>
<td>62.50 ± 3.47</td>
</tr>
<tr>
<td>Third</td>
<td>8</td>
<td>34.37</td>
<td>45.12 ± 6.33</td>
</tr>
</tbody>
</table>

albumen showed a tendency to decrease with continued inbreeding; solids in the thin albumen diminished; the phosphorus content of thin and thick albumen declined. There was, however, no critical evidence for the conclusion that any of these alterations in egg composition had a causal relationship to parallel changes in hatchability.
Is it inbreeding per se (i.e., increasing homozygosity) that depresses the hatching quality of eggs? Or, are the deleterious consequences of inbreeding brought about by genes with harmful effects of a specific nature for which the stock had been heterozygous? Both alternatives, in fact, appear to be important mechanisms in inbreeding degeneration. Recent advances of population genetics have furnished impressive evidence for the role which heterozygosity plays in safeguarding reproductive fitness and in the equilibration of developmental events (Lerner, 1954). The results of selection experiments, to be reviewed presently, have shown, on the other hand, that a considerable measure of success can be attained in preventing deleterious recessive mutants from coming to the surface. The difficult problem of the proper controls for selection experiments has been discussed by Gow, Johnson, Downs, Gibson, Mountain, Strain and Tinne (1959).

Inquiries by Briles (1954) and by Briles and Krueger (1955) relative to the adaptive value of blood group genes of fowl were addressed to the problem of the importance of certain levels of obligate heterozygosity for maintenance of a high degree of reproductive fitness. Hatchability was one of the traits under scrutiny. Their results prove conclusively that embryo survival and hatching were superior in those matings in which the parents had been heterozygous for the blood group genes under study.

A number of investigators have attempted to combine inbreeding with selection for high hatchability. In Dumon's experiments with White Leghorns hatchability declined in spite of selection, but Waters (1932) and Waters and Lambert (1936 a and b) were more successful in this respect. Working also with White Leghorns, they used rigid selection on the basis of high hatchability for choosing their breeding birds, with large family size and good vigor as next important considerations. Entire families in some instances were excluded from the experiment because hatchability was unsatisfactory. The degree of inbreeding for each generation was, in general, less intensive than that obtained by brother and sister or parent and offspring matings.

The results of these experiments are shown graphically in Figure 51. If the eggs of all inbred lines are considered, it is evident that hatchability declined with an increasing coefficient of inbreeding, although in comparison with experiments on inbreeding without selection the decline was relatively slight. But those individuals which were chosen to be parents of the next inbred generation did not show any loss in the hatching quality of their eggs, even if inbreeding amounted to as much as 80 percent. These birds may be assumed to have been relatively free of genetic factors interfering with normal embryonic development.

Further and similar inbreeding experiments confirmed these conclusions (Waters, 1945; Knox, 1946). In another publication Waters (1938) produced evidence showing that the crossing of random-bred White Leghorn females to highly inbred White Leghorn cocks improved
Figure 51

Trends showing the average percent of fertile eggs hatched for all inbreds and for those inbreds chosen to be parents, together with the number of birds in each group. Inbreeding experiments with White Leghorns (From Waters and Lambert, 1936 a).
hatchability. It follows from all this evidence that there is no simple and direct relation between coefficient of inbreeding and percentage of hatchability. The results are determined by the amount and success of selection which accompanies inbreeding.

Convincing evidence for the conclusion that a great many genetic factors influence hatchability is furnished by the fact that through many steps of inbreeding it remained necessary to exercise close selection in order to obtain sibs with high hatchability, and by the observation that even highly inbred groups showed an enormous range of variation in the hatchability of the eggs of individual hens (Waters and Lambert, 1936a).

Support for this conclusion can also be seen in Dunn's (1924) observation that differences appeared between various inbred lines with regard to the age distribution of embryonic mortality. Thus in one family more than 40 percent of all deaths occurred before the sixth day of development, while in another line only 8 percent of the mortality fell into this period. If for the whole inbred material embryonic mortality was compared with the outbred stock, the age distribution appeared to be similar in the two sets of data, though the total mortality was much increased among the inbred embryos. But if the inbred families were considered individually, consistent differences in distribution became apparent, and these may be ascribed to the fact that the different lines had become homozygous for different sets of genetic factors interfering with development at one or another period. Segregation for various specific causes of death had obviously taken place. This conclusion is supported by the observation of Byerly (1930) that the frequency of teratological abnormalities is reduced by heterosis.

The improvement of hatchability which may be obtained by crossing breeds, as compared with intra-breed matings, is illustrated by some data (Table 61) taken from a publication by Warren (1942). Similar facts were reported by Horlacher, Smith and Wiley (1941). Kushner and Kitaeva (1951) claimed, presumably under the influence of Mitchurinist doctrines, that the unfavorable effects of inbreeding on hatchability can be lessened by factors of the environment in which the animals are raised.

<table>
<thead>
<tr>
<th>Females</th>
<th>Mated to males of same breed</th>
<th>Mated to males of a different breed</th>
<th>Breed (if different) from own</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of fertile eggs</td>
<td>Hatched %</td>
<td>Number of fertile eggs</td>
</tr>
<tr>
<td>White Leghorn</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strain W</td>
<td>289</td>
<td>61</td>
<td>406</td>
</tr>
<tr>
<td></td>
<td>167</td>
<td>84</td>
<td>387</td>
</tr>
<tr>
<td></td>
<td>192</td>
<td>73</td>
<td>584</td>
</tr>
<tr>
<td>White Leghorn</td>
<td>199</td>
<td>73</td>
<td>231</td>
</tr>
<tr>
<td>Australorp</td>
<td>199</td>
<td>72</td>
<td>114</td>
</tr>
</tbody>
</table>

Table 61
With regard to the general effect of inbreeding and crossbreeding on hatchability, Byerly, Knox and Jull (1934), in a discussion of experiments with White Leghorns and Rhode Island Reds, justly remark that “crossing breeds is a very effective means of increasing hatchability if the hatchability of a strain or breed is low. The increase in hatchability to be expected in eggs from purebred females mated to males of an unrelated breed, over the hatchability obtained in matings of the same females within the breed, is inversely proportional to the average hatchability of eggs from the latter matings. If hatchability within the breed is low, mating to an unrelated breed will probably improve it markedly. But if hatchability in matings within breeds is high, in the present data over 80 percent, crossbreeding is at least as likely to decrease hatchability as to increase it.” More recent work of Dudley (1944) led to similar results, and the observations of Henderson (1951, 1957) on reciprocal crosses of White Leghorn and Dark Cornish fowl, as compared to the parental breeds, can probably be explained in the same manner.

The relative contributions of mother and father to hatchability

It is of considerable interest to know what are the relative contributions of mother and father to the hatchability of eggs. In the case of autosomal lethal mutations we know, of course, that the two parents play the same role in transmitting such factors. On the other hand, it has been shown that physiological disturbances may occur in the mother’s organism which affect the hatchability of her eggs (pp. 131-136).

Where no evidence is available concerning the presence of such specific factors of one or the other type, the relative role of the two parents can be studied by the correlation technique. Comparisons of this kind have been made by Hays and Sanborn (1924) and by Bronkhorst (1933). For the relationship between hatchability of the mothers’ eggs and hatchability of their daughters’ eggs, Hays and Sanborn found for 811 Rhode Island Reds a correlation coefficient of 0.196 ± 0.034, and Bronkhorst obtained for the same correlation among 1142 White Leghorns a coefficient of 0.177 ± 0.028. Similar correlation coefficients were reported by Jull (1931) as follows: 74 Rhode Island Red dams and their 148 daughters r = 0.21 ± 0.07, and 60 White Leghorn dams and their 105 daughters r = 0.16 ± 0.09. Between sisters Pearl and Surface (1909) had already reported a correlation of 0.188 ± 0.089. These coefficients indicate a significant, though slight, influence of mothers on the hatching quality of their daughters’ eggs.

Perhaps a better demonstration of the influence which mothers have on the hatching quality of eggs laid by their daughters is offered by Jull’s (1931) procedure of dividing the dams 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 comparing the mean hatchability of the eggs of the daughters from each group of dams. The data for Rhode Island Reds are given in Table 62, and those for White Leghorns in
Table 63. In both cases, the dams with higher mean hatchability produced daughters whose eggs hatched significantly better than those from the daughters of the dams who in regard to hatchability were below the mean for the whole group.

### Table 62

<table>
<thead>
<tr>
<th>Dams' hatchability, Range in %</th>
<th>Number of dams</th>
<th>Mean of dams' hatchability %</th>
<th>Number of daughters</th>
<th>Mean of daughters' hatchability %</th>
</tr>
</thead>
<tbody>
<tr>
<td>68.0—94.5</td>
<td>51</td>
<td>80.65 ± 0.67</td>
<td>105</td>
<td>75.10 ± 1.91</td>
</tr>
<tr>
<td>41.0—67.5</td>
<td>23</td>
<td>59.95 ± 1.16</td>
<td>43</td>
<td>66.36 ± 2.94</td>
</tr>
<tr>
<td>Difference</td>
<td></td>
<td>20.68 ± 1.35</td>
<td></td>
<td>8.74 ± 3.81</td>
</tr>
</tbody>
</table>

In order to make a similar test for the father's role in determining the percentage hatchability of eggs laid by his daughters, it is necessary to make indirect comparisons such as the performance of dams and daughters of the same sires, dams and mates, mates and daughters, sires' mates and sons' mates, or first and second-year daughters of the same males. The figures in Table 64 show the principal results obtained in such correlation studies. The only possible interpretation of these data seems to be that the male plays a less important role than the female in determining hatchability, but that there is some evidence indicating an effect of the male's genotype. In evaluating the different coefficients, it should be kept in mind that the correlation between the average of the performance of a male's mates and that of his daughters is least conclusive, since in this case the effect of both parents enters the comparison. The relationship between dams and mates of the same male probably gives the best measure of the influence which the males have on hatchability.

### Table 63

<table>
<thead>
<tr>
<th>Dams' hatchability, Range in %</th>
<th>Number of dams</th>
<th>Mean of dams' hatchability %</th>
<th>Number of daughters</th>
<th>Mean of daughters' hatchability %</th>
</tr>
</thead>
<tbody>
<tr>
<td>74.0—94.5</td>
<td>36</td>
<td>81.24 ± 0.53</td>
<td>62</td>
<td>63.40 ± 2.85</td>
</tr>
<tr>
<td>53.0—73.5</td>
<td>24</td>
<td>64.36 ± 1.13</td>
<td>43</td>
<td>52.33 ± 2.88</td>
</tr>
<tr>
<td>Difference</td>
<td></td>
<td>16.88 ± 1.25</td>
<td></td>
<td>11.07 ± 4.05</td>
</tr>
</tbody>
</table>

The outstanding feature of these correlation coefficients, as they relate to the effect of either parent on hatchability, obviously is the smallness of the values, and this may be taken as an indication of the complex nature of hatchability. The greater role of the female, expressed in higher coefficients of correlation, is explained by the fact that, in addition to her contribution to the genetic constitution of the embryo, hatchability is influenced by her own heredity as well as by her diet and by physio-
logical disturbances of her organism as they affect the structure and composition of her eggs. Hatchability estimates by Brunson, Godfrey and Goodman (1956) and by Crittenden, Bohren and Anderson (1957 a) support the same conclusions. Champion (1957) reported on experiments in which reciprocal crosses were made between two strains of White Leghorn fowl and in which the resulting F1 generations were then backcrossed to the original stocks in all possible combinations. Highly significant differences in hatchability were found between some of these combinations, but Champion concludes that maternal effects and/or sex linkage played no significant role in their origin. Krzanowska (1959), on the other hand, found important maternal effects on the early growth of embryos.

Convincing proof for the influence of sires on hatchability was presented by Waters (1944) from studies on White Leghorn fowl in which he employed the method of diallel crossing, i.e., the mating of the same hens to different sires. An analysis of variance of his results showed that there were highly significant differences between cocks. Similar implicit evidence had, of course, already existed in the comparative results from crosses of inbred and distantly related stocks. But none of these data allow us to distinguish between the effects of heterozygosity (heterosis) and the action of specific genes transmitted by the sires.

An interesting demonstration of the importance of maternal factors for hatchability has been provided by studies of van Schalkwyk and Liebenberg (1952) and Eranmus (1958) on Black Australorps, White Leghorns and reciprocal crosses between these two breeds. Several consecutive tests showed consistently that of the two pure breeds the eggs of the Black Australorps hatched better than those of the White Leghorns, but that in the crosses the eggs from White Leghorn females bred to Black Australorp males hatched better than did those from the reciprocal matings. Eranmus gave proof of the statistical significance of these
differences. He found no evidence for sex-linked genes and ascribed the results to, as yet unanalyzed, factors of egg composition; factors which influence survival and hatching of the F₁ embryos on account of superiority (for the hybrids) of the internal environment of eggs laid by Leghorn mothers as compared with that of eggs laid by Australorp hens. One hopes that attempts will be made to test the validity of this hypothesis. Similar and highly significant differences in hatchability between these reciprocal crosses were recorded by Morris and Skaller (1958) who suspect dissimilarities in sperm age (rate of fertilization) as the cause. A somewhat similar situation, but presumably based on quite different factors, was discussed earlier with reference to crosses involving Creeper fowl (p. 141).

Are there specific hatchability genes?

Studies to determine whether or not the “hatching quality” of eggs is a separate genetic trait were first undertaken by Pearl (1911), but the significance of his results remained doubtful. On the basis of their correlation studies with Rhode Island Reds, Hays and Sanborn (1924) suggested that there is one incompletely dominant gene (H) which determines high hatchability: “There is no sex linkage and all results obtained are to be expected in a simple mono-hybrid ratio.” Hays and Sanborn believed that the flock under consideration could be grouped into three general classes or phenotypes, as follows: (1) Those showing hatchability of 85 percent or above, we call high. (2) Those with a hatchability of 55 to 84 percent, we call medium. (3) Those below 55 percent, we call low. Since factor H has a cumulative effect, the range for the medium class is twice as great as for the high class.” Dominance of H was assumed to be incomplete, the homozygous zygotes having a higher hatchability than the heterozygous ones. Hays assumed, in addition, that “both HH and Hh males probably give about the same hatching record from HH hens.”

The latter hypothesis, genetically unexplained, presumably helps to account for the greater influence of females than of males on hatchability. The data of Hays and Sanborn can hardly be used to substantiate their hypothesis of a monofactorial interpretation of high hatchability. Jull (1931, 1940) has already pointed out that the low values found by Hays and others for hatchability correlations between parent and offspring groups militate against the assumption of simple inheritance, since with only one genetic factor for high hatchability a relatively high correlation should result between the hatchability of dams and daughters. Bronkhorst (1933) came to similar conclusions.

If the interpretation of Hays and Sanborn were correct, high hatching females should produce exclusively high hatching daughters. This is not invariably true. Snyder (1930) reported the case of a hen which produced a 96.5 percent hatch during her first laying year, and an average hatch of 91 percent over a three-year period (263 eggs), while out of eight
of her first-year daughters six gave hatches of 83 to 90 percent, but the remaining two gave only 66.6 and 49.7 percent. Bronkhorst (1933) refers to similar instances. A good idea about the complexity of the situation may be gained from heritability estimates. Such estimates, in terms of embryo viability, were made by Hill, Dickerson and Kempster (1954), Bruinson, Godfrey and Goodman (1956) and Crittenden, Bohren and Anderson (1957 a) and yielded heritabilities of between 4 and 8 percent. Further heritability estimates, in terms of hatch of fertile eggs, were reported by Wilson (1948) and by Shoffner and Sloan (1948) from intra-sex daughter on dam regressions and by Crittenden, Bohren and Anderson (1957 a) from flock-mated pedigreed pullets; they showed similar values (4 to 16 percent). Additional details are reported by Crittenden (1958). These results are another expression of the great importance of external agencies (maternal nutrition, incubation practices, etc.) for the success of incubation. In evaluating the results of such calculations it must not be forgotten that the ability of organisms to respond to fluctuations of the environment is anchored in the genotype and will to a certain extent respond to selection. It is also clear that heritability values will be subject to variation according to the more or less ideal conditions of management. Hays (1959) has recently given a summary of an experiment, extending over eleven years, in which an effort was made to establish separate lines of Rhode Island Red fowl with "high" and "low" hatchability. The results demonstrate, if demonstration was needed, that the concept "hatchability" is an abstraction with much too complex physiological connotations to be useful as a guide to selection.

Hays (1926) reported an interesting case, interpreted by him as a demonstration of the importance of the male in regard to hatchability, and as an indication that "hatching power is inherited in Mendelian fashion." The data are shown in Table 65. The same seven Rhode Island Red females were bred to two different males during the first two laying years. The author did not state the actual numbers of eggs involved in his observations. The differences in hatchability are striking; in fact, they are much too great to prove Hays' point. The data suggest the interesting possibility that a dominant lethal mutation had occurred early in the development of the testes of cockerel C 8081.

<table>
<thead>
<tr>
<th>Females</th>
<th>C 7129</th>
<th>C 7132</th>
<th>C 7297</th>
<th>C 7310</th>
<th>C 7482</th>
<th>C 7716</th>
<th>C 7738</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fertility %</td>
<td>67</td>
<td>100</td>
<td>92</td>
<td>100</td>
<td>88</td>
<td>48</td>
<td>100</td>
</tr>
<tr>
<td>Fertile eggs hatched %</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>10</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Females</th>
<th>C 7129</th>
<th>C 7132</th>
<th>C 7297</th>
<th>C 7310</th>
<th>C 7482</th>
<th>C 7716</th>
<th>C 7738</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fertility %</td>
<td>97</td>
<td>98</td>
<td>94</td>
<td>89</td>
<td>50</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Fertile eggs hatched %</td>
<td>53</td>
<td>55</td>
<td>73</td>
<td>55</td>
<td>0</td>
<td>0</td>
<td>82</td>
</tr>
</tbody>
</table>
There is overwhelming evidence for the conclusion that the hatching quality of eggs is influenced by a large number of factors, and there may be many others, yet to be discovered. The fact that mutations affecting morphological traits, such as rumplessness, even in heterozygous condition cause a certain loss of hatchability (Dunn and Landauer, 1934), suggests that many genes may indirectly influence the chances of the embryo to survive and to hatch. In addition, there are probably numerous physiological factors of more vital importance for survival and hatchability. Many of these factors may be difficult to analyze in Mendelian terms, and in the absence of such analyses heritability estimates may in specific situations serve as useful guides for determining whether selection in a particular direction is effective.

**EMBRYO DEVELOPMENT AND HATCHABILITY**

**Embryo growth and hatchability**

Changes in embryonic growth rate may be instrumental in producing serious distortions of development, resulting in malformations and in death of the embryo (Landauer 1941b). It remains to be determined, however, how important is the role of this mechanism. According to Nicolaides (1933) and Hays and Nicolaides (1934) the most common embryonic stages found in eggs at the time of laying are pre-gastrula and early gastrula for hens with low hatching records, but well advanced gastrula for high-hatching hens. Taylor and Gunn (1935), on the other hand, were unable to detect a correlation between embryo size in newly-laid eggs and hatchability of other eggs from the same hens; nor could they find relationships between the size or degree of differentiation of various parts of the blastoderm and hatchability. Baczkowska (1959), however, reported rising hatchability with increasing size of the blastodisc.

In a further analysis of their material the same authors (1939) found that the amount of overgrowth in the peripheral part of the area opaca of the blastoderm was significantly greater in the high-hatchability group than in the group with medium hatchability. A difference in the same direction, but of borderline significance, was found between the high and low hatchability groups. The correlation between the amount of overgrowth and hatchability was found to be 0.3158 ± 0.1313, with a correlation ratio of 0.5328. It was mentioned previously (p. 123) that McNally and Byerly (1936) found a relationship between mean somite number after 48 hours of incubation and hatchability. In an analysis of the performance of 23 Rhode Island Red hens, Neel (1942) calculated a coefficient of correlation of 0.77 ± 0.08 between developmental rate for 6-hour intervals from 24 to 72 hours of incubation (expressed as number of somites) and hatchability. A positive correlation between size of the blastodisc after 24 hours of incubation, as seen by a special candling device, and subsequent hatchability was reported by Baintner and Bögre (1955).
Detailed observations by Bernier (1947) and Bernier, Taylor and Gunnis (1951) on the relation of early embryo size to hatchability are of considerable interest. Their data were derived from brother-sister matings in a production-bred line of White Leghorns (DB) and from a stock obtained by crosses of that line with a White Leghorn stock which had been selected for small embryo size (SEOB). The pertinent data are shown in Table 66. In interpretation of their results the authors offer the following comments:

"The relation between early embryo size and hatchability is positive in the individual matings of the OB origin of females in 1940. Large mean blastoderm size and large number of somites were indicative of high hatchability in a given mating. The most interesting fact is undoubtedly the increase in the value and significance of the correlation coefficients as the embryos increase in age. In eggs occupying a clutch position subsequent to the first, and in which embryonic development has been under way, in the oviduct for approximately 26 hours, the correlation is +.193, not significant but indicative of a trend. In eggs occupying first clutch position, which are known to have remained in the oviduct longer than those occupying a subsequent clutch position, the correlation is +.291 and still not significant. In eggs occupying clutch positions subsequent to the first and incubated for 38 hours, the correlation between mean number of somites and hatchability is +.496 which is significant at P.01. Finally, in eggs occupying first clutch position and incubated for 38 hours the correlation between mean number of somites and hatchability is +.632 which is significant at P.05. The older the embryo from a given mating, the higher the correlation observed between their mean size and hatchability in the same mating, as far as the OB females were concerned in 1940."

No such correlations existed in the SEOB data. Bernier interprets his results with the OB material as "evidence that inbreeding resulted in homozygosity for deleterious genes in many of the zygotes produced by these OB females. These deleterious genes started expressing themselves shortly after fertilization and their outward manifestation was a retardation in embryonic development. The higher the frequency of deleterious genes in a particular mating, the larger the proportion of zygotes affected, the greater the reduction in mean blastoderm size or number of somites and percentage of hatchability, and hence, a positive correlation between mean early embryo size and hatchability."

Among the SEOB females heterozygosity for such deleterious factors presumably was less common, hence the lack of a similar relationship. It is justly pointed out by Bernier, however, that the reduction in mean early embryo size in inbred stocks may be the result of growth retardation which in turn may be a manifestation of impending death of some of the embryos, and that actually impending embryonic mortality rather than true embryonic growth rate may have been measured. These observations and conclusions are likely to find an application in such relations
as exist between rate of production, time of the day when the eggs were laid, interval between eggs, and clutch position on the one hand and hatchability on the other.

In this respect Bernier makes the following statement: "The normal relation between blastoderm size at time of oviposition and hatchability is a curvilinear one. This is supported by the demonstration that: eggs in first and last clutch positions, eggs laid early in the morning and late in the afternoon, and eggs with unusually long time intervals all contain embryos relatively more advanced in development while eggs with short time intervals contain embryos relatively less advanced in development, and all of these classes do not hatch as well as those in intermediate clutch positions, laid in the middle part of the day, and with a time interval of 23 to 27 hours."

The situation is undoubtedly a very complex one. Such factors as the reduced shell porosity of first eggs in a clutch (Tyler, 1945) suggest that we may witness an interplay of diverse physiological agencies.

Russian students of incubation have made experiments on a large scale in efforts to eliminate in early stages of incubation infertile eggs as well as eggs with small germ discs (Orlov, 1954; Kuchkovskaya, 1954; Tret'yakov and Pel'tser, 1954). They found that after a pre-incubation period of 15 hours at 37.5 to 40.5° C. (100 to 105° F.) candling permitted to eliminate the infertile eggs, and to sort the remaining ones into eggs with small and large germ discs. The eggs could then be stored for at least six days without appreciable loss of vitality, and if only those eggs were set which had shown a large germinal disc, an improvement in hatchability was obtained. The authors recommend their method not only on account of the better utilization of incubator space, but also because the rejected eggs had not shown an appreciable loss in nutritive value. The report by Baintner and Bögre (1955), already referred to, and a more recent one by Bögre and Varga (1956) point to similar conclusions.

For later stages Bronkhorst (1933) has made a comparison between high (above 75 percent) and low (below 50 percent) hatching hens with regard to embryo growth (Figure 52). The most interesting feature of his data is that the maxima of growth generally occurred earlier among the embryos of the high-hatching than among those of the low-hatching group. A particularly striking difference between the two sets of embryos was found at the end of the incubation period where the embryos of the high-hatching group showed a much greater increase in body weight than the low-hatching embryos. Absolute weights as well as daily weight increments are much more variable among the embryos of the low than among those of the high-hatching eggs. It is, of course, impossible to judge from such data whether the observed differences indicate that retarded growth was a causal factor in reduced hatchability, or whether
## Correlation between embryo size and hatchability

<table>
<thead>
<tr>
<th>Class of eggs</th>
<th>Measurement</th>
<th>Number of matings</th>
<th>Correlation</th>
<th>Number of matings</th>
<th>Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td>All eggs, irrespective of clutch position</td>
<td>Blastoderm size</td>
<td>30</td>
<td>+.137</td>
<td>60</td>
<td>+.125</td>
</tr>
<tr>
<td></td>
<td>Number of somites</td>
<td>29</td>
<td>+.4731</td>
<td>61</td>
<td>+.093</td>
</tr>
<tr>
<td>Eggs in first clutch position</td>
<td>Blastoderm size</td>
<td>15</td>
<td>+.201</td>
<td>45</td>
<td>+.128</td>
</tr>
<tr>
<td></td>
<td>Number of somites</td>
<td>15</td>
<td>+.6322</td>
<td>47</td>
<td>+.028</td>
</tr>
<tr>
<td>Eggs in clutch position subsequent to first</td>
<td>Blastoderm size</td>
<td>30</td>
<td>+.103</td>
<td>57</td>
<td>-0.017</td>
</tr>
<tr>
<td></td>
<td>Number of somites</td>
<td>28</td>
<td>+.4061</td>
<td>50</td>
<td>-0.044</td>
</tr>
</tbody>
</table>

*significant at 1% level; 2significant at 5% level
Figure 52

Growth curves showing the daily increment of weight among embryos of a high (−) and a low (−−) hatching line of White Leghorns (From Bronkhorst, 1933).

the reduced size of the embryos is an expression of retardation preceding death from unanalyzed causes. It is interesting in this connection, however, that Byerly (1934) found in an inbred strain of White Leghorns a postponement of hatching by about twelve hours as compared with other matings. It is not known whether this was due to retarded growth or to a delay in the act of hatching itself.

Energy metabolism of the developing chicken embryo is influenced by many factors. Barott (1937) has shown that temperature, humidity, carbon dioxide and oxygen concentration all have definite effects in this respect; effects which are reflected in the rate of embryonic development and in the chances of the embryo to survive and to hatch. The influence of incubation temperature on time of hatch is shown in Figure 53. Further observations concerning the influence of temperature on length of the incubation period have been recorded by Bouges (1923), Henderson (1939) and Romanoff (1939). Penquite (1938) demonstrated
that the conditions of temperature and humidity have important bearings on growth of the chicken embryo, and Penionschkewitsch and Schechtman (1939) showed that these conditions are directly reflected in the caloric value of the embryos. According to Golovkov (1939) the hatching of Leghorn eggs takes place about six to eight hours earlier than that of eggs from heavy breeds (Rhode Island Red, Orloff).

Demuth (1939) found that in pure oxygen growth of the chicken embryo is retarded, but that differentiation suffers little, if at all.

A functional relationship of the thymus to hatchability is suggested by observations of Dmitrieva (1939). She found that in 21-day normal (crossbred Leghorn) chicks the thymus weighed 37.53 ± 3.00 mg., whereas in 21-day chicks (of the same stock) which had failed to hatch, thymus weight was only 17.50 ± 1.33 mg. The two groups had the same body weight (35.89 ± 0.69 g, and 35.95 ± 0.73 g., respectively). No difference could be detected in the structure of the thymus (such as development of epithelial and lymphoid elements or ratio between medullary and
cortical substance). Dmitrieva believes that there is a hereditary basis for retarded thymus growth, but proof for this conclusion is lacking. In any event, however, the author's findings, if verified, should furnish a basis for many interesting inquiries.

In tissue cultures from an embryo with posterior duplication Kemp and Engelbreth-Holm (1930) observed an increased frequency of tripolar mitoses. Similar findings were reported by di Grazia (1937) for tissue culture material from a diccephalic chicken embryo. This may be an expression of early growth disturbances. High incubation temperature may be one of the causative factors (Stilwell, 1947). The problem deserves further attention.

**Malpositions**

Before hatching, chicken embryos normally assume a characteristic position within the egg so that the long axis of the embryo coincides with the long axis of the egg and the beak is located underneath the right wing, with the tip of the beak directed toward the air space in the blunt end of the egg.

It was first recognized by Sanctuary (1924-1925) that among chicken embryos which had failed to hatch, i.e., among embryos which had either died after the eighteenth day of development, or which were still alive at the end of the incubation period, but had not emerged from the shell, somewhat more than 50 percent are found to be in positions different from that which is "normal" just previous to hatching.

On the basis of studies by Sanctuary (1924-1925), Hutt (1929), and Smith (1931) the following classification of malpositions has been accepted by the majority of investigators working on these problems.

| Malposition I | Head between thighs |
| Malposition II | Head in small end of egg |
| Malposition III | Head to left instead of under right wing |
| Malposition IV | Embryo rotated in such a way that the beak is not directed toward the air cell |
| Malposition V | Feet over head |
| Malposition VI | Beak above right wing instead of underneath it |

Combinations of two malpositions may occur in the same embryo, e.g., I and II or II and III. Malpositions V and VI are rather uncommon and will not be considered further in the following discussion. In fact, malposition VI is a normal variant according to Dove (1935). For the first four types of malpositions Byerly and Olsen (1936 b) have summarized from the work of various authors the frequencies shown in Table 67. The material included in this tabulation came from hatches of between 72.5 and 84.8 percent, i.e., from eggs which had been under favorable incubation conditions.
Table 67

Average incidence and range of frequencies of malpositions in percent of 18-day living embryos

<table>
<thead>
<tr>
<th>Orientation of eggs during incubation</th>
<th>Malpositions</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
<td>II</td>
<td>III</td>
<td>IV</td>
</tr>
<tr>
<td>Large end up</td>
<td>Average</td>
<td>1.16</td>
<td>1.76</td>
<td>3.38</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>1.08-1.95</td>
<td>0.20-2.12</td>
<td>1.95-3.94</td>
</tr>
<tr>
<td>Horizontal</td>
<td>Average</td>
<td>1.66</td>
<td>5.67</td>
<td>1.56</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>0.95-1.94</td>
<td>2.27-4.18</td>
<td>1.36-2.14</td>
</tr>
</tbody>
</table>

Among embryos which had died between the eighteenth day and the end of the incubation period Byerly and Olsen (1936 a) observed the frequencies of embryos which had pipped the shell shown in Table 68.

Data collected by Asmundson (1938) show a similar distribution. These figures indicate that embryos rarely, if ever, pip the shell when they are in malpositions I or III, or in combinations of I and II or II and III.

Table 68

Embryo position | Number of eggs | Pipped %
-----------------|---------------|--------
Normal           | 12,690        | 41.2   |
Malposition I    | 1,168         | 0.6    |
Malposition II   | 1,575         | 25.7   |
Malposition III  | 3,240         | 1.1    |
Malposition IV   | 745           | 9.8    |
Malpositions I and II combined | 142 | 2.1 |
Malpositions II and III combined | 183 | 2.2 |

Occasional hatching from malposition III has, however, been observed (Byerly and Olsen, 1934), and there is also evidence that shifting of the embryo from malpositions I and IV to the normal hatching position may still occur after the nineteenth day.

The first question which arises with regard to these malpositions is whether or not they are related to the orientation of the early embryo. Taylor (1932) and Cavers and Hutt (1934) found that such a relationship exists for malposition II. Eggs in which the embryo deviates from its normal position at four or six days of incubation show later a much higher incidence of head-in-small-end malposition than do others. No similar relationship exists with regard to other malpositions. Heterotaxia apparently does not interfere with normal hatchability (Taylor, 1934).

The problem of whether or not the orientation of the egg during incubation influences the origin of malpositions has been studied extensively by Byerly and Olsen (1931, 1933, 1936 b, 1937), Cavers and Hutt (1934) and Hutt and Pilkey (1934). The differences between eggs incubated with their large end up versus those kept in a horizontal position, as far as the incidence of malpositions is concerned, can be seen from
the figures in Table 67. It is evident that malpositions II and IV are more common among horizontally incubated eggs than among those incubated with the large end up, whereas the reverse is true for malposition III.

The incidence of malposition I seems not to be affected appreciably by this difference in incubation practice. It has been demonstrated also that malposition II (head-in-small-end) can be produced experimentally with high frequency by incubating eggs for the first 18 days with their small end up, or by coating the large end with paraffin and incubating the eggs with the large end up. On the other hand, the incidence of malposition II is reduced in eggs incubated with the small end up if the small end is paraffin-coated. Byerly and Olsen concluded from these results that the occurrence of malposition II is accounted for by gravity, but that air-hunger of the embryo is another regulating factor. These agencies seem to play no role in the causation of other malpositions.

There are other, more general factors which increase the occurrence of at least some of the malpositions. Excessively high incubation temperature was found to raise the frequency of malpositions I and III, whereas malposition II was found to be more than ordinarily common at temperatures below as well as above the optimum (Byerly, 1938). Frequent turning of the eggs during incubation tends to reduce the incidence of malpositions (Insko and Martin, 1933), increasing maternal age may have a tendency to raise it (Steele and Insko, 1948).

Low hatchability on account of poor feed rations is accompanied by an increased occurrence of malpositions (Smith, 1931); this relationship has been noted especially with reference to malposition III (Byerly and Olsen, 1934). In comparison with normal feeding it was observed that vitamin A deficient diets are responsible for the occurrence of more malpositions of all types, except V; the differences between the two groups were statistically significant for the total of all malpositions and for malposition VI (Pöhl and Sipe, 1940). Similarly, vitamin D (cod liver oil) was reported to decrease the frequency of malpositions (Insko, 1934). Inbreeding tends to raise the incidence of malpositions (Upp, 1934). Malposition III, according to Hutt (1938), occurs more frequently in large eggs than in small ones, but Asmundson (1938) failed to find significant differences in this respect.

Serious criticism has been levelled by Byerly and Olsen (1934), Dove (1935) and Waters (1935 a and b) against the interpretation that all embryonic malpositions represent agencies responsible for embryo mortality and, hence, for reduced hatchability. Byerly and Olsen as well as Dove concluded from their observations that malposition III, head under left wing, is a consequence of delayed embryonic development. The work of Waters indicates that a somewhat similar situation exists with regard to malposition i, head between thighs, and this has been confirmed by Byerly and Olsen (1936 b; 1937), Byerly (1938) and Munday (1953).
With regard to these two malpositions, at any rate, one is forced to conclude from evidence available at present that in general they represent symptoms of noxious factors which at an earlier period of incubation had interfered with development. Yet, in respect to malposition III the curious fact remains that, according to Asmundson (1938), breed differences of frequency exist. Malposition III occurred in his material almost exclusively in White Leghorn and Rhode Island Red stock, whereas it was very rarely found in Barred Plymouth Rock embryos. This aspect deserves further attention.

For other malpositions (IV and VI) no evidence has been advanced which would indicate that they represent the effect of delay in development, and such an explanation certainly does not hold for malposition II. There is little doubt that in certain instances, such as the majority of cases of malposition II, the embryonic position itself is a true barrier to hatching; in many other cases the existence of a malposition is merely a symptom of developmental retardation or an expression of the fact that the embryo died at a time when the particular position was normal.

The occurrence of embryo malformations as an index of incubation conditions

In the absence of malformations of known genetic nature, teratological abnormalities account for a relatively small proportion of all the embryos which die. There are various indications that different agencies may influence the frequency of occurrence of malformed embryos, and some of this evidence is of interest in connection with general problems of embryonic mortality and of hatchability.

One rather common type of malformation is known as chondrodystrophy. Embryos of this kind were first reported from the Storrts Agricultural Experiment Station (Landauer and Dunn, 1926; Landauer, 1927). The chief external abnormalities consist in a marked shortening of the extremities (micromelia) and frequent deformities of the skull. In extensive breeding experiments Dunn (1927b) could not establish a hereditary basis for this type of defect. In a later experiment the influence of the male was tested with regard to the occurrence of chondrodystrophic embryos. After some such embryos had been observed in a mating of Frizzle fowl, a Leghorn cock was substituted for the Frizzle cock, and still later the Frizzle rooster was put back into the mating. The results are shown in Table 69. Both types of matings produced chondrodystrophic embryos. There was, however, a decline in frequency from the first to the third mating. This is in agreement with the observations of Dunn (1927b), Hutt and Greenwood (1928-1929a), Munro (1932), Smith (1934), and Otrygancico (1936c; 1938). All these authors found that there is a definite seasonal change in incidence of chondrodystrophic embryos, the frequency decreasing with advancing spring.
Table 69

<table>
<thead>
<tr>
<th>Mating</th>
<th>Incubation period (1934)</th>
<th>Number of fertile eggs</th>
<th>Number of chondrodystrophic embryos</th>
<th>Percent of chondrodystrophic embryos</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frizzle x Frizzle</td>
<td>February 20 to April 3</td>
<td>201</td>
<td>10</td>
<td>4.98</td>
</tr>
<tr>
<td>Frizzle x Leghorn</td>
<td>April 10 to April 24</td>
<td>91</td>
<td>3</td>
<td>3.30</td>
</tr>
<tr>
<td>Frizzle x Frizzle</td>
<td>May 8 to June 12</td>
<td>209</td>
<td>1</td>
<td>0.50</td>
</tr>
</tbody>
</table>

In subsequent investigations it was found that certain nutritional deficiencies are responsible for micromelia and beak defects. This is true for deficiencies in riboflavin (Ogorodniy, 1939 a; Romanoff, 1940) or biotin (Cravens, McGibbon and Sebesta, 1944; Couch, Cravens, Elevjem and Halpin, 1948 a). It appears likely from available information that the sporadic occurrence of chondrodystrophy is brought about by vitamin deficiencies, and among these a shortage in biotin (Fig. 51) probably is especially important. Chicken embryos respond to a great variety of other experimental conditions with a chondrodystrophy-like syndrome. These conditions include the adding of sulphur supplements to the diet of laying hens (Holmes, Halpin and Herrick, 1941), treatment of 48-hours embryos with eserine sulfate or various sulfa drugs (Ancel, 1945 b), the injection of thallium into the yolk sac of 4-days embryos (Karnofsky, Ridgway and Patterson, 1950), or similar treatment of embryos with insulin (Landauer, 1947 a and b), pilocarpine (Landauer, 1953, 1956 c), 6-amino-nicotinamide (Landauer, 1957 d), and yet other substances. In experiments at the Storrs Agricultural Experiment Station it could be shown that chicken embryos can be wholly or in part protected against the effects of many of these teratogenic compounds (e.g. insulin, eserine, sulfanilamide, pilocarpine and 6-aminonicotinamide) by giving simultaneous supplements of nicotinamide (Landauer 1948 a and b, 1953, 1956 c, 1956 d; Zwilling 1948, 1949 b; Zwilling and DeBell, 1950). These findings make it likely that an interference with normal carbohydrate utilization by the early embryos is responsible for the origin of malformations of this type.

Seasonal trends have been observed in the incidence of various sporadically-occurring malformations of chicken embryos. Thus, Upp (1934) found that eye deformities, by far the most frequent kind of malformation of chicken embryos, in his material (collected in Iowa and Louisiana) became more frequent as the hatching season advanced. No explanation was offered for this trend, but it is interesting to note that the averages of temperature and precipitation in the two localities during the same period of the year follow a course closely similar to that of the incidence of eye defects. This suggests the possibility that the developmental stage of the blastoderm at the beginning of incubation or humidity conditions in the incubators (the latter perhaps affecting the oxygen tension and/or concentration of carbon dioxide) may have been causative agencies determining the frequency of these developmental disturbances. Upp's observations were confirmed by Landauer (1943).
Micromelia and parrot beak as occurring in eggs produced on a biotin deficient diet (From Gravens, McGibbon and Sebesta, 1944).

Otrygan'ev and Kuchkovskain (1941) reported that abnormalities of the head tend to occur after excessively high incubation temperatures during the first three days of development and that overheating between the third and fifth day is likely to produce ectopia viscerum. Further proof that high temperature is the causative agent in the origin of ectopia of heart and viscera was given by Otrygan'ev (1941 b) and Ance (1947).

It is generally recognized that unfavorable incubation conditions, caused by a variety of different factors, may increase the incidence of malformed embryos, and this seems to be especially true with regard to abnormal development of the eyes and the head. A good illustration of the change in frequency of malformations as an index of incubation conditions is offered by the following data (Table 70), collected at the Storrs Agricultural Experiment Station, incident to changing from an old-type still-air incubator with water pans to a forced-draft incubator with humidity control and separate hatching compartment. The number of embryos which showed malformations of the head, chiefly microphthalmia, anophthalmia, otocephaly and cerebral hernia, was tabulated for the last two years with the old incubator (1930 and 1931), and for the first two years with the new incubator (1932 and 1933), and their frequency calculated in percent of all fertile eggs put into the incubators. The average
frequency of such malformations occurring during the two two-year periods dropped from 1.41 percent to 0.22 percent; that is, under better incubation conditions malformations of the head occurred only one-sixth as often, a highly significant difference. It seems likely that an improvement in humidity conditions, with a coincident rise in the efficiency of ventilation, was the principal factor in reducing the frequency of abnormalities.

A great deal of excellent work has been done in recent years by Ancel and Fintemberger (1925 a and b, 1927), Wolff (1933, 1934, 1936, 1948), Szejtsenwal (1933, 1934), Galler (1935-1936), Frölich (1936), Morita (1936, 1937), Kryayevoy (1938), Tarnawsky (1938), Lallemend (1939), Kosin (1944), and Ancel (1945 a and b, 1946-1947, 1950) in producing various types of malformations of chicken embryos experimentally. It can be concluded from these studies that many malformations of chicken embryos are probably due to disturbances of the organizing centers. Such disturbances presumably can be brought about by many different factors, either located within the egg itself or acting through the environment.

Experiments by Buchanan (1926), Hinrichs (1927), Hyman (1927), Tazelaar (1928), and Rulon (1935), concerning the presence of physiological gradients in the developing chicken embryo suggest the existence of still other mechanisms through which unfavorable agencies may lead to distortions and malformations of various parts or organs. Recent work by Gray and Worthing (1941) is also of interest in this connection. That the susceptibility of chicken embryos to disturbing agencies varies with age was shown by Wilson (1935) with regard to gamma rays of radium, by Fell and Landauer (1935) with regard to varying tissue culture conditions, by Lallemend (1939) and Gabriel (1946) in relation to the effects of colchicine, and by Landauer (1947 a, 1954) and Landauer and Bliss (1946) with reference to insulin and other teratogenic compounds. Important differences exist also, however, between breeds and stock of fowl in the frequencies with which various malformations occur sporadically or can be induced experimentally, and this has led to the conclusion that a complex genetic basis (in degree of susceptibility to environmental agencies) exists for many of these deviations from normal development (Landauer 1955, 1957 c).

### Table 70

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of fertile eggs</th>
<th>Head abnormalities %</th>
</tr>
</thead>
<tbody>
<tr>
<td>1930</td>
<td>7883</td>
<td>1.29</td>
</tr>
<tr>
<td>1931</td>
<td>11121</td>
<td>1.49</td>
</tr>
<tr>
<td>1932</td>
<td>9977</td>
<td>0.24</td>
</tr>
<tr>
<td>1933</td>
<td>8982</td>
<td>0.19</td>
</tr>
</tbody>
</table>

Prenatal and postnatal mortality

Do the same agencies which cause chicken embryos to die at one or another period of incubation continue to have effects after hatching?
If lack of 'vigor' were one of the principal factors in causing low hatchability, it might be expected that siblings with high embryo mortality also would show high chick mortality. This problem was investigated by Dunn (1921-1922) at the Storrs Agricultural Experiment Station. Using the records of two consecutive years, he grouped chick mortality during the first three weeks after hatching according to hatchability of the mothers' eggs, and obtained the data shown in Table 71.

Table 71

<table>
<thead>
<tr>
<th>Fertile eggs hatched %</th>
<th>Number of chicks</th>
<th>Chick mortality during the first three weeks %</th>
</tr>
</thead>
<tbody>
<tr>
<td>20 - 39</td>
<td>162</td>
<td>17.90 ± 1.97</td>
</tr>
<tr>
<td>40 - 59</td>
<td>610</td>
<td>12.95 ± 0.92</td>
</tr>
<tr>
<td>60 - 79</td>
<td>595</td>
<td>11.43 ± 0.88</td>
</tr>
<tr>
<td>80 - 99</td>
<td>210</td>
<td>14.76 ± 1.66</td>
</tr>
</tbody>
</table>

The highest chick mortality had occurred in the groups with lowest and highest percentages of hatchability. The difference in chick mortality between these two classes is 3.14 ± 3.83 percent. This obviously is not significant, and shows that the high embryonic mortality of the low-hatch progenies was not selective; that is, it did not reduce mortality after hatching. The coefficient of correlation between prenatal and postnatal mortality of individual progenies was found to be -0.003 ± 0.090, indicating an entire lack of correlation. This can only be interpreted to mean that different sets of factors are responsible for embryo and for chick mortality. Similar results were obtained by Hull (1927-1928) who extended the analysis to early (previous to eighteenth day) and late (eighteenth to twenty-first day) embryo mortality. Neither the early nor the late death rate of embryos was significantly correlated with chick mortality. Observations by Briles and Krueger (1955) and by Coles and Cumber (1956) point to the same conclusion. It is evident, however, that certain conditions, such as nutritionally deficient diets of laying hens or the presence of pathogens in hatching eggs, may have an adverse effect on hatchability as well as on chick viability.

Peaks of embryo mortality and their significance

Embryo mortality is not distributed at random over the entire incubation period. Payne (1919-1920) first found that there is a distinct early and a still more pronounced late peak of embryonic mortality, and his results were, with minor modifications, confirmed by subsequent investigations. There is evidence for the conclusion that increased embryo mortality, due to various causes, tends to be expressed chiefly at these periods.

Interesting observations, bearing on this problem, were reported by Brankhorst (1933), who compared the mortality distribution among the
eggs of high (above 75 percent) and low-hatching (below 50 percent) White Leghorn hens. The material consisted of 857 fertile eggs with a mortality of 63.13 percent in the low-hatching group, and of 1,810 fertile eggs with an embryo mortality of 19.39 percent in the high-hatching group. The distribution of actual mortality in the two groups is shown in Figure 55. The peaks of mortality occur at similar periods, but are much exaggerated in the low-hatching group. If percentage distribution of mortality is considered (Figure 56), it can be seen that in the low-hatching group early and late mortality were similar in extent, while in the high-hatching group by far the greatest part of mortality occurred toward the end of development.

The effects of inbreeding and outcrossing on embryo mortality are also chiefly expressed at these two critical periods (Byerly, 1934). In the case of crosses the reduction in mortality seemed to be greater for the eggs laid by F₁ hens (F₂ embryos) than for the first crosses (F₁ embryos), another indication of the importance of the mothers' physiology on hatching quality of eggs.

In a study concerning the effect of different incubation temperatures
on embryo mortality, Byerly (1938) made the interesting observation that the increase in mortality, due to temperatures above or below the optimal level, is of nearly the same order for eggs from hens with high hatchability records as it is for those from hens with low hatching records. Eggs from hens which produce high hatches at normal temperatures give still relatively high hatches at abnormal temperatures and, vice versa, eggs from mothers with poor hatches at normal temperatures tend to give the poorest results under abnormal temperature conditions, but the distribution of viability, i.e., the relative numbers of progeny from the different mothers, remains about constant.

![Relative distribution of embryonic mortality within a high (---) and a low (--) hatching line of White Leghorns (From Bronkhorst, 1933).](image)

Various other agencies are known to increase embryo mortality preferentially at one of the two periods at which the death rate normally tends to be greatest, though it should not be forgotten that there are also factors which cause mortality at other stages of development. There can
be little doubt, however, that critical periods exist in the life of the chicken embryo at which, presumably due to fundamental changes in the physiological functioning of various parts and organs, death is more likely to occur than at other times. Similar periods exist in the development of other birds (Riddle, 1930). Explanations have been put forward by Schmalhausen (1926), Brody (1927), Riddle (1930), Needham (1932), Pringle and Barott (1937), Ogorodniy (1939 a and b) and Penionzhkevich (1945) to account for these critical periods, but definite evidence is still lacking. It is likely that the early peak of mortality is related to important changes in the metabolic activity of the embryos. It is interesting in this connection that a sudden increase in metabolic rate, as measured by carbon dioxide elimination, occurs on the third day of development (Noyons and Pascal de Hesselle, 1939). Observations of Seek (1911) on heat production by the chicken embryo also point to the conclusion that changes in intensity and/or kind of metabolism may be responsible for peaks of mortality.

MATERNAL INFECTIOUS DISEASE AND HATCHABILITY

Pulmonary disease is the only bacterial infection of laying hens for which there is definite evidence of an influence on hatchability. Rettger and Stoneburn (1909, 1911) first established at the Storrs Agricultural Experiment Station that Salmonella pullorum may be present in ovarian ova of infected hens and in the yolks of fresh or incubated eggs from infected stock. The albumen of such eggs always reacts negatively to the agglutination test (Frank and Edgington, 1937). It has been demonstrated repeatedly that eggs which had been laid by infected hens hatched less well than those laid by healthy hens (Beaudette, Bushnell and Payne, 1923; Canfield, 1925; Bushnell, Hinshaw and Payne, 1926; Dearstyn, Kaupp and Wilfong, 1929; Runnels, 1929; Beach and Michael, 1930). The extent to which hatchability may be reduced by this agency can be seen from the figures in Table 72.

It is known that not all of the eggs of positive reactors to the pullorum agglutination test harbor Salmonella pullorum. On the other hand, it has been reported by Dearstyn, Kaupp and Wilfong (1929) that a relationship exists between mean serum titre of the infected mother and percent hatchability of her eggs. This is shown by the figures in Table 73. The number of eggs contaminated as well as the extent of contamination of individual eggs may play a role in this situation. Conversely, Bushnell, Hinshaw and Payne (1926) observed in a hen which was apparently recovering from pullorum disease that increasing hatchability of her eggs occurred pari passu with decreasing agglutinin content of her blood serum (Table 74).

Another demonstration that the infection of embryos with Salmonella pullorum is responsible for mortality during incubation was provided by Mallmann and Moore (1936) in a comparison of the average in-
Table 72

<table>
<thead>
<tr>
<th>Authors</th>
<th>Non-infected stock</th>
<th></th>
<th>Infected stock</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of laying hens</td>
<td>Number of fertile eggs</td>
<td>Hatch %</td>
<td>Number of laying hens</td>
</tr>
<tr>
<td>Bushnell, Hinshaw and Payne (1926)</td>
<td>164</td>
<td>4585</td>
<td>63.4%</td>
<td>19</td>
</tr>
<tr>
<td>Beach and Michael (1930)</td>
<td>202</td>
<td>1842</td>
<td>72.2%</td>
<td>96</td>
</tr>
</tbody>
</table>

Incidence of *Salmonella pullorum* in embryos which had died during the latter part of the incubation period and in newly-hatched chicks of the same stock (Table 75).

The frequency of the infection of eggs with *Salmonella pullorum* decreases with progressing spring (Rennells and van Roekel, 1926-1927 a and b; Mallmann and Moore, 1936).

Table 73

<table>
<thead>
<tr>
<th>Mean serum titre</th>
<th>Number of hens</th>
<th>Number of fertile eggs</th>
<th>Hatch %</th>
</tr>
</thead>
<tbody>
<tr>
<td>over 200</td>
<td>9</td>
<td>218</td>
<td>28.4%</td>
</tr>
<tr>
<td>100 - 200</td>
<td>6</td>
<td>187</td>
<td>36.4%</td>
</tr>
<tr>
<td>under 100</td>
<td>10</td>
<td>303</td>
<td>45.5%</td>
</tr>
</tbody>
</table>

*Salmonella aetbycke*, the organism which causes paratyphoid of fowl, frequently invades the ovary, and it seems likely that, similar to *Salmonella pullorum*, it may be responsible for losses in hatchability.

Table 74

<table>
<thead>
<tr>
<th>Date of test</th>
<th>Titre of serum</th>
<th>Percent hatchability for corresponding period</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 11, 1921</td>
<td>1 : 640</td>
<td>25.3%</td>
</tr>
<tr>
<td>January 25, 1922</td>
<td>1 : 160</td>
<td>65.7%</td>
</tr>
<tr>
<td>April 13, 1922</td>
<td>1 : 40</td>
<td>90.6%</td>
</tr>
</tbody>
</table>

Except by organisms of the *Salmonella* group, infection of egg yolks on the ovary, in the oviduct, or in fresh eggs appears to be uncommon (Rettger, 1913; Beckwith and Horton, 1914), and there is no evidence

Table 75

<table>
<thead>
<tr>
<th>Material</th>
<th>Number tested</th>
<th>Percent positive during entire season</th>
<th>Range of percent positive in different hatches</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unhatched dead chicks</td>
<td>241</td>
<td>51.5%</td>
<td>24.3 - 85.1</td>
</tr>
<tr>
<td>Newly-hatched chicks</td>
<td>236</td>
<td>11.4%</td>
<td>5.0 - 20.4</td>
</tr>
</tbody>
</table>
to indicate that such infection plays a significant role in hatchability (Hadley and Caldwell, 1916), although statements to that effect have been made from time to time by various authors. Harry (1957, 1958) has shown that under certain conditions bacteria of the alimentary tract and skin of hens, belonging chiefly to the coli-aerogenes group, may penetrate through the shell and may, on reaching the yolk sac, become pathogenic, causing embryo mortality especially during the first two days of incubation. He suggested that such contamination may be a significant source of reduced hatchability if dirty eggs are washed with chilled water. He reported further on two outbreaks of yolk infection with Staphylococcus aureus which could be traced to persons who were carriers of this organism and who had handled the eggs during candling on the eighteenth day of incubation. A report by MacLaury and Moran (1959) deals with related problems. The organism of fowl typhoid (Shigella gallinarum) has been isolated from eggs containing embryos that had died early in incubation and may have been the cause of death (Busa, 1958; Karasszon, 1958).

According to Carr (1943-1944) there is no impairment of the hatching quality of eggs laid by hens which are carriers of the Rous No. 1 sarcoma. The infective virus is not transmitted via the egg, but the carrier hens do transmit virus-neutralizing antibodies to the yolk of their eggs.

Lorenz and Newlon (1944) found that as an aftermath of avian pneumoencephalitis infection (Newcastle disease) chickens are likely to lay for some time eggs with abnormal shells, inferior quality of albumen and free floating air bubbles in place of the regular air space. There is a serious loss in the hatching quality of such eggs. The pathology of these effects on reproduction was studied by Biswal and Morrill (1954). From observations at Storrs it appears that excessive embryo mortality, due to maternal infection with Newcastle virus, is accompanied by an increased incidence of morphological malformations. Blattner and Williamson (1951) found after experimental infection with Newcastle virus a high incidence of defects of the lens and auditory sac. Another virus disease, infectious laryngotracheitis, has similarly harmful consequences for hatchability (J. B. Smith, 1933; Scott and Brandly, 1934).

Hays (1951a) observed an abnormally high rate of early embryo mortality after a mild outbreak of infectious bronchitis among laying hens. Broadfoot and Smith (1954) published confirmatory evidence. Taylor, Gunn, Grau and Lehpovsky (1953) discussed in some detail the consequences on hatchability of an epidemic of atypical infectious coryza which may have been complicated by infectious bronchitis. They found that many of the infected hens had (permanently?) become unable to produce eggs with a normal structure of albumen and shell. The incidence of embryo malformations was high; hatchability was low. It seems likely from the foregoing reports that all respiratory infections of laying
hens are detrimental to the production of eggs with a normal structure, and hence to the hatching quality of these eggs.

Coles and Underwood (1954 a) and Coles (1955) concluded from a study of their flock records that the eggs of mothers, among the progenies of which lymphomatosis had occurred, hatched significantly better than the eggs of mothers whose progenies had remained free of the disease. Hutt and Cole (1955) have shown, however, that this conclusion was based on an inadmissible statistical treatment of the data, and that such a relation does not in reality exist.

Taylor, Lowry and Raggi (1955) made observations of great interest on changes in hatchability coincident to an outbreak of avian encephalomyelitis. They found that for a short period egg production fell sharply or ceased altogether in the majority of birds in the affected pens. Cessation of laying was of short duration (average 5.9 days). "Eggs produced just before and during the period of depressed egg production showed decreased hatchability and an increased embryonic mortality during the last three days of incubation." There was evidence that virus contamination of the eggs occurred only during the initial period of maternal illness, viz., parallel with decline in production.

No evidence has been put forward with regard to the possible effect on hatchability of parasitic diseases of chickens, other than bacterial and viral infections. It appears, however, that in dirty nest boxes fungi (Aspergillus) may penetrate through the shell of eggs and may thereby become a cause of reduced hatchability (B. S. Hanson, personal communication). It should be recorded that according to Schlolthauer and Essex (1933) eggs of turkeys affected with enterohepatitis (due to protozoan invasion) hatched less well than those of unaffected turkey hens. Their data need confirmation. Cecal coccidiosis of fowl does not affect hatchability (Bressier and Gordonuk, 1951).

At the end of our quest into the riddles of hatchability we are reminded of Denis Diderot's saying about nature and her secrets: C'est une femme qui aime à se travestir, et dont les différents déguisements, laissant échapper tantôt une partie, tantôt une autre, donnent quelque espérance à ceux qui la suivent avec assiduité, de connaître un jour toute sa personne.
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